

## The role of particulate matter in the productivity of surface waters

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**ABSTRACT:** Except for the special cases of upwelled water and the spring blooms in temperate and boreal waters, the productivity of the oceans is largely governed by the rate of nutrient regeneration in surface waters. This rate of regeneration is a function of the number of actively metabolizing bacteria present, which in turn appears to be a function of the particle content of the water. Thus, particle content may be the basic control on the productivity of the open oceans. The possibility of increasing productivity by artificially increasing the particle content of the water should be considered for regions characterized by low particle count, such as the Sargasso Sea. Since silicate can only be resupplied by re-solution of diatom tests, a process taking place at depth, plankton blooms following regeneration kinetics will typically be dinoflagellate rather than diatom blooms.

### INTRODUCTION

Since the work of Riley (1963) it has been recognized that a correlation exists between the productivity of a water mass and its content of particulate matter. It has generally been considered that the causes of the increased particulate matter were the increased debris from the greater burden of decomposing phytoplankton and the addition to the surface water of plankton-derived surface-active materials relatively easily transformed into particles by processes associated with wave action (Sutcliffe, et al., 1963, 1971; Barber, 1966; Sheldon, Evelyn & Parsons, 1967; Riley, 1970; Sheldon, et al., 1973). In this paper I will investigate the implications which can be drawn from the distributions of particulate matter in the oceans, both in time and in space.

### MECHANISMS OF FORMATION OF PARTICLES

After fifteen years of active research, the question of the mechanisms of particle formation is still largely unsolved. Many mechanisms have been proposed, and all of them do produce particles; however, no single one of them fully satisfies the experimental evidence from the oceans.

It has long been considered that a major source of particulate organic matter in

the coastal regions is the outflow from rivers. This may indeed be the case under exceptional circumstances, but evidence is accumulating to suggest that river outflow is a minor source of organic matter outside of the estuary itself. As the particulate matter carried by fresh waters enters the saline environment of the estuary, the surface charge on the particles approaches zero (Neihof & Loeb, 1972) and the particles begin to coagulate (Ries & Meyers, 1968; Teot & Daniels, 1969; Edzwald, et al., 1974; Kranck, 1975). Almost all of the particulate matter sediments within the estuary (Sakamoto, 1972; Hair & Bassett, 1973; Gardner & Menzel, 1974; Meade, et al., 1975). This process is effective even for such major rivers as the Mississippi (Shultz & Calder, 1976) and the Amazon (Milliman, et al., 1975). Furthermore, intensive investigations into the chemical nature of humic and fulvic acids in marine sediments have shown that these compounds differ from their fresh water counterparts (Nissenbaum & Kaplan, 1972; Nissenbaum, 1974).

Oceanic particulates are also considered to be products of the decomposition of phytoplankton. The correspondence between particle-rich areas and areas of high productivity has been pointed out by a number of workers (McAllister, et al., 1961; Antia, et al., 1963; Riley, Wangersky & Van Hemert, 1964; Finenko & Zaika, 1970; Otsuki & Hanya, 1972). However, careful study of the nature of the particulate matter demonstrates that recognizable phytoplankton constitute a major portion of the particles only during bloom periods, and that through a considerable portion of the year there is no close correlation between phytoplankton populations and particulate matter. Thus, the correlation between productivity of the surface waters and content of particulate organic carbon (POC) exists in space, but not in time; at any given instant the more productive waters contain more particulate matter than do the marine deserts, but the yearly cycles of phytoplankton and POC at any given station are not necessarily correlated (Riley, 1959; Hobson, 1971; Nakajima, 1973; Manuels & Postma, 1974; Nishizawa & Tsunogai, 1974; Takano, 1974; Melnikov, 1975).

Possible reasons for the lack of temporal correlation became more apparent as mechanisms for the production of particulate matter were discovered. Baylor, et al. (1962) demonstrated the formation of particles by the bubbling of surface sea water, while Wheeler (1975) produced particles by the compression of surface films. Sharp (1972) found that particles could be produced by shaking filtered sea water, and Johnson (1976) showed that organic aggregates could be formed by the collapse of bubbles due to the solution of the enclosed gases. All of these mechanisms involve the collection of surface-active material, either in solution or in the form of colloidal micelles, at an interface, followed by compression of the interface. While the interfaces cited are all gas – liquid interfaces, density or shear interfaces might also serve as collection sites.

