

# Phytoplankton growth and zooplankton grazing in oligotrophic oceans

George A. Jackson

Institute of Marine Resources, Food Chain Research Group, Scripps Institution of Oceanography, University of California, San Diego, La Jolla, California 92093

Central oceanic regions such as the Sargasso Sea and the North Pacific Gyre have traditionally been thought of as biological deserts<sup>1,2</sup>. New phytoplankton production estimates<sup>3</sup> and interpretations of physiological data<sup>4,5</sup> have suggested that these areas are, in fact, highly productive and that nutrient exchanges supporting these high growth rates are extremely transient. Fast phytoplankton growth rates must be balanced by equally fast zooplankton-caused mortality. Zooplankton abundances and their filtration rates, however, are consistent with slow phytoplankton growth rates, not fast. It is shown here that the dominant grazers in oligotrophic areas seem to be microzooplankton, and that molecular diffusion limits the effect of nutrient pulses, implying that bulk nutrient concentrations are most important. Present growth studies imply that phytoplankton can meet their growth needs with nanomolar ammonia concentrations.

Ambient concentrations of such nitrogenous nutrients as ammonia are below detection limits with conventional chemical methods in surface waters of central oceanic oligotrophic areas<sup>6,7</sup>. Indirect evidence suggests that the concentrations of ammonia and urea in the North Pacific central gyre<sup>7</sup> are less than 50 nM. This is far lower than average values for unpolluted coastal waters<sup>8,9</sup>, and very low compared with half-saturation concentrations for most phytoplankton grown in cultures<sup>10</sup>.

Growth rates for phytoplankton growing with steady-state nutrient kinetics at such low concentrations would be low, a fact supported by <sup>14</sup>C incubation measurements in the central North Pacific Gyre. Average specific growth rate, calculated as carbon assimilation rate divided by living carbon concentration<sup>7</sup>, is about 0.1 per day.

Phytoplankton growth measured by other techniques can yield much higher rates. The shortest doubling time reported is 3 h in the Sargasso Sea, calculated from ATP concentration changes in incubated water samples<sup>3</sup>. This is equivalent to a specific growth rate of 2.8 per day for a 12-h growth day.

Cellular nutrient status determines and can, therefore, indicate growth rate. Phytoplankton grown in cultures have their carbon, nitrogen and phosphorus contents in the same relative proportions as those in oceanic phytoplankton (in the Redfield ratio) only when growing at maximal rates<sup>5</sup>. If the physiology of oceanic phytoplankton is the same as that of

cultured phytoplankton then oceanic cells also grow at maximum rates<sup>5</sup>. Oceanic cells with the same maximum growth rate as cultured cells would grow at 2-3 per day.

These high growth rates cannot be supported for cells growing in a steady state with measured nitrogenous nutrient concentrations. Because slightly N-depleted phytoplankton display elevated uptake rates when compared with N-sufficient algae and because a source of regenerated nitrogen is zooplankton excretion, McCarthy and Goldman<sup>4</sup> suggested that phytoplankton in oligotrophic oceans may obtain their nitrogen needs by rapid, transient uptake of excreted nitrogen. They noted such nutrients should be present at concentrations well above average in the wakes of swimming animals. They recognised that such elevated concentrations would persist only briefly. Thus, phytoplankton might appear to be growing successfully at the expense of virtually undetectable small-scale nutrient pulses.

The predominant source of phytoplankton mortality in low nutrient input regions such as mid-ocean gyres is zooplankton grazing. Calculation of grazing rates by multiplying typical laboratory-measured filtration rates and field-measured grazer densities (Table 1) shows that microzooplankton, especially protozoa, are dominant herbivores in the loss to grazers of 11% per day (0.11 per day) in the oligotrophic Pacific.

The conclusion that microzooplankton in the North Pacific Gyre are the dominant grazers explains the low rate of zooplankton excretion measured there<sup>11</sup>. Specific regeneration rate of the macrozooplankton, calculated by dividing 2.4 nM per day nitrogen regeneration rate<sup>11</sup> by the 0.2 μM particulate nitrogen concentrations, is 0.012 per day. Microzooplankton feeding at a total filtration rate 5.4 times as fast (Table 1) will increase this rate to 0.007 per day.

