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The Dynamics of Nitrogen and Phosphorus Cycling in the Open Waters of the Chesapeake Bay

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The use of radioisotopes and rare stable isotopes in field investigations of plankton nutrition both in lakes and the ocean is now widely practiced. The introduction of the ^{14}C technique to measure phytoplankton photosynthesis (1) revolutionized the study of aquatic primary productivity. The use of ^{32}P in plankton studies has received less attention (2,3,4), and more recently ^{15}N has proven to be a useful tool (5,6). The literature of the last two decades which includes various applications of these isotopes in studies of aquatic biology is heavily burdened by discussions of problems in experimental design and data interpretation (7,8,9,10). In general the application of such techniques to aquatic biology has progressed more slowly than in other fields of study, and ecologists have been criticized (11) for their naive and often erroneous use of isotopes in studies of transfer processes within aquatic ecosystems. Recently, innovative applications of isotope tracer studies to plankton nutrition have included tritiated substrates in the study of heterotrophy (12) and ^{29}Si (13) and ^{68}Ge (14)in the study of the silicious nutrition of diatoms.

Direct and indirect evidence supports the contention that nitrogen is often the element most likely to limit plant productivity in the sea (15,16,17). In addition, studies of the nitrogenous nutrition of plankton are attractive in that nitrogen provides perhaps the simplest perspective from which to view a material balance in a planktonic ecosystem. Whereas cellular nitrogen is primarily bound in structural material,both carbon and phosphorus are largely involved in cellular metabolic activities in addition to their structural roles.

Blue-green algae capable of fixing gaseous nitrogen are considerably more common in fresh-water than in the sea and partially because of this, the availability of nitrogen is considerably less likely to regulate plant productivity in fresh-water. Phosphorous is frequently looked to as the most important nutrient in both the regulation of productivity and limitation of biomass in fresh-water and the open waters of estuaries

(18).

In most natural waters dissolved combined nitrogen is present in more than a single form. Concentrations of nitrate, nitrite, and ammonium in the sea vary temporally and spatially (19) and recently, urea has been reported from all areas which have been investigated (20,21,22,23). Amino acids are usually detected (24,25), and although the concentrations are always low, they may at times contribute to phytoplankton nitrogenous nutrition (26,27).

Although we know what forms of combined inorganic nitrogen do and do not commonly exist in the sea, we are largely ignorant of the identity, origin, and fate of a sizeable pool of dissolved organic nitrogen. This material is temporally and spatially ubiquitous (27,28,29) and the implication is that the bulk of it is highly refractory and has little potential in algal nitrogenous nutrition (27,28).

The availability of ^{15}N labeled forms of the plant nutrients thought to be of greatest importance, enables one to assess the relative significance of several forms of nitrogen in the nutrition of natural plankton assemblages. A few oceanographic laboratories in this country now have the capacity to rapidly process plankton samples for ^{15}N enrichment, and the recent availability of optical emission spectrometers may greatly extend the use of ^{15}N in plankton studies. Shipboard studies with large volume cultures established by enriching natural seawater with nutrients have demonstrated that estimates of phytoplankton assimilation derived from short interval measurements of ^{15}N uptake agree closely with measurements of both the decrease in dissolved nitrogenous nutrient and increase in particulate nitrogen (30). Field studies of nitrogen fixation have also employed ^{15}N (5), but the acetylene reduction assay for nitrogenase activity (31) is far more convenient and it has become widely accepted as the method of choice.

Because of the low natural concentrations of some of the phosphorous and nitrogenous forms of interest, experiments must be initiated quickly. In most cases phytoplankton activity is measured after removal of the zooplankton; such removal certainly reduces the natural supply of the rapidly recycled forms of both phosphorus and nitrogen to the captured phytoplankton. With zooplankton inclusion, phytoplankton are consumed during the experiment, animal metabolites are released, and the interpretation of data is immensely complicated. Since ambient substrate levels should be determined before the initiation of an experiment, there has been much interest in improving the capacity to quantitate phosphorous and nitrogenous nutrients with specific, accurate, precise, and convenient methodology. Most of the techniques of choice are described in both manual and automated forms by Strickland and Parsons (1972) (32). We have streamlined these manual methods to permit us to rapidly process 5ml samples with both precision and sensitivity which exceeds

those of the automated methods. A small number of samples can be routinely analyzed by a single analyst for nitrate, nitrite, ammonium, urea, and soluble reactive phosphate within one half hour after sample collection.

