

REVIEW

Time-lag algal growth dynamics: biological constraints on primary production in aquatic environments

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ABSTRACT: Changes in the nutrient regime of phytoplankton cells induce variable time lags before the onset of cell division (quasi-instantaneous response to more than 24 h lags), dependent mainly on the algal species and the magnitude of the nutrient pulse. The latter parameter appears to be a main controlling factor in algal growth dynamics under transient conditions, overriding other variables such as temperature, irradiance and nutritional state. The presence of such phenomena puts intrinsic limits on primary production in a variable nutrient environment because algal cells are not made up of synthetic components only (*sensu* Williams 1971), but also of structural and genetic material. Under these conditions, high nutrient uptake rates over short time periods do not necessarily lead to high growth rates (defined as increase in cell numbers) over comparable time scales, even if cell quota increase very rapidly following nutrient resupply. Data from different groups of investigators on uptake-growth coupling, internal nutrient pools, growth lag, and carbon-nitrogen uptake interactions show consistent patterns as follows: for phytoplankton in a variable nutrient environment, 2 essential strategies emerge at the genus level. One is the 'growth' response, exhibited by the genera *Dunaliella* and *Chaetoceros*, which do not accumulate internal pools of inorganic nutrients, whose uptake and growth are closely coupled, and which therefore process nutrient pulses very rapidly into new cells. The other is the 'storage' response, found in genera such as *Thalassiosira* or *Amphidinium*, which have the capability of accumulating large internal nutrient pools, present extensive uncoupling between uptake and growth, and exhibit lags in cell division of up to 24 h following a single addition of the limiting nutrient. The latter response type presents an ecological advantage when nutrient pulsing frequency is lower than cell division rate; the first response type would provide a competitive advantage at high frequency pulses.

INTRODUCTION

Although the significance of elevated nutrient uptake by phytoplankton in a nutrient-poor and patchy environment has been subject of much debate (Lehman & Scavia 1982, 1984, Currie 1984a, b, Goldman 1984a, b), the relation of this phenomenon to algal cell growth has been much less studied. Algal cells can scavenge low or high levels of nutrients quite efficiently from the environment (Caperon & Meyer 1972, Eppley & Renger 1974, Goldman & McCarthy 1978, Lehman & Scavia 1982), but the mechanisms by which,

as well as the time scales over which, the material taken up is transformed into new biomass and/or new cells, are still far from well known. While uptake of silicate has been shown to be tightly coupled to cell division (Lewin 1962, Lewin et al. 1966, Darley et al. 1976, Sullivan 1977, Chisholm et al. 1978), this is certainly not the case for other nutrients such as nitrogen or phosphorus. The concept of balanced growth (Campbell 1957, Shuter 1979, Eppley 1981), which is implicit in studies of the assimilation of such compounds, has led some investigators to questionable conclusions regarding the significance of rapid uptake

rates in relation to algal growth in a nutrient-depleted environment. For example, McCarthy & Goldman (1979) implicitly assume an instantaneous response of growth rate to cell quota increases when extrapolating their laboratory results to the field situation. Such an assumption may not always be true, because time delays are sometimes involved in the relation between those parameters (Caperon 1969, Cunningham & Nisbet 1978, 1980, Gotham & Rhee 1981, Quarmby et al. 1982).

The use of several steady states to characterize the relation between uptake and growth (McCarthy & Goldman 1979, Goldman & Glibert 1982) makes this relation independent of time. Information on the time scale required to transform nitrogen or phosphorus taken up into new cells or biomass is crucial to reach conclusions concerning the possible mechanisms of survival in a nutrient-poor and probably patchy area. Nevertheless, the hypothesis presented by McCarthy & Goldman (1979) certainly stimulated further work on internal nutrient pools by noting that 'research is needed in which Q (cell quota) is partitioned into nutrient storage and active metabolic pools'. Later investigations have shown that, in the case of nitrogen uptake, many intermediate compounds can accumulate intracellularly after nitrogen is supplied to algal cells (Collos & Slawyk 1980, Collos 1982, Dortch 1982, Dortch et al. 1984) and before cell division occurs. Such phenomena complicate the interpretation of uptake data as the resulting increase in cell quota does not necessarily imply an equivalent increase in cell numbers or in nutritional value for higher trophic levels. For example, Collos & Slawyk (1977) have shown that up to 90 % of the nitrate taken up over 6 h by natural phytoplankton in upwelling areas can be found inside the cells as unreduced nitrate. More recently, Wheeler et al. (1982) observed that uptake of ammonium during short-term incubations probably represents only internal ammonium labeling, and that longer incubations are required to obtain rates of macromolecular synthesis.

Thus, the problem of relating nutrient uptake rate to cell growth defined as increases in cell numbers is essential for a good understanding of primary production (Legendre et al. 1984). It is, however, a particularly difficult problem because cell division is a discontinuous function, while nutrient uptake can be considered as a continuous one, even if non-linear phenomena are associated with it (Collos 1983). Such a distinction between nutrient uptake and cell division is particularly important for limiting nutrients and in non steady-state situations which are now thought to be the rule in the oceans (Dugdale 1977, McCarthy 1981, Goldman 1984a, b). This review presents data on the relation between nutrient uptake (mostly inorganic

nitrogen and phosphorus) under transient conditions and phytoplankton growth, as measured by increases in cell numbers, and puts the high nutrient uptake rates of algal cells recently reported into physiological (if not ecological) perspective.

The literature on phytoplankton growth under transient nutritional conditions was surveyed in order to quantify the time delays involved in the growth response of cells to a new supply of the limiting nutrient. Starting from the reasonable assumption that algal cells in oligotrophic areas may be periodically depleted or starved of nitrogen or phosphorus, published experiments on the effect of resupply of ammonium, nitrate or phosphate to nitrogen (N) or phosphorus (P)-depleted or starved cells in algal cultures have been used. Most of these experiments were not originally designed to study the lag between nutrient uptake and cell growth, and some of them did not even measure the uptake of the added nutrient. They could nevertheless be used for the present purpose because the relevant parameter was the time elapsed between a change in the nutrient regime and the beginning of growth as estimated from increases in cell numbers.