Liquid – solid interfaces have also served as collection sites for organic materials. In these cases, new particles might not be formed, but pre-existing inorganic particles might acquire an organic outer coating (Suess, 1970; Neihof & Loeb, 1974). The importance of this mechanism to sea water chemistry depends upon the completeness of the coating. If the coating were complete or nearly complete, the bulk of the particle would be out of contact with sea water, and the particle would react as though its

bulk composition were that of the coating. Suess (1970) felt that some calcite particles might be protected from dissolution in this manner. Neihof and Loeb (1974) demonstrated the presence of such films on particles added to sea water, using the change in surface charge brought about by adsorption of surface-active material. They also demonstrated the organic nature of the film by showing that destruction of dissolved organic material by ultraviolet light prevented the formation of the film.

Some zooplankton, such as appendicularians and pteropods, discard gelatinous materials in the surface waters as part of their normal activities (Gilmer, 1972; Hamner, et al., 1975; Alldredge, 1976). These materials can account for extremely high local POC values in the surface waters.

Of course, we must always allow for some contribution of particulate matter from terrestrial sources. Some will result from transport through the air of terrestrial dust (Delany, et al., 1967). Other materials originate as effluents of manufacturing processes (Carpenter, et al., 1972), or from the discarding of manufactured products difficult to degrade (Carpenter & Smith, 1972; Colton et al., 1974).

While these mechanisms must all be at work in the surface waters, they do not entirely satisfy the experimental observations (Sheldon, et al., 1967; Batoosingh, et al., 1969) of an apparent equilibrium in particle size distribution, such that the removal of particles by filtration is followed by the formation of a new crop of particles, even in the absence of bubbling or agitation, and in too short a time to be attributed to bacterial activity; the mechanisms involved must be chemical or physical, and not biological.

A mechanism which would satisfy the observations has been elucidated by Ruckenstein & Nagarajan (1975). They calculated the distribution of particle sizes to be expected with various concentrations of a surface-active material, and found that above a critical concentration the distribution shifted from unimodal to bimodal, with the second peak centered at a fairly large particle size. Their calculated distributions matched those found experimentally. If this mechanism is at work in sea water, as it must be, the removal of the larger particles by filtration should be followed by a reconstitution of the peak in the larger size range. Since the nature of the surface-active material, the ionic strength of the medium, and the temperature, rather than the concentration of surface-active material, control the size of the particles, the reconstituted particles should be fewer, but of the same size as the first crop. Repeated filtrations should ultimately remove enough of the surface-active material to take the concentration below the critical level for the formation of large particles.

We should not expect the particle size distribution in sea water to follow that calculated by Ruckenstein & Nagarajan exactly. The ionic strength of sea water will push the equilibrium in the direction of larger particle sizes. Mazer, et al. (1976) have shown that in solutions of sodium dodecyl sulfate the size of the micelles formed increased with decreasing temperature and increasing NaCl concentration. In distilled water at 85° C the micelles were spherical and about 25 Å in diameter, while at 18° C and in 0.6 M NaCl, they were ellipsoidal and greater than 1000 Å in their longest dimension. The possible effects of the other ionic constituents of sea water have not been investigated.

Also, the formation and maintenance of the peak of larger particles would not be simply an equilibrium process. While the initial formation of the micelles would come about through electrostatic forces, once the particles were formed by the agglomeration of smaller micelles they would be cemented together by the organic materials extruded by the bacteria present (Marshall, et al., 1971). The reversible equilibrium distribution would thus become irreversible, and the distributions could be expected to be skewed towards the larger particle sizes. This sequence of events has been demonstrated with the use of  $^{14}\text{C}$ -labelled organic materials fed to bacteria (Paerl, 1974).