In the study of plankton nutrition one has to select an incubation technique which best suits the particular problem under investigation. An in situ incubation involves the collection of a water sample, enclosure in a suitable bottle, addition of isotope tracer material, and resuspension of the bottle to the depth from which the sample was collected. The objective is to execute the incubation at near natural light and temperature. Careful and rapid handling are required to minimize physiological shock which may result from exposure of deep water samples to both full incident solar irradiation and great changes in temperature. Any potential problems related to pressure differentials are usually ignored. The in situ incubation has been perfected with a single unit which captures, inoculates with material of choice (e.g. isotope stocks), and serves as an incubation chamber (33). After the completion of the incubation the chamber is brought to the surface and the sample is processed. Advantages of such a system are obvious, but the disadvantages are primarily that for nutrient assimilation studies one must make isotope tracer additions without specific knowledge of the ambient nutrient levels. Also, zooplankton which consume phytoplankton and release plant assimilable forms of nitrogen and phosphorus cannot be excluded from the incubation chamber.

Because major sea-going vessels usually cannot remain on stations for extended periods, and there may not be an opportunity to return to a buoy, biological oceanographers frequently use simulated in situ incubations. A deckboard incubator is fitted with optical filters to simulate light at depth of sampling, and flowing seawater controls temperature. Some of the problems associated with measuring light and selecting appropriate filters have been investigated and discussed (34).

The Chesapeake Bay is a highly productive coastal plain estuary with a well defined two-layer circulation (35). It is approximately 300 km in length and it is primarily an estuary of the Susquehana River. The nutrient loading resulting from both the Susquehana River drainage from western Pennsylvania and central New York and the metropolitan discharges of the District of Columbia and Baltimore, Maryland, are potentially large. It is indeed interesting to note in the data presented by Carpenter, Pritchard, and Whaley (1969) (36), that the effect of nutrient loading from the adjacent metropolitan areas is virtually undetectable as dissolved inorganic nutrient in the Bay proper below both Baltimore and the junction of the Potomac River with the Bay. It has been demonstrated that the heavy winter-spring runoff from the Susquehana River is the primary source of nitrate in the Bay, but no point sources for either ammonium or phosphate can be identified.

Data from some coastal regions, such as for Buzzards Bay, Massachusetts, suggest that transport of nitrogen remineralized in the sediment interstitial water to the overlying water may contribute significantly to the phytoplankton nitrogen requirement (37). In another study, vertical transport from the sand bottom off La Jolla, California, was shown to provide an insignificant portion of the nitrogen utilized by the phytoplankton in the overlying water (38). Carpenter, Pritchard, and Whaley (1969) (36) concluded from calculated vertical exchange rates for spring and summer that the transport of dissolved nitrogen and phosphorus from the sediments into the euphotic zone was insufficient to account for more than a few per cent of the approximated rates of phytoplankton nutrient utilization. More recently, Bray, Bricker, and Troup (1973) (39) calculated that upward diffusive flux across the sediment-water interface in the Chesapeake Bay would amount to a weekly addition of 5% to the total orthophosphate in the water column. This is considerably less than the rate at which phytoplankton remove phosphorus from the euphotic zone of the Bay (40).

It can be seen, therefore, that the observations relating to nutrient availability and plankton biomass in the Chesapeake Bay are apparently paradoxical: High phytoplankton standing stocks and high phytoplankton productivity persist in the presence of low ambient levels of dissolved inorganic nitrogen and phosphorus throughout much of the year. The short-term temporal stability in these patterns suggests an equilibrium in the biological and chemical processes, and Carpenter, Pritchard, and Whaley (1969) (36) hypothesized that the productivity of the open waters of the Chesapeake Bay is regulated largely by a dynamic nutrient-phytoplankton-zooplankton-nutrient cycle.

Our initial efforts to stimulate primary productivity by enriching natural water samples from various locations within the Chesapeake Bay were unsuccessful. The results clearly demonstrated the unsuitability of the nutrient enrichment-incubation technique in the investigation of a highly dynamic planktonic ecosystem, and supported the hypothesis that only through short-term isotope tracer experiments could one come to an understanding of the plankton nutrition in this estuary.

The phytoplankton may grow at rates sufficient to double their biomass in one or two days and yet such increases in biomass are rarely observed in the Bay. In fact, with the exception of localized blooms, the phytoplankton standing stock varies only by approximately a factor of 5 in the entire main body of the Bay throughout an annual cycle. Consider further a summer condition of nearly constant low levels of plant nutrients in waters containing a population of small herbivorous zooplankters capable of ingesting 2 to 3 times their body mass daily, and one can begin to appreciate both the dynamic nature of estuarine planktonic communities and the great effort required to investigate their nutrition.