Nitrate was also considered here because, even though this compound is not relevant to the current micropatch nutrient debate, such data are of importance in stratified oceanic areas where deep nutrient supply may be of a pulsed nature (Klein & Coste 1984).

Nutrient starvation was generally reached in batch cultures either by letting cells deplete the N or P source during the course of growth (Ketchum 1939, Spencer 1954, Thomas & Dodson 1968, Eppley & Thomas 1969, Finenko & Krupatkina-Akinina 1974, Dortch 1982), or by washing and transferring cells to new medium lacking N or P (Yentsch & Vaccaro 1958, Eppley & Thomas 1969, Guérin-Dumartrait et al. 1970, Berland et al. 1973). The term 'starved' refers to the absence of an essential nutrient such as N or P and, even though some studies did not actually measure nutrient levels, it could be estimated from mass balance that the nutrients in question were indeed depleted by the cells at the time of the experiment. Sometimes, the nutritional status was estimated from intracellular parameters, such as in the study of Berland et al. (1973) where it was obvious from carbon-to-nitrogen composition ratios that the cells were not N depleted at the beginning of the experiments. Therefore, data were selected on the basis of the evolution of particulate nitrogen (PN) or protein concentration, i.e. only when the PN or the protein stopped increasing were the cells considered as starved. This corresponded roughly to the depletion of the N source supplied by the culture inoculum in the above study.

The following equivalences between names of algal

species which have changed have been used: *Thalassiosira pseudonana* clone 13-1 = *T. oceanica*; *Thalassiosira fluviatilis* = *T. weissflogii*; *Exuviella mariae-lebourae* = *Proocentrum minimum*; *Gymnodinium splendens* = *G. sanguineum*; *Asterionella japonica* = *A. glacialis*; *Anacystis* sp. = *Synechococcus* sp. The second name, which is the more recent one, will be used throughout this paper.

V_{max} is defined as the maximum specific uptake rate in units of time⁻¹; P_{max} is the maximum absolute uptake rate in units of mass cell⁻¹ time⁻¹.

CHOICE OF GROWTH PARAMETER: RESULTING VARIABILITY IN LAG ESTIMATES UNDER TRANSIENT NUTRIENT CONDITIONS

Table 1 illustrates that growth lag may vary considerably depending on the parameter chosen to assess 'growth'. For example, the lag in growth following N resupply to N-starved cells of *Skeletonema costatum* or *Pavlova lutheri* ranges from zero when growth is estimated from increases in particulate nitrogen (PN) to 48 h when cell numbers are used, with intermediate

Table 1. Variations in estimates of growth lags as a function of the parameter chosen to measure algal growth

Species	Nutrient state	Perturbation type	Growth estimate	Lag (h)	Source
<i>Scenedesmus quadricauda</i>	N-starved 2 d	10 µM NH ₄ pulse	Cell no.	12	Healey (1979)
			Protein	0	
			PC	12	
			PN	0	
			Chl a	7	
	P-starved 3 d	10 µM PO ₄ pulse	Cell no.	12	Healey (1979)
			Protein	4	
			PC	10	
			PN	10	
			PP	0	
<i>Skeletonema costatum</i>	N-starved 7 d	Complete medium pulse 500 µM NO ₃ 25 µM PO ₄	Cell no.	48	Sakshaug & Holm-Hansen (1977)
			IVF	24	
			PC	24	
			PN	0	
			Chl a	12	
	P-starved 3 d	Complete medium pulse 500 µM NO ₃ 25 µM PO ₄	Cell no.	48	Sakshaug & Holm-Hansen (1977)
			IVF	48	
			PC	48	
			PN	48	
			Chl a	48	
<i>Pavlova lutheri</i>	N-starved 15 d	Complete medium pulse 500 µM NO ₃ 25 µM PO ₄	Cell no.	48	Sakshaug & Holm-Hansen (1977)
			IVF	24	
			PC	36	
			PN	0	
			Chl a	12	
	P-starved 3 d	Complete medium pulse 500 µM NO ₃ 25 µM PO ₄	Cell no.	24	Sakshaug & Holm-Hansen (1977)
			IVF	0	
			PC	12	
			PN	0	
			Chl a	12	
<i>Synechococcus</i> sp.	N-starved 1 d	11.8 mM NO ₃ pulse	Cell no.	8–10	Allen & Smith (1969)
			Protein	1–2	
			RNA	1–2	
			DNA	8–10	
			Chl a	2–3	
			Carotenoid	3–4	
			Phycocyanin	4–5	
no.: number		Chl a: chlorophyll a			
PC: particulate carbon		IVF: <i>in vivo</i> fluorescence			
PN: particulate nitrogen		RNA: ribonucleic acid			
PP: particulate phosphorus		DNA: deoxyribonucleic acid			

values when using particulate carbon (PC), *in vivo* fluorescence (IVF) or chlorophyll *a* (Sakshaug & Holm-Hansen 1977). This study, as well as that of Healey (1979) and Allen & Smith (1969) – all of which have used at least 5 different parameters to estimate algal growth under transient conditions – show that growth lag is greatest when the cell numbers are used. This applies to ammonium, nitrate and phosphate additions as well. The above examples also show that – for phytoplankton in a varying nutrient regime, i.e. any situation other than steady-state in a chemostat culture – the estimate of growth can vary from zero to any value depending on the chosen parameter. In a similar way, conclusions on species competition may vary considerably depending on whether nutrient uptake or cell division is considered as an estimate of phytoplankton growth. In the remainder of the paper, the term 'growth' will therefore be defined as reproduction of cells by binary fission.

LAGS IN CELL DIVISION: INFLUENCE OF SPECIES AND NUTRIENT PULSE MAGNITUDE

Tables 2, 3 and 4 summarize published data on the delay involved between a resupply of nutrient and the change in cell numbers. The lags observed here are different from the well-known lag phase in cell division following transfers of batch cultures to fresh medium (Fogg 1971). The main difference lies in the

fact that cells used in the experiments presented here are starved of a particular compound: N or P.