Continuous, steady state uptake has specific growth rates equalling specific uptake rates. To achieve a 0.1 per day growth rate, concentrations less than now measurable would be adequate. For example, *Thalassiosira pseudonana* growth rate is 2.6 per day (81% of maximum) for ammonia concentrations at the detection limit, 0.1 μM (refs 22, 23). If growth follows the Monod equation,

$$\mu = \mu_{max} \frac{C}{C + K_s} \quad (1)$$

with  $\mu$  the specific growth rate,  $\mu_{max}$  the maximum growth rate,  $C$  the ammonia concentration, and  $K_s$  the half-saturation concentration, then a  $K_s$  value of 23.5 nM can be calculated from the above concentration and growth rate. Such a cell could maintain a growth rate of 0.1 per day at an ammonia concentration of 0.8 nM. A growth rate of 2.6 per day would, of course, require 0.1 μM ammonia.

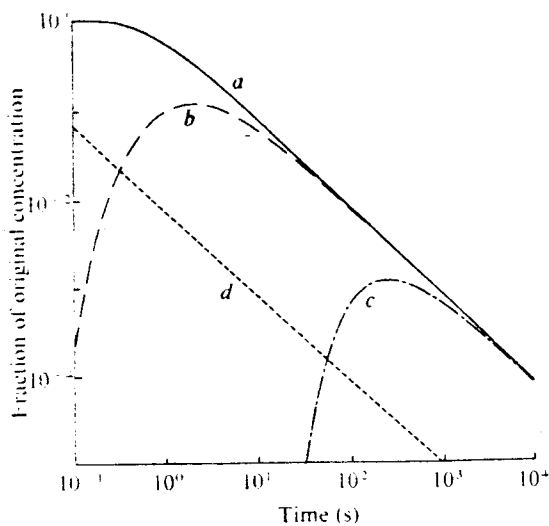
Short term non-steady state ammonia uptake rates can be much faster than growth rates: instantaneous ammonia uptake rates are as high as 15 per day, equivalent to doubling times of 0.05 days or  $4.3 \times 10^3$  s (ref. 4). Phytoplankton cells would have to take up nitrogen at maximum capacity for this length of time to accumulate enough nitrogen to support one cell division.

Table 1 Biological scales for central N. Pacific Gyre region

	Phytoplankton	Microzooplankton			Macrozooplankton	
		Protozoa	Nauplii	Post-nauplii	Copepods	Thaliaceans
Concentrations (C) (individuals per litre)	600,000*	655*	3*	1*	0.1 <sup>†</sup>	$1 \times 10^{-4} \pm$
Separation distance (D) (cm)	0.1	1.1	5	10	21	—
Swimming speed (S) (m per day)	—	120§	—	—	1,200	—
Daily path separation (cm)	—	0.01	—	—	0.29	0
Individual filtration rates (ml per individual per day)	—	0.120*	2#	10#	168**	500 <sup>††</sup>
Total filtration rate (ml per litre per day)	—	75	6	10	16.8	0.05

Total filtration rate is 108 ml per litre per day, equal to a 0.11 per day grazing rate. Separation distance is  $C^{-1/3}$ . Daily path separation assumes all swimming paths are parallel and equally spaced,  $(C^{-1}S^{-1})^{1/2}$ .

\* Ref. 17; † M. M. Muliin, personal communication; ‡ doliolids are dominant Thaliaceans (J. A. McGowan, personal communication); § ref. 18; || ref. 19; \* ref. 15; # ref. 20; \*\* ref. 21; †† Filtration rate is that of *Doliolitta gegenauri* (D. Deibel, personal communication).



**Fig. 1** Concentrations through time after a plume is created. Concentrations are fractions of original plume concentration. *a*, *b*, *c* show the effect of a 100  $\mu\text{m}$  wide plume which is representative of a copepod's passage. *a*, At centre of plume; *b*, 100  $\mu\text{m}$  from plume centre, 50  $\mu\text{m}$  from initial plume edge; *c*, 1,000  $\mu\text{m}$  from plume centre; *d*, effect of 10  $\mu\text{m}$  wide plume representative of protozoa passage at centre of plume.

Phytoplankton growing at 0.1 per day could meet their nitrogen needs at uptake rates 1% of the maximum 15 per day.

A discontinuous nutrient source would be excreta from animals swimming near a phytoplankter. From the moment the animal excretes them, nutrients diffuse away. A phytoplankter will see a different range of nutrient concentrations depending on where it is relative to the plume. The concentration in a plume with square cross-section can be easily calculated. The relative concentration,  $f$ , at a given time after excretion,  $t$ , at a distance away from the centre along the centre line,  $x$ , for a plume of initial width,  $2a$ , and diffusivity,  $D$  ( $= 10^{-5} \text{ cm}^2 \text{ s}^{-1}$ ),

$$f = \frac{1}{2} \left\{ \operatorname{erf} \left( \frac{a-x}{2(Dt)^{1/2}} \right) + \operatorname{erf} \left( \frac{a+x}{2(Dt)^{1/2}} \right) \right\} \times \operatorname{erf} \left( \frac{a}{2(Dt)^{1/2}} \right) \quad (2)$$

where  $\operatorname{erf}(z)$  is the error function of  $z$  (ref. 12, p. 56).

