This Week's Citation Classic® CC/NUMBER 5 JANUARY 29, 1990

Eppley R W, Holmes R W & Strickland J D H. Sinking rates of marine phytoplankton measured with a fluorometer. *J. Exp. Mar. Biol. Ecol.* 1:191-208, 1967.

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A fluorometer was used to detect chlorophyll fluorescence of phytoplankton as it settled. Cells from growing cultures settled more slowly than senescent ones. Sinking rate was a function of cell size, with interesting exceptions. [The *SCI*® indicates that this paper has been cited in over 200 publications, making it the most-cited paper from this journal.]

Sinking Rates of Ocean Phytoplankton

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May 17, 1989

In 1965 Carl J. Lorenzen was at Scripps, working in the Tuna Oceanography Group. Carl was interested in the oceanographic applications of a fluorometer to measure the fluorescence of chlorophyll within living phytoplankton.[1] My boss, and the intellectual leader of the phytoplankton people at Scripps, John D.H. Strickland, saw the importance of this work and got one of Carl's specially modified fluorometers for our group. Meanwhile, Ted Smayda at the University of Rhode Island was publishing papers on phytoplankton sinking rates, determined laboriously by watching individual cells with a microscope. It occurred to us that the fluorometer could be used to follow the sinking of populations, while only the largest phytoplankters contained enough pigment for the fluorometer to detect individual cells. We constructed an appropriate sinking vessel and set to work measuring population sinking rates.

Robert W. Holmes had established a large collection of phytoplankton cultures in Strickland's group at Scripps, so he and I went through the collection systematically, measuring sinking rates, cell volumes, growth rates, and other features that might influence sinking rates. We soon had a massive data set, compared with the information available in the literature, and were able to draw/confirm some generalities. One clear result was that a phytoplankter's sinking velocity changed with its physiological state. There were essentially two states: growing and senescent. We also observed aggregation and accelerated sinking in a diatom that produced extracellular chitin fibers. Dr. E. Paasche arrived from the University of Oslo, bringing with him cultures of the coccolithophorid, *Emiliania huxleyi*, and the secret of how to remove the calcium carbonate coccoliths from the cells without damage. Thus we were able to determine *E. huxleyi* sinking rates with and without its coccoliths. Other ideas and observations crept into the paper from the active work going on at that time, such as growing plankton in the Scripps Deep Tank and a cruise to the Peru upwelling region. There were also red tides off Scripps in 1964-1965, due to dinoflagellates, and Holmes had cultures of some of the causative organisms. Thus we were able to determine sinking rates of swimming cells to compare with nonmotile diatoms.

Strickland joined in writing the paper, contributing, among other things, calculations of the specific gravity of diatoms and its variation with cell size. We also included a recipe for the seawater culture medium then in use in the group, which no doubt accounts for some of the citations of this paper. Most, however, cite the results and the physiological generalities and implications of the work. In 1970 Smayda wrote an extensive review of the subject[2] and included much of our work, even a modification of one of our figures showing dramatically the influence of cell size and physiological state on sinking rate. This was very gratifying. It has found its way into textbooks.

Later, Paul K. Bienfang at Hawaii developed yet another clever way of assessing phytoplankton sinking rates. He reinterpreted much of the earlier work in his papers a decade or so after ours.[3] A recent seminal paper considers the evolutionary survival value of the sinking of diatoms and their senescent aggregates.[4] Such aggregates have been photographed on the deep-sea floor in the North Atlantic following the spring bloom.[5] Since sinking biogenic material transports organic carbon to the ocean interior, where it may remain for decades to centuries, the measurement of particle flux with sediment traps[6,7] has become an important component in the study of the oceans' role in global change.

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2. **Smayda T J.** The suspension and sinking of phytoplankton in the sea. *Oceanogr. Mar. Biol.* 8:353-414, 1970. (Cited 295 times.)
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4. **Smetacek V S.** Role of sinking in diatom life-history cycles: ecological, evolutionary and geological significance. *Mar. Biol.* 85:239-51, 1985. (Cited 45 times.)
5. **Billet D S M, Lampitt R S, Rice A L & Mantoura R F C.** Seasonal sedimentation of phytoplankton to the deep-sea benthos. *Nature* 302:520-2, 1983. (Cited 25 times.)
6. **Honjo S.** Seasonality and interaction of biogenic and lithogenic particulate flux at the Panama Basin. *Science* 218:883-4, 1982. (Cited 90 times.)
7. **Martin J H, Knauer G A, Karl D M & Broenkow W W.** VERTEX: carbon cycling in the northeast Pacific. *Deep-Sea Res.* 34:267-85, 1987.

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