What follows is a description of our recent effort to study the plankton nutrition in the Chesapeake Bay with isotope tracer techniques. This program remains in progress, and most of our results to date are either in press or in a state of preparation. Our intention here is to demonstrate through a preview of some of our data the utility of isotope tracers in developing a dynamic image of plankton nutrition which permits insight into the mechanisms by which planktonic productivity is regulated.

We conducted a series of 7 cruises of 2 weeks duration and at 6 week intervals to sample and study 8 geographically fixed stations in the open waters of the Chesapeake Bay and one station on the adjacent continental shelf (Figure 1). Nutrient measurements were made and experiments were initiated to quantitate phytoplankton incorporation rates for carbon, nitrogen, and phosphorus. Numerous other physical, chemical, and biological measurements were made, and the collected biota were also used for additional experiments. Each station required a full day of effort. With the exception of the previously mentioned modifications, all shipboard analytical methods followed the procedures outlined by Strickland and Parsons (1972) (32).

All nutrient, biomass, and nutrient uptake rate measurements which will be reported are averages of two samples from different depths in the euphotic zone, and they are considered to be representative of the upper layer of the estuary. The near constancy of chorophyll a concentrations (hereafter referred to as chlorophyll) with depth in the profiles throughout the upper layer supports the notion that this layer, and likewise the euphotic zone, is well mixed. In order to minimize the effect of any small scale inhomogeneities, all individual measurements were made with material collected in a composite sample (the contents of 6 Van Dorn bottles which were cast to the same depth were mixed and aliquots were withdrawn).

^{14}C labeled carbonate, ^{32}P labeled phosphoric acid, and ^{15}N labeled nitrate, nitrite, ammonium, and urea were added to separate bottles and each was incubated on the deck of the ship under simulated in situ conditions. At the termination of the experiments the particulate material was analyzed for isotopic enrichment. ^{14}C and ^{32}P were determined by liquid scintillation spectrometry and ^{15}N by mass spectrometry. The dissolved organic phosphorus and dissolved polyphosphate were also examined for enrichment, and similar measurements for dissolved organic carbon and nitrogen are part of our continuing program. Because of the frequent condition of low nutrients, high biomass, and hence rapid turnover of available nutrient, incubations were of only a few hr duration at midday and extrapolations to daily rates were made using occasional 24 hr sequences of short incubations.

The distribution of plant biomass, as chlorophyll, is rather surprisingly uniform in the main body of the Chesapeake Bay (Figure 2). In April and June higher biomass was observed in the vicinity of the Potomac River discharge, and in June and

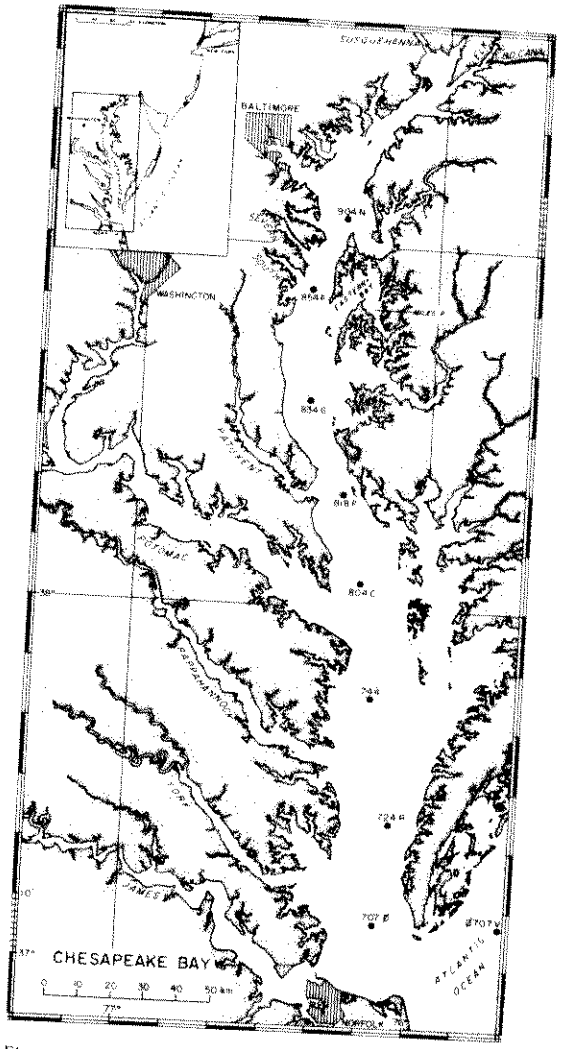

Figure 1. Location of the Chesapeake Bay and station positions

August higher biomass was observed below Baltimore. But in general, there is little temporal or spatial heterogenity: > 50% of the chlorophyll values were between 10 and 20 $\mu g \cdot liter^{-1}$, and 90% were between 5 and 25 $\mu g \cdot liter^{-1}$. The cause of the increased biomass below Baltimore may be the result of greater nutrient availability, but there is not evidence for this in either the nitrogen or phosphorus data throughout most of the year. There is sufficient nitrogen in this region to support a greater plant biomass than is observed and, as demonstrated by Taft, Taylor, and McCarthy (1975) (40), there is no apparent relationship between plant biomass and soluble reactive phosphorus. The same conclusions with respect to nitrogen and phosphorus apply to the area immediately below the Potomac River in August when compared to the stations further north.