The results (Fig. 1) show that even within the plume, nutrient concentrations drop rapidly. Three hundred seconds after a copepod-sized pulse (100  $\mu\text{m}$  across) is released, concentrations have dropped by three orders of magnitude at the pulse centre and are a maximum 0.1 cm away that is  $< 0.001\%$  of the initial concentration. Molecular diffusion away from protozoan wake will be faster. Concentration at the centre of a 10  $\mu\text{m}$  plume will have dropped to 0.1% of the initial concentration within 0.1 s. Because they will be further from the pulse most phytoplankton will see even lower concentrations.

Ammonia concentration in a plume behind a swimming herbivore can be calculated several ways. A grazer could be viewed as converting the particulate nitrogen in the water it filters to ammonia. By continually converting the 0.2  $\mu\text{M}$  particulate nitrogen<sup>7</sup> to ammonia, it would leave a trail of 0.2  $\mu\text{M}$  ammonia. This supposes continual conversion. Sporadic excretion would raise concentration in a given pulse but decrease water volume affected. McCarthy and Goldman<sup>4</sup> calculated that such a sporadic pulse could contain 5  $\mu\text{M}$  ammonia around a copepod. Thus, the maximum nutrient concentration behind a protozoan will have decreased from 200 to 2 nM within 1 s; the same concentration change behind a copepod would occur within 100 s. These times are much shorter than the 4,300 s earlier calculated as the length of time required to accumulate sufficient N for a doubling. Individual nutrient pulses are not sufficient to be the main nitrogen source for phytoplankton.

These calculations neglect concentration decreases caused by nutrient uptake and assume that only molecular diffusion is important. Phytoplankton and turbulence cause concentrations to decrease faster than has been calculated here.

Usefulness of these molecular diffusion calculations depends on nutrient recycling occurring on small scales. Comparison of feeding rates for potential oceanic herbivores shows that small grazers—protozoa and copepods—dominate the larger thaliaceans, accounting for 99% of water filtered. The marine copepod *Paracalanus parvus* incorporates 37% of ingested particulate nitrogen and recycles the rest<sup>13</sup>. If mid-oceanic grazers recycle at the same 63%, then microzooplankton and copepods recycle at least 62% of ingested primary production for uptake by surviving phytoplankton, either directly or through bacteria. Thus, nitrogen cycling occurs predominantly on the microscale. Inputs on a larger scale, from salp aggregates or fish schools, may be more visible but less important.

Importance of nutrient interactions on a small scale is analytically convenient because diffusion-based mixing processes are so much better understood than those based on turbulence. Additionally, the complete range of phytoplankton-herbivore interactions would be occurring at any given time in the medium scale water sample. This would imply that the mean nutrient concentration through time at a given phytoplankter (that is, what a cell sees) would be the same as the mean concentration through space at a given time (that is, a water sample). A linear uptake-ammonia relation would imply that mean nutrient uptake rate is linearly related to the mean concentration through time at the cell, which is in turn linearly related to the measured concentration. As long as uptake rate is a linear function of ammonia concentration, the amount of ammonia will provide a useful mirror of an individual phytoplankter's environment. Less than linear uptake rates, indicative of saturation of cellular systems, would cause a linear model to overestimate cellular nutritional status.

Microzooplankton, which control N cycling in the temporally and spatially uniform central North Pacific Gyre<sup>14</sup>, need not dominate elsewhere: in the very heterogeneous coastal California protozoa are relatively unimportant<sup>15</sup>. The northern Sargasso Sea, where cold core rings introduce variability not seen in the central Pacific<sup>16</sup>, may have different grazers. However, similarity in zooplankton volumes for the North Pacific and the North Sargasso Sea<sup>14,16</sup> suggest that the two oligotrophic systems are similar.

Why, then, do oceanic phytoplankton show nutritional composition characteristic of nutritionally fit cells? If oceanic algae grow at a rate of 0.1 per day and if the relationship between cellular nutrient status and maximum growth rates found in culture studies<sup>5</sup> apply to all phytoplankton, then algae from oligotrophic oceanic areas have lower maximum growth rates. This would imply that the algae have adapted to perpetually low growth rates by losing the ability to grow fast. Further understanding of nutrient cycling in these oligotrophic areas will depend on the development of techniques to measure these low concentrations.

