

dering or roaming, used of ships in poetry, the word as we employ it started out as an adjective. Neither *planktic* nor *planktonic* therefore can have any ultimate authority in ancient Greek. We must however use one of them, since we have turned the original singular adjective into a collective noun.

Planktic, with its terminal hard "c" coming so close to the identical sound of the "k," is definitely less pleasant to me than is planktonic; the latter is the only form given in the Oxford English Dictionary, though it is described as an irregular formation for the hypothetical planktic. Since there is, to me, no compelling reason in favor of planktic on linguistic grounds, I shall continue to use planktonic solely as the more euphonious of the two. Speakers of other languages must clearly be left to decide whether they prefer *planktonisch* to *planktisch*, *planctonique* to *planctique*, *planctonico* to *planctico*, etc. I see no reason to insist on uniformity even within a language. It may be worth noting that if someone speaking colloquially in the laboratory referred to a collection just submitted to him as looking *planktonish* (the strict cognate of *planktonisch*) it would sound natural and comprehensible; in these circumstances *planktish* would be meaningless.

Planctonicus sounds well as a Latin adjective and has often been used as a specific name; even though its formation can have no classical authority, it seems to fit.

The aesthetic objection to planktic does not apply to *benthic*, which is doubtless preferable to *benthonic*. I should however, be quite happy if we never got anything worse than the latter. We do, whenever we run into *biodegradable* or any of the other horrid bigenerous words of unkindly procreation with which the environmental crisis has polluted our language. But even such words may ultimately settle down, as has apricot, part Arabic, part Hellenized Latin, though filtered through the Portuguese.

It is obviously impossible to impose strict consistency, particularly in derivatives of somewhat synthetic nouns such as *plankton*, or for that matter *electron*, a word which is an accidental reconstruction of the original Greek, but with quite a different meaning. I do not suppose that anyone has proposed an editorial policy requiring that *electric* should be systematically substituted for *electronic*.

My position is that there is no need to enforce rigid rules if people will try to write clearly and with elegance. If they do not, little can be done, even with the strictest precepts. Perhaps that ardent Pauline scholar, E. A. Birge, would have preferred "not of the letter, but of the spirit; for the letter killeth, but the spirit giveth life."

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. . . occasionally, by raising our eyes from
the immediate problems that confront us,
we can achieve a partial synthesis which
gives fresh direction to our enquiries.

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Environmental control of phytoplankton cell size

Two apparently divergent views have recently been expressed concerning the environmental control of phytoplankton cell size in the oceans. Semina (1972) offers what can be characterized as a physical

argument emphasizing the role of hydrodynamic forces in favoring the retention of large cells within the planktonic biotope. According to Semina mean cell size of a planktonic population is a result of 1) the

direction and velocity of vertical water movement, 2) value of density gradient in the main pycnocline, and 3) phosphate concentration. The numerical assignments are those of Semina and reflect the emphasis given to the individual factors in her discussion. The effects of these factors on cell size are mutual, with the response to a change in any one of them being a function of the level of the other two. Semina's argument is largely inductive, being based on correlations, but she finds that these factors can, as a first approximation, account for the observed distribution of cell sizes in the Pacific.

Parsons and Takahashi (1973), while acknowledging the utility of Semina's approach, feel that her explanation contains discrepancies and oversights on which improvements could be made. They offer an alternative model that incorporates several additional factors, making it more complex and comprehensive. They cite 1) the rate of nitrate or ammonia input to the cell, 2) the extinction coefficient of the water, 3) the mixed layer depth, 4) the surface light intensity, 5) the sinking rate of phytoplankton, and 6) the upwelling velocity of the water. Again the numerical assignment is theirs and can be taken as indicative of the relative significance they attach to these factors.

As well as adding several factors largely to describe the light environment, Parsons and Takahashi obviously consider nutrients, especially nitrogen, to play a key role, while hydromechanical considerations are reduced in importance. Parsons and Takahashi suggest that nutrient availability, through controlling growth rates by Michaelis-Menten kinetics, determines which species can occur or dominate the plankton. They generalize that small cells have low K_s values; consequently, where nutrient concentrations are low, small cells should predominate, while in nutrient-rich areas large cells should be favored. Assigning values from the literature to the required parameters of the model for certain water masses and representative large and small species, they make predictions about cell

sizes to be favored in the water masses considered. They contend that predictions from their deductive model fit the observed distributions well also. The most notable difference between the expected distributions of Semina and Parsons and Takahashi concerns the cell sizes to be found in tropical upwellings. Semina concludes that small cells should predominate while Parsons and Takahashi predict large cells. Each proponent cites appropriate authorities for substantiation. This discrepancy, although bothersome, we accept as legitimate disagreement and it won't concern us further. Neither do we wish to debate the merits of nitrogen versus phosphorus as the limiting nutrient in the ocean.