There are numerous possible explanations for the occasional association of higher plant biomass with regions downstream from the discharges of Baltimore and District of Columbia, and some of the more obvious include: greater availability of minor nutrients; unidentified stimulating material associated with the discharge of the metropolitan wastes; less herbivorous grazing potential which may or may not be related to the discharges; and reduced thickness of the near surface mixed layer. We have no data to permit evaluation of hypotheses concerning minor nutrients and other stimulating materials. It would be exceedingly difficult to detect the small reduction in herbivorous grazing potential which could within a few days result in plant biomass increases comparable to those observed. The pycnocline was quite shallow below Baltimore in August, and we are further evaluating the relationship of both phytoplankton biomass and phytoplankton productivity on a volume basis to thickness of both the upper mixed layer and the euphotic zone. McCarthy, Taylor and Loftus (1974) (41) demonstrated that throughout the Chesapeake Bay and over an annual cycle, approximately 90% of both the biomass and the productivity of the phytoplankton community is found in the unicellular forms which pass 35 μm mesh.

There are well documented occurences of algal blooms of moderate proportions in the Chesapeake Bay. During our study a major visible bloom was never identified on our regular stations. Loftus, Subba Rao, and Seliger (1972) (42) followed the development and dissipation of a bloom which appeared in the open Bay near the Severn River following an intensive rain storm. Their data demonstrate that for the portion of the bloom in the Bay proper there was never adequate nitrogenous nutrient available to permit more than a fractional doubling of plant biomass (1-13%). Therefore, with nutrient limited growth, the bloom was either doomed to dissipate through physical forces or sufficient nutrient had to be delivered through rapid recycling processes within the bloom. Oxytoxum sp. was the dominant phytoplankter and the dominant herbivore, a rotifer (Euchlanis sp.), reached densities of 10^5 individuals$\cdot liter^{-1}$. They

demonstrated that this density of Euchlanis sp. could almost totally consume maximum observed bloom phytoplankton densities (4×10^2 μg chlorophyll$\cdot liter^{-1}$) in 12 hr. A rotifer of similar size (Brachionus sp.) ingests 3 times its mass per day (43), and it can be concluded that the high metabolic rate per unit biomass for such small zooplankters would result in considerable return of ingested nitrogen and phosphorus to the water in dissolved forms.

Time permits the consideration of only a single cruise in any detail, and we have chosen to discuss PROCON 10 of June 1973. It represents an extreme in chlorophyll variations along the major axis of the Bay, and it demonstrates the preferential algal utilization of the more reduced and rapidly recycled forms of nitrogen in the presence of high concentrations of NO_3^-.

Time course measurements with multiple samplings during an incubation of a few hours repeatedly demonstrated that ^{32}P uptake occurred initially at a rapid rate which could not, from comparisons with photosynthesis as measured by ^{14}C fixation, be equated with net uptake associated with growth (40). The subsequent phase of reduced uptake can however, with a few exceptions be shown to approximate phytoplankton synthesis of new cellular material. Table I and Figure 3 demonstrate this phenomenon.

TABLE I. ATOMIC RATIO OF CARBON TO PHOSPHORUS UPTAKE (40)

Station	Initial Phase	Subsequent Phase
834G	0.16	44
818P	0.001	28
744	0.001	60
724R	0.002	88
707Ø	0.015	410
Ø707V	0.45	6

From the laboratory culture data of Parsons, Stephens, and Strickland (1961) (44), one can calculate atomic ratios for carbon to phosphorus composition of marine phytoplankton which were grown in a phosphorus sufficient medium. For 8 phytoplankters the values ranged from 28 to 102 and had a median of 81. A phosphorus deficient natural phytoplankton population existing in a medium which contains a low constant level of orthophosphate (and no alternate source of phosphorus) would be expected to have less intracellular phosphorus than phytoplankton in a phosphorus sufficient medium (45). The well documented phytoplankton "luxury uptake" of orthophosphate (46) complicates efforts to make meaningful extrapolation from short-term rate measurements. That is to say, that even after taking into consideration the above mentioned dual phase uptake, rate measurements for the second phase may still suggest greater net uptake per unit time than can be reasonably anticipated from independent estimates of