Under identical experimental conditions, the time lag can be quite variable, ranging from zero for *Dunaliella tertiolecta* to more than 24 h for *Thalassiosira pseudonana* and *Amphidinium carterae* (Dortch et al. 1984) for ammonium pulses (Table 2), and from zero for *Chaetoceros lauderi* to 72 h for *Skeletonema costatum*, *Prorocentrum minimum* and *Chlamydomonas magnusii* (Berland et al. 1973) for nitrate pulses (Table 4). Species of the genus *Chaetoceros* stand out as being able to grow rapidly following a phosphate (Table 3) or a nitrate (Table 4) pulse. The same can be said of *Dunaliella* following an ammonium (Table 2) or nitrate (Table 4) pulse. In contrast to those, species such as *T. pseudonana* exhibit growth lags of 24 h or more after an ammonium (Table 2) or nitrate (Table 4) pulse.

Additional data from Olson & Chisholm (1983) could not be presented under the chosen table format because their experiments are more sophisticated than those in Table 2. Essentially, they supplied a single ammonium pulse to N-limited cells of unicellular algae at different times of the L-D cycle. For *Hymenomonas carterae* and *Amphidinium carterae*, cell division patterns were controlled more by the photocycle than by the ammonium pulse; the reverse was true for *Thalassiosira weissflogii*.

In the case of phosphate uptake, Nyholm (1978) differentiated between phosphate pulses (about

Table 2. Time lag between ammonium resupply to N-starved cells and beginning of growth estimated from cell counts

Species	Duration of starvation (h)	Light regime	Perturbation type	Lag (h)	Source
<i>Scenedesmus quadricauda</i>	48	24 L	10 µM pulse	12	Healey (1979)
<i>Platymonas striata</i>	24	24 L or 16 L–8D	714 µM pulse	>24	Edge & Ricketts (1977)
<i>Isochrysis galbana</i>	72	24 L	50 µM pulse	9	Dortch et al. (1984)
<i>Dunaliella tertiolecta</i>	72	24 L	10 µM pulse	0	Dortch et al. (1984)
<i>Amphidinium carterae</i>	72	24 L	10 µM pulse	>26	Dortch et al. (1984)
<i>Skeletonema costatum</i>	72	24 L	10 µM pulse	4	Dortch et al. (1984)
<i>Thalassiosira pseudonana</i>	72	24 L	10 µM pulse	>24	Dortch et al. (1984)
<i>Thalassiosira nordenskioldii</i>	72	24 L	10 µM pulse	8	Dortch et al. (1984)

N: nitrogen
L: light hours
D: dark hours

15 μM) and phosphate shocks (above 150 μM) and observed, along with Burmaster (1979) that the latter seemed to inhibit algal growth estimated from cell numbers. While reductions in growth rates following N pulses are sometimes due to methodological artefacts (Plumley & Darley 1985), unquestionable dramatic changes in cell integrity can occur under such circumstances. For example, considerable losses of cellular matter due to protoplasm lysis during spermatogenesis induced by recovery from N starvation have been observed in a *Stephanopyxis* sp. (Stosch & Drebes 1964) and in *Skeletonema costatum* (Sakshaug & Holm-Hansen 1977).

An important feature resulting from the compilation is the lack of effect of the N source on the growth lag. Although N-starved cells are known to exhibit enhanced ammonium uptake and depressed nitrate uptake (Dortch et al. 1982), the difference between the effect of these 2 N sources at the level of cell division is nil, as, for example, *Skeletonema costatum* exhibited an identical time lag (4 h) in cell division after addition of ammonium or nitrate (compare Table 2 and 4, data from Dortch et al. 1984). The same phenomenon was observed in cultures of *Cylindrotheca fusiformis* (Plumley & Darley 1985).

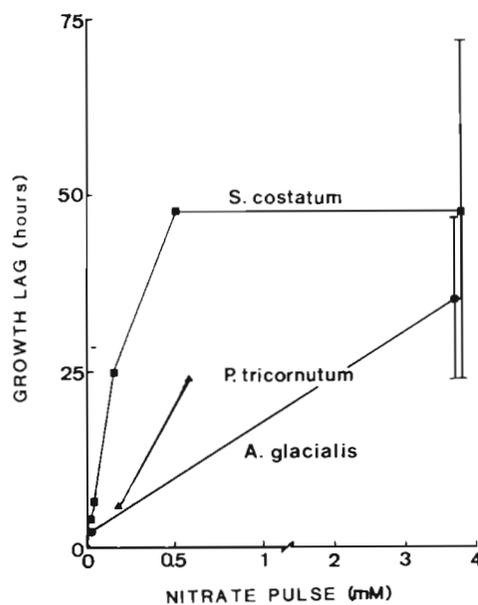


Fig. 1 Effect of magnitude of a single nitrate pulse on growth lag of N-starved cells of 3 diatoms. Data from Yentsch & Vaccaro (1958), Carlucci et al. (1970), Berland et al. (1973), Sakshaug & Holm-Hansen (1977), Dortch et al. (1984). Vertical bars: range of values obtained on 4 different strains of *Skeletonema costatum* by Berland et al. (1973)

Table 3. Time lag between phosphate resupply to P-starved cells and beginning of growth estimated from cell counts

Species	Duration of starvation	Light regime	Perturbation type	Lag (h)	Source
<i>Scenedesmus quadricauda</i>	3 d	24 L	10 μM pulse	12	Healey (1979)
<i>Phaeodactylum tricornutum</i>	3–4 d	Natural	2 μM pulse	3 in L 11 in D	Ketchum (1939) Ketchum (1939)
	na	24 L	7 to 70 μM pulses	20–80	Spencer (1954)
<i>Pavlova lutheri</i>	3 d	24 L	25 μM pulse	24	Sakshaug & Holm-Hansen (1977)
<i>Skeletonema costatum</i>	3 d	24 L	25 μM pulse	48	Sakshaug & Holm-Hansen (1977)
	x d*	7 L–17 D	0 to 5 μM pulses	0	Finenko & Krupatkina-Akinina (1974)
<i>Cerataulina bergonii</i>	x d	7 L–17 D	0 to 5 μM pulses	24	Finenko & Krupatkina-Akinina (1974)
<i>Chaetoceros socialis</i>	x d	7 L–17 D	0 to 5 μM pulses	0	Finenko & Krupatkina-Akinina (1974)
<i>Chaetoceros curvisetus</i>	x d	7 L–17 D	0 to 5 μM pulses	0	Finenko & Krupatkina-Akinina (1974)
<i>Chaetoceros gracilis</i>	na	24 L	0.02 to 1.0 μM pulses	0	Thomas & Dodson (1968)
<i>Nitzschia actinastroides</i>	na	24 L	3.2 μM pulse	6–8	Müller (1972)

