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On the philosophy of modeling—reply to a comment by M. R. Droop

In his comment on our recent silicon uptake model (Davis et al. 1978) Droop (1978) asserts that it would be wise to simplify the model and ignore the internal pool which on the average is only a few percent of the total cell silicon (though up to 50% in certain cases: Azam and Chisholm 1976). We agree this might be a reasonable approach for some uses, for example, to incorporate silicon uptake kinetics into an annual ecosystem model for management purposes. However, Droop suggests ignoring the internal pool for all nutrients for all modeling purposes and to this we strongly object.

Modeling of biological systems has been sold to the public and the granting agencies as a tool for ecosystem prediction and management, and the approach has been to use the simplest possible model for the system at hand ignoring biological truths which do not apply to that lake, that year, etc. This approach has had limited success to date but it holds considerable promise for the future, particularly as we become more knowledgeable as to what to include and what to leave out of the model.

The more fundamental use for modeling is to combine the available knowledge of a system to test ideas of how the system works and to see how sufficient our knowledge is and where we need further study. This was the purpose of our recent model, and we feel it successfully achieved those goals. It demonstrated that inclusion of the internal silicon pool allowed us to model the observed transient states, confirming the biochemical evidence for the existence of the internal pool. The model demonstrated that our knowledge of silicon utilization by diatoms was fundamentally complete; however, at the same time it pointed to specific aspects which need further study such as the feedback control mechanisms. The simplified version suggested by Droop would be totally inadequate for this task; in fact, it was the inadequacy of the two-compartment model which inspired our modeling effort.

For certain uses, for example, as a component of a large management model, we agree it may be reasonable to use a two-compartment model for silicon or vitamin B_{12} uptake as Droop suggested. However, the two-compartment model is clearly unacceptable for modeling uptake of nitrogen and phosphorus, which are the major limiting nutrients in marine and freshwater systems. Phosphorus is the prime example, where much of the research of the past 25 years on freshwater phytoplankton has focused on the importance of internal phosphorus pools. Mackereth (1953) observed a 25-fold de-

crease in phosphorus per cell in the diatom *Asterionella formosa* during phosphorus starvation. He also noted that phosphorus-depleted cells could take up large quantities of phosphorus with no detectable growth and concluded that *A. formosa* must form large nonfunctional internal pools of phosphorus. Similar behavior has been observed for marine yeasts (Button et al. 1973), blue-green algae (Healey 1973), and green algae (Rhee 1974), to name a few examples. It is known that phosphorus is stored in polyphosphate bodies which have been induced by excess phosphorus supply (Jensen and Sicko 1974; Sicko-Goad et al. 1975).

The folly of ignoring the internal pool for phosphorus can be demonstrated by a simple example, using Mackereth's (1953) data. Assume that one wishes to predict the outcome of species competition in a phosphorus-limited lake in July. Ignoring the internal pool, one would look at the available phosphorus level in the lake and the K_s for phosphorus uptake for the species involved and make the predictions. By so doing, one may be in fact ignoring the actual competition and looking at two almost unrelated pieces of data. If indeed *A. formosa* can store 25 times its minimal phosphorus requirement, as Mackereth's data suggest, then it may well have stored sufficient phosphorus for a considerable portion of the following summer's growth during winter and spring when phosphorus supplies were more abundant. In fact, the actual competition for the uptake of phosphorus may have taken place months before this midsummer period.

Internal pools are equally important in considering nitrogen metabolism, but for different reasons. Internal nitrate pools may represent 30% of the cell's nitrogen (Bhovichitra and Swift 1977), a significant but not overwhelming amount as in the case of phosphorus. More importantly, nitrogen is available to the phytoplankton in fresh or salt water as nitrate, nitrite, ammonium, urea, and a variety of other organic forms. It is well documented that many species take up ammonium preferentially over nitrate at ammonium levels >0.5 μg-atom N liter^{-1} (Eppley et al. 1969; Strickland et al. 1969). Recent conceptual models of nitrogen uptake by phytoplankton (Grenney et al. 1973; Conway 1977; DeManche et al. unpublished) have followed the pathways documented for yeasts and higher plants (e.g. Simms et al. 1968) which include internal pools for nitrate, nitrite, ammonium, and amino acids. A series of enzymes connect the pools in the above order with the final end product being amino acids and proteins. It is presently thought that when ammonium is available the internal ammonium pool increases and through a specific feedback control mechanism inhibits the activity of either the permease for nitrate or nitrate reductase. Thus inorganic nitrogen pools can be a significant part of the total cell nitrogen (30%) and can be important in regulating uptake as well. For nitrogen, as for phosphorus, it would be imprudent to ignore the internal nutrient pool and use the same simplified model for all nutrients as Droop suggests.

The second part of Droop's comment concerns our use of particulate silicon as a biomass indicator in the silicon uptake model. Many biomass measures have been used, including cell nitrogen, cell carbon, chlorophyll *a*, total biomass, cell surface area, and cell numbers. Each of these has a unique Q, the factor for converting the particular measure in question to cell biomass. One may do the same manipulation of equations Droop has done in his comment with any pair of these and come up with equally odd equations. One could therefore conclude, as Droop has done, that there is no valid biomass indicator except biomass itself. This would immediately embroil one in the controversy over what is biomass, total biomass or live biomass. Is it correct to compare a naked flagellate with a diatom which is 50% silicon on the basis of total biomass or of live biomass? We have concluded that the best biomass indicator is one which is readily and accurately measured—in our case particulate silicon. We did relate particulate silicon to

cell volume as a better biomass indicator through eq. 3 and 7 (Davis et al. 1978) and the results of the model output compared with actual measurements showed excellent agreement (fig. 3A; Davis et al. 1978).

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