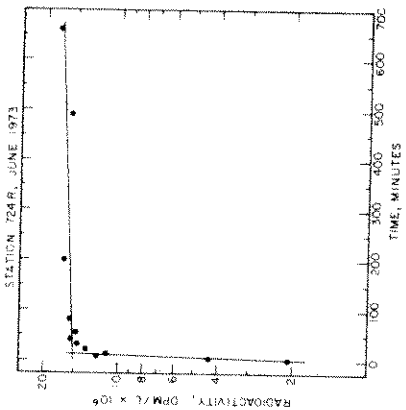

Figure 3. Uptake of ^{32}P orthophosphate into the particulate fraction with time, after Ref. 40.

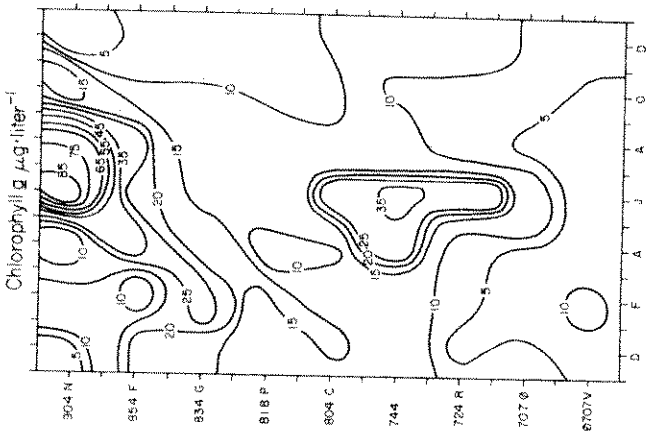

Figure 2. Chlorophyll concentration in the Chesapeake Bay from December 1972–December 1973

phytoplankton growth. If the algae are phosphorus stressed as a result of lengthy exposure to medium with lower than usual levels of orthophosphate, and sufficient phosphorus suddenly becomes available, an extremely rapid uptake would be expected in the second phase. Such a stress would result in a low carbon to phosphorus uptake value such as that observed at station Ø707V (Table 1). Conversely, ample intracellular stores of phosphorus could support high rates of algal carbon fixation concurrent with very slow phosphorus uptake resulting in a high carbon to phosphorus uptake ratio such as that observed at station 707Ø . Stations 707Ø and Ø707Vwere anomalous in other respects as well.

The high specific activity of ^{32}P preparations permits one to make estimates of uptake without measurably increasing the orthophosphate in the medium (radioactive isotope additions contributed $< 2 \times 10^{-4}$ μg atom P · liter $^{-1}$ in these experiments). In that significant changes in substrate were avoided, one is left to conclude that, except for stations 707Ø and Ø707V, our ratios for the subsequent phase of reduced uptake are reasonable approximations for cellular synthesis in Chesapeake Bay phytoplankton.

It should be obvious from the data which we have presented that one cannot make meaningful interpretations from single time determinations of ^{32}P uptake by phytoplankton in the Chesapeake Bay. In practice, aquatic biologists are often far too casual with their assumptions that the processes under investigations can be adequately evaluated with a single measurement per experiment.

Taft and Taylor (1975) (47) have described the annual cycle of phosphorus in the Chesapeake Bay, and they note that within the dissolved component, organic phosphorus is often as abundant as orthophosphate. As with dissolved organic nitrogen, much of this phosphorus remains unidentified, but phytoplankton can, with alkaline phosphatase, utilize phosphomonoesters (48,49). Taft, Loftus, and Taylor (50) have determined that throughout the year phosphomonoesters are never more than a small fraction of the total dissolved organic phosphorus in the Bay. The kinetics of algal alkaline phosphatase activity were investigated with ^{32}P labeled glucose-6-phosphate, and continuing efforts are concentrating on the nutritional value of other components of the natural dissolved organic phosphorus pool.

Nitrate concentrations (Figure 4) ranged from 0.3 to 33 μg atom N·liter with a rather sharp gradient between 904N and 724R. NH_4^+ concentrations (Figure 5) ranged from < 0.05 to 5.9 μg atom N· liter^{-1} and showed the sharpest gradient between 834G and 744. NO_2^- concentrations ranged from < 0.05 to 1.0 μg atom N·liter^{-1} and in general varied with NO_3^- concentrations. Urea-N concentrations ranged from < 0.05 to 1.0 μg atom N·liter $^{-1}$ and were highest in mid and upper Bay.