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## Stromatolites 3,400-Myr old from the Archean of Western Australia

Donald R. Lowe

Department of Geology, Louisiana State University, Baton Rouge, Louisiana 70803

Internally laminated conical mounds characterise a regionally extensive chert unit near the top of the 3,400-Myr old Warrawoona Group in the Pilbara Block of Western Australia. The chert formed by silicification of a carbonate-evaporite sequence deposited in shallow subtidal to intertidal environments. The morphology and internal organisation of the mounds described here suggests that they are conical stromatolites similar but not identical to members of the common Proterozoic group *Conophyton* Maslov.

The Warrawoona Group of the eastern Pilbara region of Western Australia (Fig. 1) is a typical Archean greenstone belt volcanic sequence<sup>1,2</sup>. The 10-km thick section consists largely of volcanic rocks interstratified with cherty sedimentary units generally <30 m thick. Low greenschist-grade metamorphism has affected the entire sequence, but, in the areas studied, shearing is largely absent. Cherty units commonly show only minor recrystallisation.

During sedimentological studies in the eastern Pilbara, I identified a distinctive stromatolitic chert unit near the top of the Warrawoona Group in at least three of the Pilbara structural belts (Fig. 1). Here this unit is called the Strelley Pool chert for outcrops at Strelley Pool (21°06'33"S, 119°08'14"E) in the Pilgangoora Syncline (Fig. 1). The unit averages a relatively constant 20-25 m in thickness, although it reaches 50 m on the

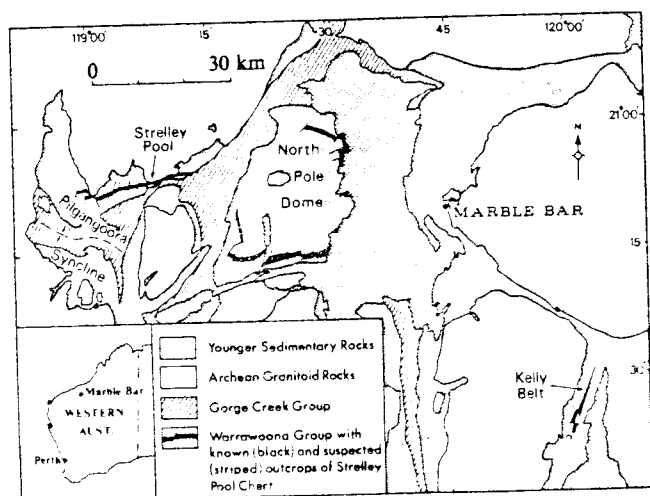


Fig. 1 General geological map of the northeastern Pilbara region showing known and suspected outcrops of the Strelley Pool chert.



Fig. 2 Photomicrograph of alternating light and dark flat laminae from area between conical stromatolites. Arrows point to layers containing detrital quartz grains. Micronodular character of translucent laminae resembles fenestral texture of modern algal mats. Scale bar, 0.5 cm.

north flank of the North Pole Dome (21°00'43"S, 119°28'52"E). An excellent section in the Kelly Belt occurs near Spinaway Creek at 21°35'S, 120°01'01"E.

The Strelley Pool chert displays a nearly constant internal stratigraphy in the three structural belts in which it was identified. It can be subdivided into two main members. The lower 10-15 m consist largely of finely laminated chert. The rock shows thin, varve-like alternating laminae of light grey chert and dark grey carbonaceous and pyritic chert or of calcareous and non-calcareous chert (Fig. 2). The laminae may be flat and even but commonly form isolated or clustered conical mounds here interpreted to be stromatolites. This subdivision characteristically includes units up to 1 m thick composed of massive, coarsely crystalline silicified evaporite. These units are present in every section examined. In the Pilgangoora Syncline, a quartzite layer is present locally at the base of the chert, and thin laminae and wisps of detrital quartz occur irregularly in the overlying laminated chert (Fig. 2). Along at least two horizons, underlying laminae are truncated and cut by desiccation cracks filled with detrital sand, but, overall, coarse clastic layers, current structures, and evidence of exposure are rare. This subdivision was deposited in a subtidal to lower intertidal environment and originally consisted of interlayered evaporite and carbonate sediments.

The upper part of the Strelley Pool chert includes a variety of dark to light grey, white, and greenish cherts. Layers of large silicified evaporite crystals occur towards the base. Large pods of silicified collapse breccia and cavities containing silicified stalactitic and stalagmitic fill indicate the existence of considerably greater amounts of original evaporite and extensive post-depositional exposure, leaching, and solution collapse. Small intraformational conglomerates, scours, and other features