L: light
D: dark
na: data not available
* Several days, not specified in source

Growth lag can sometimes be related to the magnitude of the nutrient pulse. Fig. 1 & 2 illustrate such a relation for 3 diatoms which had been initially N or P-starved. The consistency of the relation shown in Fig. 1 and concerning *Skeletonema costatum* is striking in view of the fact that data were obtained from 5 different sources, implying varying experimental conditions. For example, temperature ranged from 17°C (Dortch et al. 1984) to 20°C (Carlucci et al. 1970) and starvation from 1 d (Berland et al. 1973) to 7 days (Sakshaug & Holm-Hansen 1977). Additional data on *Thalassiosira weissflogii* (Yoder et al. 1982) presented

the same trends (4 and 10 h lags for 1.7 and 20 µM pulses respectively), but was not shown for the sake of clarity. Concerning ammonium, Plumley & Darley (1985) observed that the lag in cell division of N-limited *Cylindrotheca fusiformis* increased with the magnitude of ammonium additions. Fig. 3 shows growth lag of 4 species of unicellular algae as a function of ammonium pulses. In this particular case (Thomas et al. 1980), cells were not N-depleted, but these data were retained because they exemplify the interspecific variability in response to ammonium pulses. Some species, such as *Gonyaulax polyedra* and

Table 4. Time lag between nitrate resupply to N-starved cells and beginning of growth estimated from cell counts

Species	Duration of starvation	Light regime	Perturbation type	Lag (h)	Source
<i>Chlorella pyrenoidosa</i>	4 d	14 L–100	Complete medium added	8	Guérin-Dumartrait et al. (1970)
<i>Phaeodactylum tricornutum</i>	4 d	24 L	192 µM pulse	6	Yentsch & Vaccaro (1958)
	1 d	24 L	588 µM pulse	24	Berland et al. (1973)
<i>Platymonas striata</i>	1 d	24 L	714 µM pulse	>24	Edge & Ricketts (1977)
<i>Chlamydomonas magnusii</i>	1 d	24 L	3800 µM pulse	24–72	Berland et al. (1973)
<i>Monallantus salina</i>	1 d	24 L	3800 µM pulse	72	Berland et al. (1973)
<i>Prorocentrum minimum</i>	1 d	24 L	3800 µM pulse	24–72	Berland et al. (1973)
<i>Asterionella glacialis</i>	1 d	24 L	3800 µM pulse	24–48	Berland et al. (1973)
<i>Chaetoceros lauderi</i>	1 d	24 L	3800 µM pulse	0	Berland et al. (1973)
<i>Skeletonema costatum</i> (4 strains)	24 h	24 L	3800 µM pulse	24–72	Berland et al. (1973)
	36 h	24 L	150 µM pulse	24	Carlucci et al. (1970)
	36 h	24 L	50 µM pulse	12	Carlucci et al. (1970)
	7 d	24 L	500 µM pulse	48	Sakshaug & Holm-Hansen (1977)
	72 h	24 L	10 µM pulse	4	Dortch et al. (1984)
<i>Thalassiosira pseudonana</i>	72 h	24 L	10 µM pulse	>34	Dortch et al. (1984)
<i>Dunaliella tertiolecta</i>	72 h	24 L	10 µM pulse	0	Dortch et al. (1984)
<i>Amphidinium carterae</i>	72 h	24 L	10 µM pulse	>26	Dortch et al. (1984)
<i>Thalassiosira weissflogii</i>	10 h	12 L–12 D	1.7 µM pulse	4	Yoder et al. (1982)
			20.0 µM pulse	10	
<i>Pavlova lutheri</i>	15 d	12 L–12 D	500 µM pulse	48	Sakshaug & Holm-Hansen (1977)

L: light hours
D: dark hours

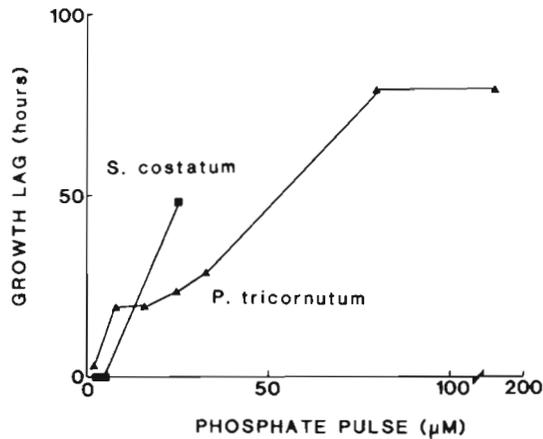


Fig. 2. Effect of magnitude of a single phosphate pulse on growth lag of phosphate-starved cells of 2 diatoms. Data from Ketchum (1939), Spencer (1954), Finenko & Krupatkina-Akinina (1974), Sakshaug & Holm-Hansen (1977)

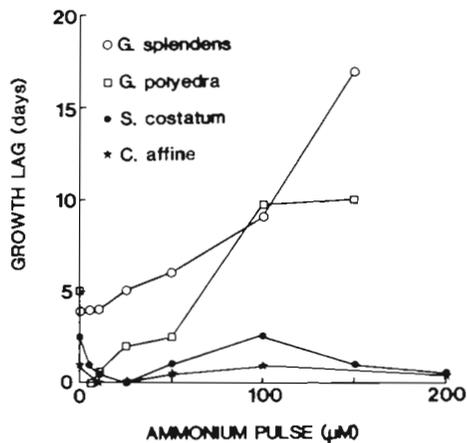


Fig. 3. Effect of magnitude of a single ammonium pulse on growth lag of several phytoplankters. Data from Thomas et al. (1980). Final growth rate was not significantly different from controls. Data on *Dunaliella tertiolecta* and *Asterionella glacialis* not shown (see text)

Gymnodinium sanguineum, are very sensitive to large ammonium pulses, while others, such as *S. costatum* and *Chaetoceros affine*, adapt much faster to similar perturbations in the nutrient regime. *Dunaliella tertiolecta* and *Asterionella glacialis* were also tested in the same study. The first species exhibited no lag in growth rate whatever the magnitude of the pulse and the second species presented 24 h lags only at ammonium pulses above 50 µM.