Another feature of the distribution of POC is a logarithmic decrease with depth in the ocean (Wangersky, 1976; Gordon, 1977). It has usually been considered that such a decrease must be attributed to in situ metabolic activity. A recent paper (Rodriguez & Offen, 1977) demonstrates that at high pressure the peak of the distribution of micelles will be shifted towards smaller sizes. This shift in the equilibrium would not affect those particles cemented together by bacterial activity; it would result in a change in the size of the particles being formed and as yet uncolonized. As a further result, we should see an apparent decrease in POC, as more of the new particles fell below our arbitrary dividing line between dissolved and particulate material. Thus, at least part of the decrease with depth could be due to physical and chemical, rather than biological, causes.

We should therefore expect that the concentrations of POC should reflect the concentrations of surface-active materials in the dissolved organic matter (DOM), and should be more plentiful in regions of high productivity. The mechanisms of micelle aggregation through electrostatic forces should result in a basic bimodal particle size distribution, with the peak in the smaller size range below the cutoff size of our filters. Superimposed on this distribution would be the particles created by all of the other mechanisms. The final distributions would thus display the effects of wind speed (Sutcliffe et al., 1971), windborne terrestrial material, and bubble growth from cresting internal waves (Ramsay, 1962).

#### PARTICLE CONCENTRATIONS AND BACTERIAL METABOLISM

The discovery of mechanisms for particle formation other than simple decomposition of phytoplankton and zooplankton remains led to an upsurge of research into the possible direct utilization of these particles by zooplankton. If the concentration of particles in a given water mass is determined by some sort of equilibrium with the dissolved organic carbon, the pool of organic carbon available for exploitation by zooplankton is vastly greater than the standing crop of particles alone. Baylor & Sutcliffe (1963) demonstrated that the growth of *Artemia salina* could be supported on a diet of the organic particles produced by bubbling natural sea water; experiments by other investigators using other zooplankton organisms have largely proved equivocal. One of the reasons for this indifferent success may be the choice of experimental organisms. The distribution of POC in deep water suggests that the major users of this material may be the microzooplankton, rather than the larger forms usually chosen by experimenters (Wangersky, 1974).

There is little doubt that marine bacteria are closely associated with the particulate matter. This is not to say that the microorganisms are concentrated on the particulate matter; almost every investigator has found that as much as 80% of the bacteria in the water column are to be found floating free (Sieburth, 1968; Sorokin, 1971; Jannasch & Pritchard, 1972; Wiebe & Pomeroy, 1972). However, recent work has indicated that the bacteria not attached to particulates may be in a resting stage, and may need 6 to 12 hours of incubation at high nutrient levels before they begin to metabolize the added nutrients (Jannasch & Pritchard, 1972; Wiebe & Pomeroy, 1972).

While at first glance this circumstance might seem surprising, it is exactly what we should have expected to find. Bacteria are of a size and specific gravity which should allow them to remain suspended indefinitely in sea water. In the presence of any turbulence, they should move together with the parcel of water in which they are floating. They see only the envelope of water which immediately surrounds them, and which travels with them wherever they go. Organic nutrients must reach them only by molecular diffusion through this envelope; except in the most organic-rich waters, they should exist in a perennial state of malnutrition.

In contrast, those organisms attached to particles are constantly exposed to new water; depending upon particle size and specific gravity, the particles must travel either faster or slower than the surrounding water. The particles also supply a larger adsorbing surface, thus collecting more organic matter from the surrounding water than the bacteria could all by themselves. Even a particle completely lacking in any nutritive qualities of its own must still be a veritable travelling garden for its microbial passengers. If the particle can itself be metabolized, the advantage to the bacteria is greater still.

These findings help to explain a long-standing mystery, the well-known discrepancy between numbers of bacteria estimated by direct counts and those calculated from colony counts. Typically, direct counts have shown from 10 to 1000 times as many bacteria as have the various plating-out techniques (Jannasch & Jones, 1959). This discrepancy has been accounted for by a variety of reasons, including the choice of media and the likelihood of finding only one colony per particle, regardless of the number of organisms present on the particle. However, if only the organisms attached to particles are in the proper physiological condition to reproduce, and all of the organisms floating free in the water are in a resting state, then the plating-out techniques may be measuring only the metabolically active forms, rather than the total number of bacteria present.