Elsewhere we have given considerable attention to the particulate nitrogen, particulate phosphorus, particulate carbon, chlorophyll and adenosine triphosphate data, and have discussed

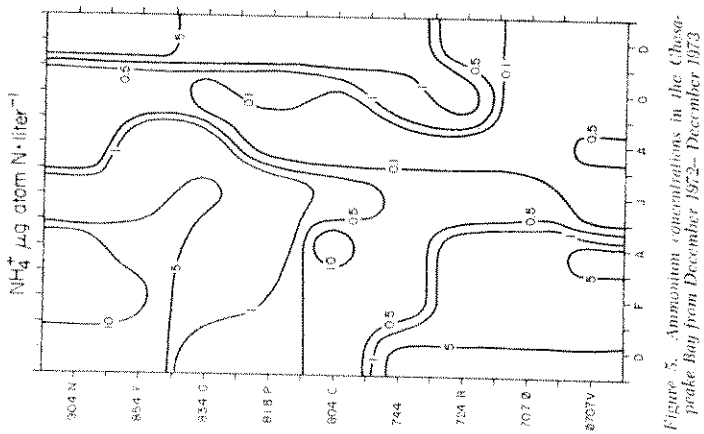

Figure 5. Ammonium concentrations in the Chesapeake Bay from December 1972–December 1973

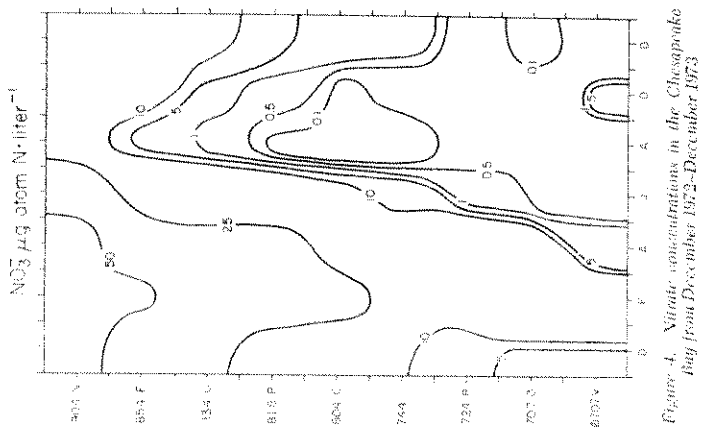

Figure 4. Nitrate concentrations in the Chesapeake Bay from December 1972–December 1973

usefulness of ratios from such data in approximating the viable, and specifically the plant,component of the total particulate material (manuscript in preparation). At this point, let it suffice to say that the chlorophyll and particulate nitrogen data (Figure 6) support the notion that the suspended particulate material below Baltimore and at the mouth of the Potomac River is as rich in chlorophyll as that elsewhere in the Bay. This does not rule out the possibility that a major difference in nature of the plant community may to some degree be masking significant detrital input. The salinity (Figure 6) in the upper mixed layer shows the anticipated increase with distance from the head of the Bay.

The stations occupied in this study were selected to represent, at ~ 30 kilometer invervals, various areas of potential interest. High turbidity is frequently encountered in regions of the Bay north of 904N (51), and under such conditions, our experiments could not be executed. The net seaward movement of the upper layer is 0.8 km·day^{-1} in the summer (36) and hence our stations on a particular cruise are dealing approximately with a parcel of water which was located one station north in the Bay on a previous cruise. For the NO_3^- data (Figure 4) one can see that in moving from top to bottom of the plot (down Bay) and from left to right (to a subsequent cruise) the NO_3^- value may be similar but is never much greater. This supports the argument that the Susquehana River (or other supply above station 904N) is the primary source of NO_3^- in the Bay proper.

One can see an interesting pattern to the availability and utilization for each of the 4 nitrogenous nutrients (Figure 7). Although NO_3^- was abundant from 804C to 904N (15-33 µg atom N·liter^{-1}) less than 2% of the total nitrogenous ration of the phytoplankton was derived from NO_3^-. At the same stations NH_4^+ was less available (1-6 µg atom N·liter^{-1}), but it invariably accounted for greater than 90% of the nitrogenous ration. From 744 to Ø707V NH_4^+ became more scarce (< 0.4 ug atom N·liter^{-1}) and although NO_3^- concentrations also became reduced, NO_3^- remained as a major component of the available nitrogenous nutrient pool. It reached maximum importance at Ø707V when a NO_3^- concentration of 0.27 µg atom N·liter^{-1} was the only nitrogenous nutrient detected. The data for both fractional availability and fractional utilization of NO_3^- and NH_4^+ are near mirror images, and throughout this series of cruises our data always demonstrated this pattern of preferential uptake of NH_4^+. The patterns for NO_2^- and particularly urea-N suggest fractional utilization in proportion to fractional availability.