It may be argued that the range of concentrations presented in Fig. 1 to 3 is not realistic. Nutrient data in micropatches or marine aggregates are few. Shanks & Trent (1979) reported maximum values of about 500, 300 and 80 µM for ammonium, nitrate and phosphate respectively in marine micropatches. These values

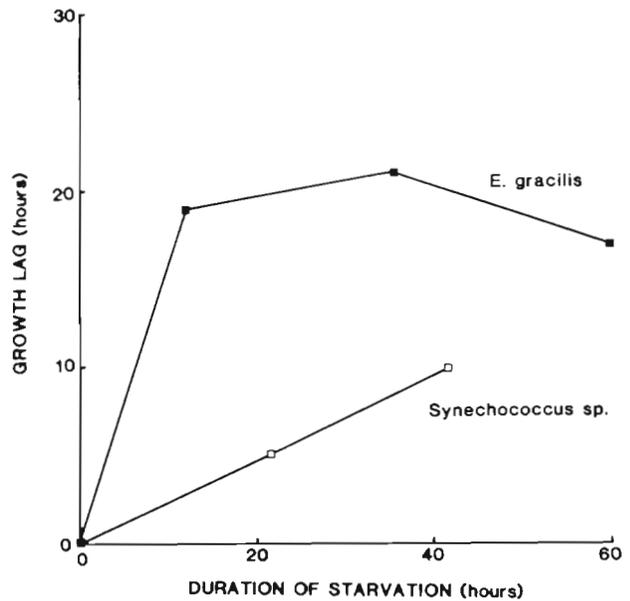


Fig. 4. Effect of duration of phosphate starvation on growth lag of 2 unicellular algae upon resupply of phosphate. Data from Buetow & Schuit (1968) and Ihlenfeldt & Gibson (1975)

indicate that, at least for Fig. 2 and 3, the concentrations used are relevant to the natural situation. Moreover, the values reported by Shanks & Trent may have to be revised upwards as they were measured on samples volumes which are too large to be considered as relevant to phytoplankton spatial scales (Allen 1977, Harris 1980).

Finally, growth lag was found to be related to the duration of starvation (Fig. 4), either with a saturation effect or not. Such patterns were expected, but starvation duration does not seem to be a major factor in phytoplankton growth dynamics as its influence was clearly overridden by that of the pulse magnitude for *Skeletonema costatum*, *Phaeodactylum tricornutum* and *Asterionella glacialis* (Fig. 1), all of which were in various nutritional states. The importance of this effect does not seem to have been recognized so far and will need to be included in modelling studies of algal competition.

UPTAKE AND GROWTH: QUANTITATIVE RELATIONS

The examples shown above indicate that, for most algal species, transformation of material taken up into new biomass is not instantaneous, but requires a certain amount of time which varies among species. For some of them, the lag in cell division is so extensive that uptake and growth do not belong to the same time domains. For example, *Thalassiosira weissflogii* takes

up nitrate during the first 12 h after resupply and divides during the following 12 h (Yoder et al. 1982). N-starved *T. nordenskioldii* cells do not start dividing before exhaustion (7 h) of the supplied ammonium pulse (Dortch et al. 1984). *Amphidinium carterae* exhausts a 10 μ M ammonium pulse in 6 h, but starts dividing only more than 26 h after the pulse (Dortch et al. 1982, 1984). Those different time scales have important implications on the interpretation of nutrient uptake rates in terms of algal growth rate estimates, as well as on the outcome of competition between species for limiting nutrients.

The first to deal in quantitative terms with the relation between uptake and growth in unicellular algae were probably Eppley & Thomas (1969). Using diatoms grown in batch cultures, they showed that uncoupling of uptake and growth could occur in N-starved (*Chaetoceros gracile*) and N-sufficient (*Asterionella glacialis*) cells. Caperon & Meyer (1972) tried to establish a relationship between growth rate (μ) and the maximum uptake rate using phytoplankters grown in steady-state continuous cultures. Although observing a great variability in response to pulses depending on the species and units used to express the rates, they concluded that V_{max} increased with μ . Later work by Eppley & Renger (1974) and McCarthy & Goldman (1979) revealed the opposite trend, i.e. that V_{max} decreased with increasing growth rate. Collos & Slawyk (1980) tried to reconcile the contradictory data sets and suggested a bell-shaped relation between the nutrient supply rate and V_{max} (Fig. 5) already apparent in some of Caperon & Meyer's (1972) data and in data from Healey (1978) and Burmaster & Chisholm (1979) on phosphate uptake (Fig. 6) and associated

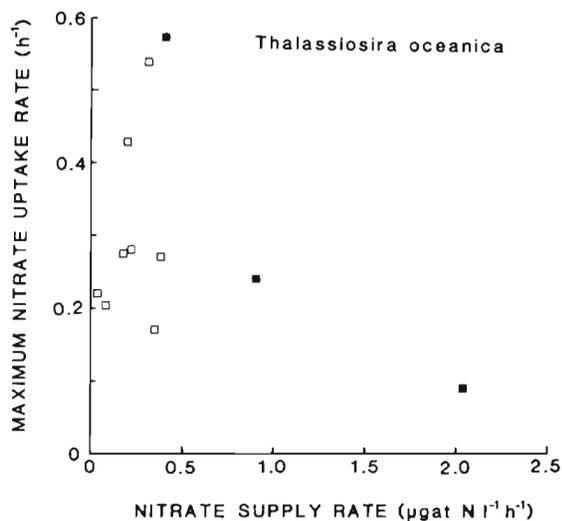


Fig. 5. Maximum nitrate uptake rate as a function of nutrient supply rate in chemostat culture. Data from Caperon & Meyer (1972) (\square), and Eppley & Renger (1974) (\blacksquare)