Although the article by Parsons and Takahashi seems to be, at least in part, a response to Semina, we feel that it has not addressed itself to the success of Semina's treatment in explaining cell size distribution. If cell size distributions, and concomitantly species composition, can be largely explained by hydromechanical considerations, it would seem to raise questions about the probable role of nutrient kinetics and competition in controlling phytoplankton composition. This question has previously been posed by Hulburt (1970), but to our knowledge has never been answered: if diffusion within a nutrient-depleted zone controls nutrient supply to the cell, and subsequently growth rate, then at population densities occurring in the ocean competition is unlikely and explanation for species successions must be sought in factors other than nutrient competition. Current North American research in phytoplankton ecology (including some of our own) is largely directed to the elucidation of kinetic parameters of phytoplankton species in culture in the hope that predictive capabilities concerning species competition will emerge. Less interest, perhaps because of experimental intractability, is expressed in the possible relationships between a measured nutrient concentration in a medium and the nutrient concentration at a cell's surface or, as in the case of phosphorus and nitrogen, inside the cell, where a calculated

K_s and μ_{\max} applies. Is physical diffusion controlling nutrient uptake or are the enzyme kinetics at the cell surface solely responsible? The difference in opinion on cell size control as epitomized by Semina and Parsons and Takahashi is symptomatic of this unresolved question. We wish to propose here that: 1) it may be premature to generalize about the relationship between cell size and uptake kinetics; 2) that if generalization can eventually be made, it will likely involve cell mobility rather than cell size if diffusion limitation of nutrient supply often obtains in natural waters; 3) because of 2) it would not be improbable to find a relationship between cell size, the hydrodynamical environment, and nutrient kinetics in the ocean; and 4) that algal ecologists might generate more imaginative and fruitful hypotheses by adopting a more biological and organismal and less chemical and biochemical approach to the phytoplankton.

In setting up a dichotomy between the physiological properties of large and small cells Parsons and Takahashi overlooked recent evidence that nutrient uptake parameters may vary considerably between clones of the same species. Table 1 summarizes data for two clones of *Thalassiosira pseudonana* isolated from different environments. Clone 3H was isolated from a eutrophic Long Island estuary, clone 13-1 from the oligotrophic Sargasso Sea (Guillard et al. 1973). These clones are more different in their physiological properties than the two species (*Ditylum brightwelli* and *Coccolithus huxleyi*) selected by Parsons and Takahashi to illustrate differences in physiological properties related to size (table 1: Parsons and Takahashi 1973). In fact the slightly larger of the two *T. pseudonana* clones has consistently lower values for each of the nutrient uptake parameters, contradicting the expectation of Parsons and Takahashi. These data suggest to us that factors other than size are probably more important in determining the physiological properties of phytoplankton in the natural environment.

There is no reason to believe that phyto-

Table 1. Physiological properties of *Thalassiosira pseudonana* clones from Guillard and Ryther (1962), Carpenter and Guillard (1971), Smayda (1970), and Guillard et al. (1973).

	Clone 3H	Clone 13-1
Diameter (μ)	2.5-10	4.0-11
μ_{\max} (Si) (doublings/day)	3.6	2.1
K_N (nitrate, μ M)	1.87	0.38
K_{Si} (silicon, μ M)	0.98	0.19
Sinking rate (m/day)	similar or lower	0.15 (healthy) 0.85 (senescent)

plankton species are unique. In terms of evolutionary theory these species presumably are endowed with a reasonable amount of genetic variability. Natural selection will act on this variability to produce populations whose nutrient uptake parameters lead to increased fitness irrespective of their size. Indeed the data presented in Table 1 strongly suggest that natural selection favors organisms whose nutrient uptake parameters reflect the nutrient environments in which they grow. The very fact that physiological races exist suggests that physiological properties are far more plastic than gross morphological ones. Rigidly linking physiological properties to cell size as Parsons and Takahashi have done denies the existence of physiological races with very different nutrient uptake parameters. Just as the data in Table 1 indicate that small cells can have relatively high K_s values, we are confident that large cells may have relatively low K_s values. We know of no a priori biochemical reason why a large cell could not have a low K_s .