Calculations for turnover time of NH_4^+ in the euphotic zone range from 3 to 20 hours and average 8 hours for PROCON 10. The rapid turnover time and lack of persistent spatial gradients argue further for local origin of NH_4^+. If one accepts the Susquehana River as the source of NO_3^-, it is clear that at the upper Bay stations there is sufficient NO_3^- for a doubling of

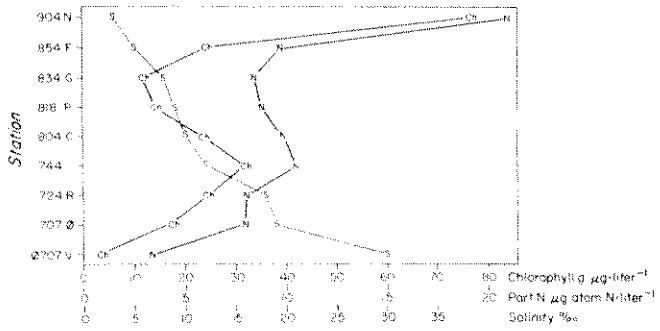

Figure 6 Salinity, particulate nitrogen, and chlorophyll a observed in PROCON 10 in June 1973

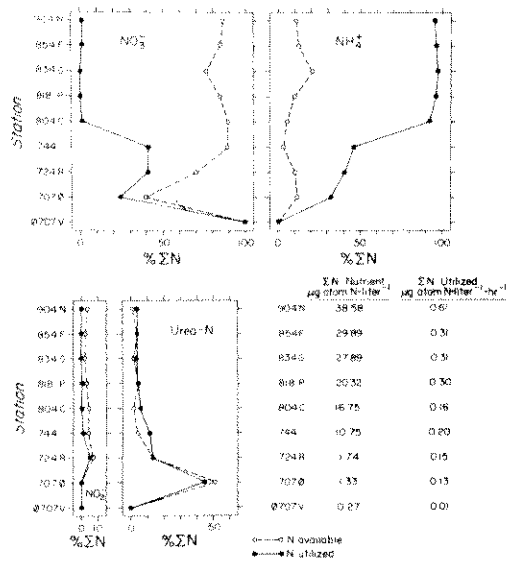

Figure 7. Percentages of both total nitrogenous nutrient available and total nitrogen utilized as nitrate ammonium, nitrite, and urea; total nitrogenous nutrient and rate of phytoplankton nitrogen utilization. Data for PROCON 10 in June 1973.

of plant biomass (~1-2 days of growth) but the NO_3^- is obviously not utilized at this rate or high levels would not be observed below Baltimore. The standing stock of the phytoplankton changes relatively little with time (although high productivity rates are constantly observed) and one is left to conclude that the herbivorous potential of the zooplankton is sufficient to permit consumption of most of the plant production. Herbivorous zooplankton release nitrogenous metabolites which can be utilized by the plants. These are primarily NH_4^+ with some urea (52,53) and under some conditions amino nitrogen (54).

Figure 8 shows the portion of the temporal and spatial coverage represented by our investigation in which there is insufficient nitrogenous nutrient for a single doubling of the particulate nitrogen. And yet one can observe few if any significant daily changes in plant biomass, plant productivity, zooplankton biomass, and nutrient concentrations at the lower and mid Bay stations throughout the summer and autumn.

During PROCON 10 the observed urea concentrations were lower than usual, and the portion of the phytoplankton ration as urea nitrogen was less than our average for the balance of the study; this was probably due to both low urea concentrations and high NH_4^+ concentrations. The observation that NH_4^+ was selected in preference to NO_3^- was consistently demonstrated, and this has also been noted in laboratory cultures (55) and in a large volume outdoor culture (56). A composite figure of most data from the present study is shown in Figure 9. The universality of the NH_4^+ preference phenomenon in the Chesapeake Bay is obvious. The conclusion from this particular analysis is that at NH_4^+ concentrations > 1-1.5 µg atom N·liter^{-1}, 95% of the nitrogenous ration of the phytoplankton will be met with NH_4^+ and urea. This NH_4^+ value is similar to that found sufficient to suppress NO_3^- utilization in the culture studies mentioned above.

If one were to determine the effect of ambient NH_4^+ concentration on NO_3^- uptake with a unialgal culture, a hyperbolic relationship might be predicted. The scatter in Figure 9 is probably the result of combining data from 120 natural phytoplankton assemblages sampled in waters with salinities ranging from 2 to 30 o/oo and temperatures ranging from 4 to 29°C.