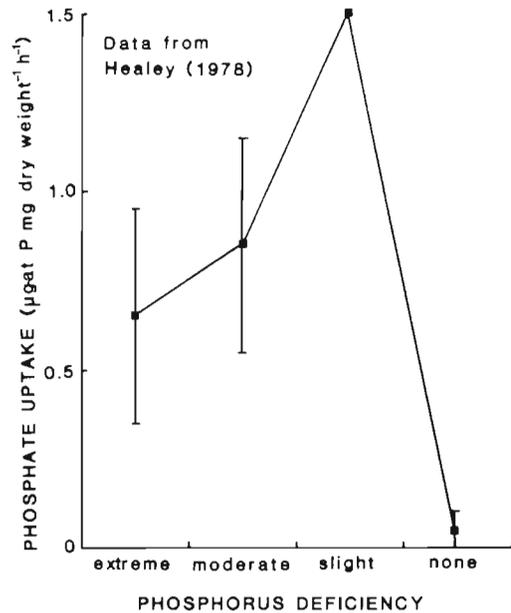


Fig. 6. Phosphate uptake as a function of phosphate deficiency. Data from Healey (1978) on a variety of unicellular algae. Vertical bars: range of values obtained on different species

enzyme activities. Goldman & Glibert (1982) experimentally confirmed such a relation for *Thalassiosira pseudonana* and several other species, but disagreed with Collos & Slawyk (1980) on which part of the curve best represents the natural situation in oligotrophic oceans. In their argumentation, McCarthy & Goldman (1979) and Goldman & Glibert (1982) selected data showing an inverse relation between ammonium uptake rate and algal growth rate (dilution rate of the continuous culture). They extrapolated such data to the field, essentially saying that phytoplankters in oligotrophic areas are able to grow fast because they can take up limiting nutrients very rapidly. Thus, the implicit assumption here is that the growth response is at least as fast as the fluctuations in limiting nutrient levels.

In the case of McCarthy & Goldman (1979), the example of *Thalassiosira pseudonana* was ill chosen because more recent work has shown that N-starved cells of this species present time lags of more than 24 h between an ammonium pulse and the beginning of cell division (Dortch et al. 1984). But, even if an instantaneous response of growth rate to a nutrient pulse can be assumed, the data of McCarthy & Goldman (1979) suggest that high uptake rates and high growth rates are mutually exclusive. Although this inconsistency was demonstrated by modelling studies (Turpin et al. 1981) and is beginning to be recognized (Goldman 1984a), it has not yet been suggested that a direct relationship between those 2 parameters could be of

advantage to a phytoplankter in a nutrient-poor and patchy area.

UPTAKE-GROWTH UNCOUPLING, INTERNAL NUTRIENT POOLS AND GROWTH LAGS

In this context, it might be of interest to establish a parallel between data sets concerning the uncoupling between V_{max} and μ , and those on accumulation of inorganic N internal pools and growth lag following a limiting nutrient pulse. Although data are lacking for certain species, it appears that those whose uptake and growth are highly coupled, such as species of *Dunaliella* or *Chaetoceros* (Goldman & Glibert 1982) accumulate very little internal inorganic N (Fig. 7) and exhibit a short growth lag (Fig. 8). These species may then process nutrient pulses into new biomass very efficiently. In contrast, algae such as *Thalassiosira weissflogii* and *Amphidinium carterae* can accumulate large amounts of ammonium (Conover 1975, Wheeler et al. 1983, Dortch et al. 1984) and present extensive uncoupling between uptake and growth (Goldman & Glibert 1982) and large growth lags upon N resupply (Dortch et al. 1984). This distinction is similar to the one made by microbiologists (Bader 1982) for substrate-limited growth: assimilative control when growth is limited by the uptake rate, and physiological control when it is limited by the rate of conversion of soluble substrates into biomass.

The relation between uptake-growth uncoupling and the internal ammonium pool (Fig. 7) could be logically expected. Indeed, it reveals a rather remarkable consistency in view of the fact that the 2 sets of variables were obtained by different groups of investigators. In contrast, the interpretation of the relation between the maximum internal ammonium pool and the growth lag is more difficult, and the arrangement of the axes as shown in Fig. 8 should not be taken to imply a cause-effect relation. Note, however, that such data are consistent with those of Fig. 3 in that species such as *Dunaliella*, *Chaetoceros* and *Skeletonema* presented very reduced lags upon ammonium pulses in the study of Thomas et al. (1980), and that the low ammonium content of *Chaetoceros* cells is also consistent with the absence of ammonium surge uptake in this genus (Conway & Harrison 1977). Thus, coming back to the relation between V_{max} and μ , it can be seen from the case of *Chaetoceros* (Fig. 7 & 8), that a direct relation between uptake and growth can be of advantage in a nutrient-poor environment. Goldman & Glibert (1982) disregarded such a possibility, but it must be recognized that such a relation has the advantage of liberating us from the paradox which is apparent in the hypothesis of McCarthy & Goldman (1979)

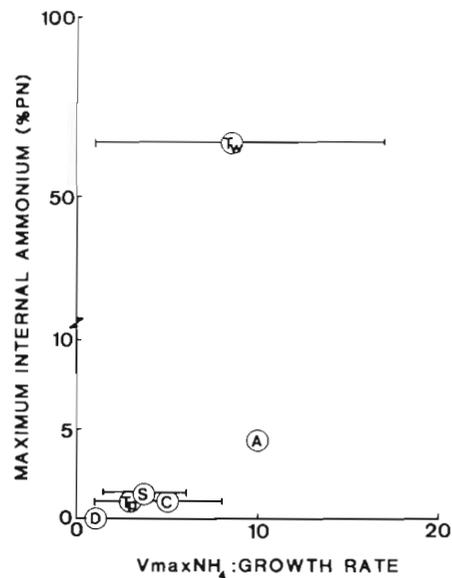


Fig. 7. Maximum internal ammonium pool as a function of the uncoupling between maximum uptake rate and steady-state growth rate. D: *Dunaliella*; S: *Skeletonema*; C: *Chaetoceros*; A: *Amphidinium*; Tp: *Thalassiosira pseudonana* 3H; Tw: *Thalassiosira weissflogii*. Data from Eppley & Thomas (1969), Conover (1975), Conway et al. (1976), Conway & Harrison (1977), Collos & Slawyk (1979), Dortch et al. (1982, 1984), Goldman & Glibert (1982), Thoresen et al. (1982). Horizontal bars: range of values found by different authors, or by the same authors under varying conditions