We don't question that the kinetic information available to and cited by Parsons and Takahashi support their generalization about cell size and kinetic parameters. But confronted with such an interesting correlation, a relevant question is why should it be so? We feel that the correlation results from diffusion controlling nutrient transfer

through a nutrient-depleted microzone (Hulburt 1970). Munk and Riley (1952) were the first to consider the advantage that sinking cells obtain in relieving diffusion limitation. Hutchinson (1967), Smayda (1970), and Hulburt (1970) have reemphasized this advantage of sinking. Sinking relieves diffusion limitation by reducing the thickness of the depleted zone on the downward-directed cell surface. This does not mean, however, that diffusion limitation is entirely overcome. Slowly sinking cells would have a thinner zone of depletion than stationary cells, but rapidly sinking cells would have an even thinner or perhaps negligible zone. In morphologically simple cells (a necessary caveat explained below) nutrient supply to the cell surface would be a function of the sinking rate. Kinetic parameters to be efficient should be attuned to this supply rate. Consequently high sinking rates would favor high K_s values and low sinking rates would require low ones. Morphological complexities, e.g. curved spines, undulating winged surfaces, etc., which could induce local shear forces to distort the nutrient-depleted zone (Smayda 1970) could obscure the expected simple relationship, especially among cells of similar sinking rate. Genetic variability, as noted above, will also weaken the relationship; however, a general trend over the large range of sinking rates in the ocean would be observable.

Marine phytoplankton tends to be dominated by mineralized, negatively buoyant diatoms and coccolithophorids and among these groups cell size, sinking rates, and nutrient kinetics could be highly correlated especially within an oligotrophic or eutrophic region. In freshwater, however, where the wide variation in physical and chemical factors often favor green and blue-green algae in addition to diatoms it is unlikely that much of a correlation between cell size and mobility exists. It seems highly likely to us that the extremely large nearly neutrally buoyant blue-green algae will be found to have exceptionally low K_s values. Smaller, rapidly sinking diatoms might, in general, have high K_s values. A correlation

with mobility could still be expected, but cell size would become independent and determined by additional selective forces. Sinking is not the only mechanism by which mobility can be achieved in phytoplankton. Actively swimming flagellate forms could have their uptake kinetics attuned to their swimming velocity. Eppley et al. (1969) found that the *Gonyaulax polyhedra* had the highest K_s among the 17 species they considered. They attributed this high value to a strategy of active vertical migration.

A necessary corollary of diffusion limitation would be a high degree of linkage in K_s values. Diffusion, being essentially a physical process, would control the transfer of all required nutrients and there would be no significant selectivity (e.g. high transfer of phosphate, low transfer of nitrate) beyond the availability of the nutrients in the medium. Nutrient concentrations in most natural situations are generally correlated with each other. In oligotrophic regions all nutrients are scarce; in eutrophic regions most nutrients are abundant. Diffusion-limited cells would then in an oligotrophic situation have low K_s values for all nutrients, but in eutrophic environments all the K_s values would be high. If nutrient kinetic parameters were determined by competition, combinations of high and low K_s values for different nutrients would be expected as one species specialized for phosphorus, another specialized for molybdenum, etc. to gain competitive advantage. Comparing the values of K_s for nitrate and ammonium uptake which Eppley et al. (1969) report for 17 species, we observe that if a species has a low K_s for nitrate it nearly always has a low K_s for ammonium, although temporal and spatial variability of these two nutrient ions might often vary inversely. Why doesn't an ammonium specialist appear? Demonstration of vastly different kinetics for oceanic and neritic species does not necessarily imply that the kinetics are a result of competition or size. Kinetics simply reflect adjustment to the total nutrient supply of the region.

