NUTRITIONAL CONTROL OF PHYTOPLANKTON SINKING RATES

A DISSERTATION SUBMITTED TO THE GRADUATE DIVISION OF
THE UNIVERSITY OF HAWAII IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

IN OCEANOGRAPHY

DECEMBER 1977

By

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ABSTRACT

An analysis of technical and theoretical problems associated with the measurement of phytoplankton sinking rates by several commonly used methods indicates that these methods are both inaccurate and imprecise. Sinking rates estimated by the discrete sample layer (DSL) method tend to systematically overestimate the mean sinking rate of the population due to the effect of inefficient detection of cells on the bottom of the settling chamber. Sinking rates estimated using the homogeneous sample (HS) method and so-called $t_{1/2}$ technique systematically underestimate the mean sinking rate if any cells in the population sink faster than twice the estimated average sinking rate.

A rigorous mathematical framework is developed which, in conjunction with certain modifications in settling chamber design, allows calculation of the mean sinking rate (assuming that no cells are positively buoyant) for both the DSL and HS methods. These theoretical and technical modifications permit mean sinking rates to be estimated more rapidly, and with greater accuracy and precision, than has been possible by previously used methods.

This work reports the mean sinking rates of steady-state phytoplankton populations whose specific growth rates and physiological states were controlled through use of continuous culture techniques. The sinking rates of these continuous culture populations were considerably lower than prior measurements on their batch culture counterparts; averaged over the entire diel cycle, the mean sinking rate was ca. 0.45 $m \cdot day^{-1}$ for the coccolithophorid and ca. 0.03-0.07

$m \cdot day^{-1}$ for the diatoms studied. The more uniform characteristics of steady-state populations, the elimination of sampling bias toward faster sinking elements, and the calculation of mean vs. median rates account for the downward revision of these sinking rate estimates. Sinking rates are not well correlated with specific growth rates or with different forms of substrate limitation. The only exception to this is the evidence for higher sinking velocities in P-limited cultures particularly at low specific growth rates. The study revealed pronounced diel sinking rate variations which are greater than the growth rate or substrate-dependent variations. The highest and lowest sinking rates were found at the ends of the dark and light periods, respectively. These mean sinking rates are positively correlated with various cell size parameters (cell volume, N/cell, C/cell) at steady state.

The effects of progressive nutrient impoverishment upon population buoyancy were inspected in nonsteady-state "bioassay" populations which were maintained for prolonged periods in batch culture. The mean sinking rates (ψ) did not show continuous, monotonic increases with subsequent senescence development such as implied in the literature. The ψ patterns differed in the nature and response rate with the substrates (NO_3^-, NH_4^+, $PO_4^{\equiv}$) primarily limiting growth. P-limited populations showed progressive ψ increases over the 18-day experiments paralleled by slow rate of maximum yield attainment. N-limited populations displayed initially high ψ (relative to steady-state values) corresponding to a more rapid attainment of maximum yield, followed by declining ψ with progressive senescence. Trials with populations of differing initial specific

growth rate and amount of intracellular limiting nutrient indicate a relationship between the bioassay growth response and the resulting buoyancy cycle. The persistence of a diel buoyancy response in the face of declining metabolic activity implies that the responsible physiological mechanism is related to a basal metabolic function. The short-term buoyancy response to a perturbation of the steady-state uptake system shows an instantaneous elevation of the population ψ. These results are consistent with the hypothesis that buoyancy regulation is related to an energy-requiring process.