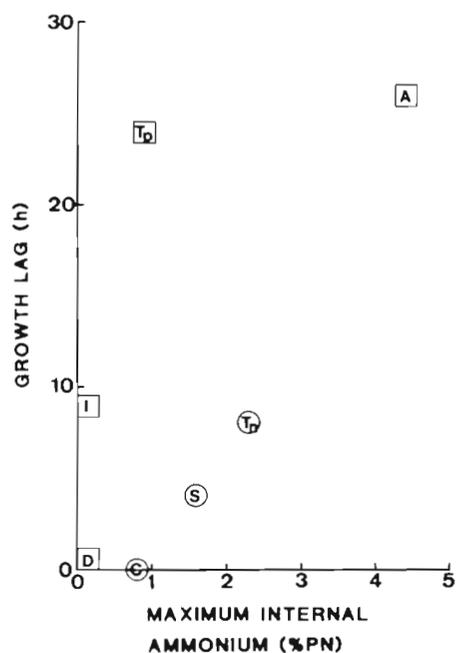


Fig. 8. Growth lag as a function of the maximum internal ammonium pool. A: *Amphidinium*; C: *Chaetoceros*; D: *Dunaliella*; I: *Isochrysis*; S: *Skeletonema*; Tn: *Thalassiosira nordenskioldii*; Tp: *Thalassiosira pseudonana* 3H. Data from Berland et al. (1973), Thoresen et al. (1982), Dortch et al. (1984). For A and Tp, growth lag values are minimum values

involving an inverse relation between μ and V : either the phytoplankton grows fast and has low uptake rates, or it grows slowly, and exhibits high uptake rates. Caperon (1969) and Caperon & Meyer (1972) suggested that the ability to accumulate internal stores of limiting nutrients was an ecological advantage in a nutrient patchy area. This might be true when the frequency of encounters with elevated nutrient areas is lower than the frequency of cell division, such as might be the case for nitrate pulses, for example, whose period has been shown to be of the order of 48 h in stratified oceanic areas (Klein & Coste 1984). However, if the nutrient pulsing frequency is high, as postulated in the current regenerated nutrient micropatch hypothesis (McCarthy & Goldman 1979, Lehman & Scavia 1982, 1984, Goldman 1984a, b), then I would suggest that growth rate has to be coupled to nutrient uptake rate for phytoplankton to survive in nutrient-poor waters. Any growth lag will be a disadvantage in terms of cell numbers.

For example, Fig. 8 indicates that, for 10 μM ammonium pulses (used by Dortch et al. 1984), *Chaetoceros* would become dominant over *Skeletonema costatum* and *Thalassiosira nordenskioldii* at pulsing frequencies greater than 1 per 4 h (4 h being the minimum growth lag of *S. costatum* on the ordinate of Fig. 8), because the latter 2 species would not have time enough to divide before the next pulse. This result is contrary to what Turpin & Harrison (1979, 1980) found, but may be explained by the lower ammonium pulses in their culture systems (a single 3 μM pulse every 24 h, or a 0.38 μM pulse every 3 h). Their conclusions and the ordering of the 3 above species as a function of ammonium pulsing frequency might well vary also as a function of the pulse magnitude, and the induced cell division lag.

NUTRIENT PULSES AND INORGANIC CARBON UPTAKE

In the microbiological literature, various causes of lag phases have been recorded (Barford et al. 1982). In the present case, interactions between C and N metabolism could be added to this list. Carbon is the main element in living matter after hydrogen, and any perturbation of its exchange between the cell and the environment is likely to have major consequences on subsequent growth and cell division. Transient changes in net C uptake following limiting nutrient pulses are presently the subject of much debate (Collos & Slawyk 1984, Elrifi & Turpin 1985, Goldman & Dennett 1985), but it appears that they depend on light levels and species. Data from Natarajan (1970) and Thomas et al. (1980) illustrate very clearly the influ-

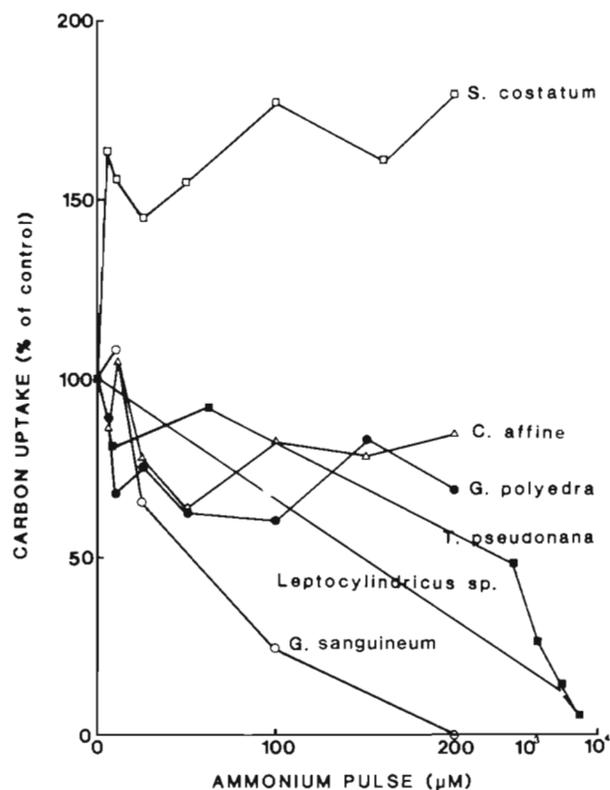


Fig. 9. Effect of varying concentrations of a single ammonium pulse on net carbon uptake by 6 species of phytoplankters. Data from Natarajan (1970) and Thomas et al. (1980)

ence of ammonium pulses on net C uptake in 6 species of phytoplankters (Fig. 9). In particular, the inhibition (*Thalassiosira pseudonana*) or stimulation (*Skeletonema costatum*) of the C uptake system by ammonium pulses is consistent with the large or reduced growth lags respectively exhibited by these species (Dortch et al. 1984).