The clones of *T. pseudonana* demonstrate

this principle of kinetic linkage admirably. The clone with a low K_s for nitrate also has a low K_s for silica and high K_s values occur in the other clone. To turn our argument on ourselves one should ask "if these cells of similar size sink at the same rate why are the K_s values so different?" The answer is simple (why else be rhetorical): Diffusive transport is a function of the concentration gradient as well as of the thickness of the depleted zone. Given a zone of similar thickness and a virtual concentration of zero at the cell surface (following Hulburt 1970), transport will then be a function of external concentrations. Higher K_s values for most all required elements will then occur in eutrophic waters, and low K_s values will be found in oligotrophic waters. This adaptation can be achieved without invoking competition or size. Demonstration by Parsons and Takahashi that a small species from an *oligotrophic* oceanic region will grow faster in an *oligotrophic* region than a large species from a eutrophic, neritic region (or vice versa) is in a sense tautological. Using *T. pseudonana* we could demonstrate the relation to nutrient supply in the preferred environment, but nothing could be said about cell size. A competitive advantage in an artificial model does not prove competition is occurring or has occurred in the natural situation.

Hulburt (1970), applying diffusion transport equations, concluded that nutrient competition could not occur in marine phytoplankton communities except at extremely high population densities. Semina's explanation of cell size could also imply that competition is a secondary factor in determining species composition and succession. Rather subtle changes in the physical environment (upward directed currents and density gradients) may favor the appearance or disappearance of certain species (large cells) or assemblages. Semina's explanation suggests that the environment may be selecting for or against sinking rate. As the sinking rate dictates nutrient supply to the cell surface, observable changes in the community kinetic parameters will also occur. These changes do not imply that

the environment is selecting, by competition, for kinetic parameters per se. Because sinking rate, cell size, and kinetics are highly correlated in the oceans, models can be constructed emphasizing any one of these characteristics and the model will apparently serve. As Kuhn (1970, p. 76) observes "philosophers of science have repeatedly demonstrated that more than one theoretical construction can always be placed upon a given collection of data." Causality is more elusive.

We believe that there are two reasons why phytoplankton ecology is not better understood today. Firstly, even though there have been two essentially competing though interrelated hypotheses to explain nutrient transfer to cells, proponents of particular hypotheses have not examined inconsistencies in their own work in terms of alternative hypotheses. The aim of most investigators has been to obtain data consistent with the hypothesis they favor rather than to critically examine competing hypotheses.¹ Secondly, the biology of the organisms involved seems to have been ignored by most investigators. Phytoplankton are usually looked at as complex solutions with particular biochemical properties rather than as organisms acted upon by natural selection. If large and small phytoplankters were heuristically looked upon as elephants and mice and basic biological questions concerning form and function were asked, we are confident that the significance of size in the planktonic environment would be more easily understood.

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¹This is not a problem unique to limnologists and oceanographers. It is a problem of the scientific community in general. This has recently been pointed out in *Nature* (1973) and by Kuhn (1970).

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A rebuttal to the comment by Hecky and Kilham

The principal challenge in the comment by Hecky and Kilham is to our assumption that there is a general relationship between the size of phytoplankton cells and their ability to take up nitrate. We have plotted Eppley's data (Eppley et al. 1969) to show the relationship between cell size and the value of K_s (Fig. 1). The data are scattered, but a general positive relationship is apparent. The source of variance in these data may be due to at least two additional factors, both mentioned by Eppley et al. (1969). These are that K_s values may be influenced by the previous history of the cells and that K_s values are temperature dependent.

Further independent data supporting our generalization are to be found in an ecological study of the growth rates of net phytoplankton and nanoplankton reported by Malone (1971, p. 815):

Two lines of evidence indicate that netplankton and nanoplankton respond differently to varying nitrate conditions. . . . netplankton tend to have higher half saturation constants for nitrate than the nanoplankton.

Malone further supports these observations with a statistical study of the incidence of

netplankton chlorophyll and the nitrate concentration.

The netplankton chlorophyll maximum was always found at depths where nitrate concentrations were $> 2 \mu\text{M}$ the nanoplankton maximum occurred at depths where the nitrate concentration was between 0.2 and $2 \mu\text{M}$. [P. 815]

We have not ignored the principal exception (Carpenter and Guillard 1971) to the general nitrate relationship as supported above since it is given in our textbook (Parsons and Takahashi 1973a). The question is, what significance does one attach to exceptions when the bulk of the data presently available supports an opposite conclusion? Exceptions to generalizations are not uncommon in biological data. A closely related case stems from some earlier studies (Parsons and Strickland 1962; Wright and Hobbie 1965) where it was assumed that low K_s values for the uptake of organic substrates were primarily due to aquatic bacteria and not to phytoplankton. However, Hellebust (1970) found a species of marine diatom that had a K_s value for organic substrates comparable to the K_s found in bacteria.