This plot does not necessarily suggest that NH_4^+ concentrations < 1-1.5 µg atom N·liter^{-1} will induce NO_3^- uptake, but rather it demonstrates that in excess of this concentration, little if any NO_3^- is utilized when available, and hence the phytoplankton are probably not growth rate limited by nitrogenous nutrient. The kinetics of phytoplankton uptake of NO_3^- and NH_4^+ for unialgal cultures are well documented (57), and if one views the uptake of NO_3^- and NH_4^+, somewhat paradoxically, as analagous to Holling's "vertebrate" feeding response (58), then the value of 1.5 µg atom N·liter^{-1} may represent a concentration of total nitrogenous nutrient above which there will be no nitrogen limitation of primary productivity.

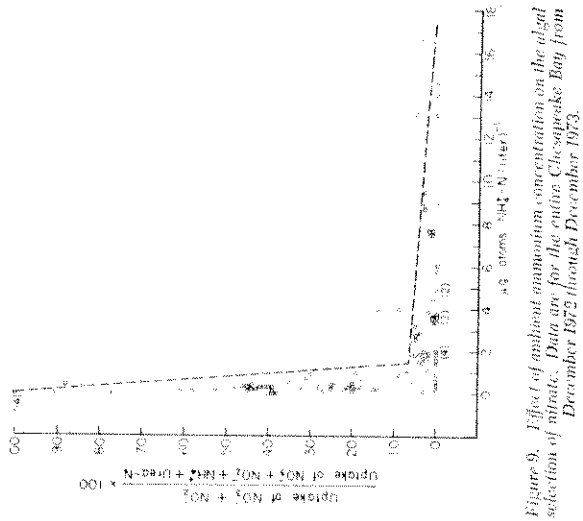

Figure 9. Effect of ambient ammonium concentration on the algal selection of nitrate. Data are for the entire Chesapeake Bay from December 1972 through December 1973.

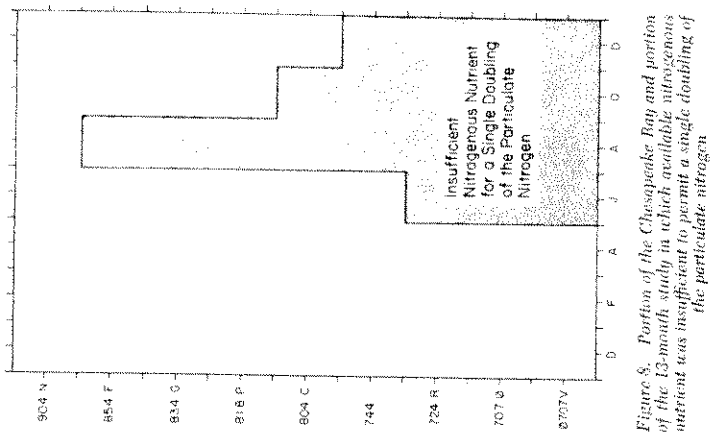

Figure 8. Portion of the Chesapeake Bay and portion of the 13-month study in which available nitrogenous nutrient was insufficient to permit a single doubling of the particulate nitrogen

At the present time our greatest uncertainty in the nitrogen and phosphorus budgets of the main body of the Chesapeake Bay rests with the question of local nutrient supply. We have concluded that in general neither vertical transport from the sediments nor rainfall (unpublished data) can be considered as major sources. A large body of data provide both direct and indirect evidence which suggests that herbiverous zooplanktors are capable of consuming the phytoplankton productivity. The smaller the zooplankton, the greater the fractional return of ingested nitrogen and phosphorus to the water via excretion. We are in the process of evaluating the importance of this pathway to local nutrient replenishment in the Bay.

Bacteria in the water column, whether free-living or associated with larger particles, may in part be responsible for both supply and loss of the plant nutrients discussed above. Unfortunately, it is extremely difficult to quantitate with even fair accuracy the role of the bacteria, and the significance of bacterial activity in these processes has not been evaluated for any large area of the open Bay. Indirect evidence suggests, however, that the role of bacteria is minor when compared to those of both phytoplankton and zooplankton.

The general impression which we would like you to obtain from this presentation is that plankton nutrition must be viewed as a dynamic process. One can be totally deceived in an effort to understand plankton nutrition solely from measurements of biomass and nutrient concentrations, and, therefore, unless one partitions the nutrient pool and actually measures rates of utilization, little useful information can be obtained from field programs designed to investigate various links in the nutrient-phytoplankton-zooplankton-nutrient cycle.

Acknowledgment

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