Reduction in net carbon uptake upon ammonium pulses was interpreted as evidence for toxicity by Natarajan (1970) and Thomas et al. (1980). It could also represent an adaptation (Stockner & Antia 1976) in the form of a transient response which is later followed by a stimulation in C uptake such as observed by Turpin (1983).

Apart from the fact that such effects have a very practical impact on estimates of primary production based on C uptake, it remains that, in the case of *Thalassiosira pseudonana*, far-reaching consequences were observed on cell division which took place only 24 h after the ammonium spike (Dortch et al. 1984). Former studies on nutrient pulsing in algal cultures (Quarmby et al. 1982) have shown a peak in C fixation 14 h after ammonium addition. Transient changes in net C uptake have also been observed following phosphate pulses to phytoplankton (Becacos 1962, Stross et

al. 1973, Stross & Pemrick 1974, Lean & Pick 1981). Thus, the assumption of uncoupling between nutrient uptake and photosynthesis necessary to rapid growth and sporadic nutrient uptake (Goldman et al. 1981) is not always supported by experimental data.

NUTRIENT PULSES AND BALANCED GROWTH

Absence of a time lag for *Dunaliella* and *Chaetoceros* in Tables 2, 3 and 4 does not necessarily imply an instantaneous response of growth rate to an increase in nutrient supply, but probably reflects the inadequate sampling frequency for cell number determinations. While immediate increases in PN or IVF are possible upon N resupply (Table 1), this is certainly not the case for cell numbers, and there are good physiological reasons for this. The simplest of these is that phytoplankton cells, like all biological material, are made not only of N or P, but also of other elements and of macromolecules. For example, in the cell model of Williams (1971), a distinction is made between a 'synthetic' portion, consisting mostly of soluble nutrient pools, chlorophyll and enzymes, and a 'structural/genetic' portion consisting mainly of genetic material, cell wall and membranes. An idea of the minimum lag in cell division for transient conditions can be obtained from the microbiological literature where values of about 1 h have been recorded following a nutritional shift-up imposed on bacterial cultures (Kjeldgaard et al. 1961, Kjeldgaard 1958, Mateles et al. 1965, Schleif 1967). This represents the time necessary for DNA synthesis and chromosome replication. In spite of such evidence, it appears that, so far, most reasoning concerning N-based growth rates have considered only the synthetic (or storage) portion of the cell. For example, McCarthy & Goldman (1979), Goldman & Glibert (1982), and Goldman (1984b) argue that the presence of micropatches of nutrients allow maximum growth rates to be reached by algal cells. The results presented here indicate that several constraints other than the one outlined by, for example, Goldman (1984b) appear. First is the magnitude of the nutrient pulse. If we assume as a starting point that the algal cells are N-limited or starved (an assumption made by McCarthy & Goldman 1979), we can see that the encounter of a 3000 μM ammonium pulse (postulated in the study of Goldman 1984b), will reduce the net C uptake of *Thalassiosira pseudonana* by about 80 % (Fig. 9) for as long as 6 to 7 h. Generally, nutrient pulses of this magnitude have been found to inhibit, rather than enhance algal growth (Nyholm 1978, Burmaster 1979).

Thus, it appears that, at least for some species, there occurs a considerable cellular rearrangement follow-

ing nutrient pulses and that, in some cases, a large amount of time (more than 24 h) may be needed in order to resume balanced growth and before cell division occurs.

The second constraint which is likely to potentially reduce the N uptake-based growth rate is the decrease of V_{max} with time. Collos (1983) has reviewed patterns of uptake as a function of time under conditions of substrate saturation for nitrate and ammonium. Concerning the latter, and on time scales shorter than either the generation time of the organisms involved or the diurnal changes in environmental conditions such as the light-dark periodicity, the vast majority of species exhibited rapid decreases in V_{max} following an ammonium pulse.

Such uptake patterns necessitate the use of appropriate time units in expressing observed rates. For example, if ammonium uptake is measured over a 1 min period, the uptake rate should be reported in units of min^{-1} and not h^{-1} unless the constancy of uptake with time is established. In the same way, extrapolations of growth rates from uptake rates should be made only under conditions of balanced growth (Eppeley & Strickland 1968).

A final constraint to primary production estimated from limiting nutrient uptake is that cell division may be restricted to a particular portion of the day-night cycle regardless of the nutrient regime (Wheeler et al. 1983).

It is probably too early to try to extend the laboratory results to the natural situation. Data on nutrient pulse magnitude and frequency in the field are clearly needed in order to assess primary production on relevant time scales. While such data are becoming available for nitrate (Klein & Coste 1984), they are still very scarce for other forms of dissolved N (Legendre et al. 1985, Smith 1986). The results presented here, however, are in agreement with Turpin & Harrison (1979, 1980) and Lehman & Scavia (1984) in that nutrient pulses should have marked effects on species composition.

For the time being, we have to rely on algal culture data in order to help interpret field results and gain insight into phytoplankton growth processes. These data show that there are transient effects of nutrient pulses on growth of nutrient-limited or starved algae, the most spectacular of these being the induced time lag in cell division. The fact that these effects can be either inhibiting or stimulating on growth processes has very practical consequences, both on estimates of primary production from C uptake and interpretations of limiting nutrient uptake rates measured over short periods of time. Concerning the latter, I suggest – following Williams (1971) – that, until we have a more complete understanding of the significance of limiting nutrient uptake relative to algal growth, uptake data lead not to extrapolations of growth rate in the particu-

late phase, but to values of 'nutrient demand', i.e. changes in the dissolved phase of aquatic environments.

Acknowledgements. Support for this research came from the Centre National de la Recherche Scientifique and the Institut Français de Recherche pour l'Exploitation de la Mer (UM 10). I thank P. J. Harrison, J. Lewin, E. Paasche and A. Sourmia for comments.

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This review was submitted to the editor; it was accepted for printing on August 14, 1986