

Caperon J & Meyer J. Nitrogen-limited growth of marine phytoplankton—I. Changes in population characteristics with steady-state growth rate.

Deep-Sea Res. 19:601-18, 1972.

[Hawaii Institute of Marine Biology, Kaneohe, HI]

Nitrate-limited growth rate of four species of algae is related to internal nitrogen content by a hyperbolic expression. Relative variation of cell carbon, nitrogen, chlorophyll-a, and volume with steady-state growth rate is examined in the context of using these measures of the physiological state of the population as indicators of nutrient-limited growth rate. [The *SCI*® indicates that this paper has been cited in over 205 publications.]

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This paper was the first of a pair on nutrient-limited growth of marine phytoplankton. In this paper we examined variation in population characteristics (e.g., nitrogen or carbon per cell) and growth rate for four species of phytoplankton, while in the second paper¹ we combined this information with data on uptake kinetics and developed a theoretical model for phytoplankton population growth. It is interesting that it is the first, very data-rich paper that has been cited so often rather than the second, which is somewhat more theoretical.

Most of this research was done while I was a research associate with John Caperon at the University of Hawaii, although part of it was from the research I did for my master's degree there. The idea for this work developed from John's earlier research on nitrate-limited growth of a single algal species,² and it was funded as part of a study on what the city of Honolulu should do with its sewage.

I think that three aspects of the paper are responsible for its citation frequency. First, we presented data on the relationship between steady-state, nitrogen-limited growth rate and

a wide range of important characteristics of phytoplankton cells, such as carbon/cell, nitrogen/carbon, cell volume/carbon, and chlorophyll-a/carbon. These data are particularly valuable to modelers of planktonic ecosystems. We were able to do this by applying continuous-flow culture techniques to the study of phytoplankton populations, which was fairly new at that time. Much of the previous work had been done with phytoplankton in batch cultures, where nutrient concentrations were variable and greatly exceeded natural oceanic concentrations, and where growth rate could not be held constant. Although they are powerful tools, chemostats also require considerable attention, and I recall a Christmas Day spent with the algae and several nights spent on a cot in the lab.

This series of experiments was also one of the first times a carbon-hydrogen-nitrogen analyzer had been used to examine N/C ratios in phytoplankton. A chemical oceanographer on the staff of the Hawaii Institute of Marine Biology had recently acquired the instrument, and John recognized its potential for determination of N/C ratios in phytoplankton. It is now a frequently used technique.

This paper has also often been cited for demonstrating that growth rate is related to internal nutrient stores of the cell rather than to the ambient nutrient concentration; in other words, growth rate reflects the prior nutrient experience of the population. This complicates models that attempt to relate algal productivity to ambient nutrient concentration. Ironically, this idea is even more clearly developed in the second, less-cited paper,¹ where we show the relationship between external nutrient concentration, uptake kinetics, and growth rate. Algal growth dynamics have recently been reviewed by Yves Collos.³

Neither John nor I have remained in the area of phytoplankton ecology. I am now a stream ecologist and am currently studying the microbial food web of a blackwater river. John has applied his scientific expertise to the growing of exotic tropical fruits on a beautiful piece of land in New South Wales, Australia.

1. Caperon J & Meyer J. Nitrogen-limited growth of marine phytoplankton—II. Uptake kinetics and their role in nutrient limited growth of phytoplankton. *Deep-Sea Res.* 19:619-32, 1972. (Cited 170 times.)
2. Caperon J. Population growth response of *Isochrysis galbana* to nitrate variation at limiting concentrations. *Ecology* 49:866-72, 1968. (Cited 80 times.)
3. Collos Y. Time-lag algal growth dynamics: biological constraints on primary production in aquatic environments. *Mar. Ecol.—Progr. Ser.* 33:193-206, 1986.