Much of the work on bacterial utilization of particles has concentrated on the decomposition of these particles. If the whole role of the bacteria present on the particles were just such decomposition, we would rightfully consider that the bacteria played only a small role in the metabolism of the ocean; the particulate organic carbon is seldom more than a few percent of the total organic carbon, and is often disregarded when DOC measurements are made, as being within the analytical error of the measurement. However, it must be considered that if an equilibrium process exists for the formation of particulate matter, the bacteria have available to them the whole of the supply of dissolved surface-active material, rather than just the

standing crop of particles. Even if we accept the concept of the DOC in deep water as being largely unusable (Menzel & Ryther, 1970), we have, in the difference between the surface DOC and that of the deep water, some 0.5 mg C/l to be decomposed. This is about a hundred times the standing crop of POC in the surface waters.

Another mechanism, one not requiring the formation of particles *de novo* for the utilization of DOC, has been suggested by Khailov and his co-workers (Khailov & Finenko, 1968, 1970; Aizatullin & Khailov, 1970, 1972). In this mechanism, the particulate matter acts as a site for adsorption of high molecular weight materials, and as a surface for bacteria. The high molecular weight substances are decomposed, and low molecular weight fragments released into solution. Particulate matter, in this view, can be considered simply as a site for the catalysis of DOC degradation.

Whatever the mechanism of bacterial activity on particles, the major users of DOC must be microbial. It seems likely that photoheterotrophy may be more important in phytoplankton than we have considered (Wangersky, 1977), and that photodecomposition in the surface layers may result in the degradation of other organic compounds (Zika, 1977), but neither of these mechanisms seems capable of all of the regeneration of inorganic nutrients taking place in the surface waters.

While there is considerable evidence from axenic culture experiments that some phytoplankton species and some bottom organisms are able to take up and use organic forms of both nitrogen and phosphorus, such utilization typically requires an extended lag or induction period. Experiments with cultures containing bacteria have shown that under more natural conditions bacterial uptake of these compounds is much more rapid; it is unlikely that any great amount of direct utilization by plankton ever occurs outside of the laboratory (Wangersky, 1977).

#### BACTERIAL REGENERATION OF INORGANIC NUTRIENTS

While many marine organisms have been shown to return simple inorganic nutrients to the oceans (Pomeroy et al., 1963; Johannes, 1964, 1965; Barlow & Bishop, 1965; Hargrave & Geen, 1968; Jawed, 1969; Whitley & Packard, 1971; McCarthy & Whitley, 1972; Yoshida & Kimata, 1972), in the long run bacterial activity must be the most important factor in nutrient regeneration. The larger organisms, no matter how effective they may be at breaking down organic nitrogen and phosphorus compounds to their simplest inorganic forms, can attack only those materials present in particulate form; many larger organisms have been shown to absorb some organic compounds directly from solution, but in only a few genera does this mechanism supply any major part of the nutritional needs of the animals (Wangersky, 1977). If a sink for nitrogen and phosphorus, in the form of dissolved matter, were present in the ocean, in a relatively short period all of these nutrients would be present only in those forms. This is a principle which we all feel we understand, but which we too seldom invoke. If there really were organic compounds in the ocean, perhaps as complex polysaccharides, which could not be broken down by marine bacteria, we would be hip-deep in maple syrup by now. If such compounds also contained even the smallest amount of nitrogen or phosphorus, the maple syrup would also be sterile.

While marine biologists have been concerned with the standing crop of nutrients, and while the literature abounds in measurements of phosphate, nitrate, and silicate, we know very little about rates of regeneration. There is no easy-to-grasp handle on this problem; in the presence of phytoplankton, nutrients furnished by regeneration will be absorbed and used. Filtration to remove phytoplankton results in the removal of the particles containing the active bacteria, and thus can furnish only a minimum regeneration rate. In temperate waters, it might be possible to estimate a regeneration rate by following the nutrient concentration in early winter, when light becomes limiting to phytoplankton growth. However, by that time the water temperature has decreased considerably; since all bacterial activity is temperature-dependent, only a minimum rate, based on cold-adapted species, can be calculated in this manner. The use of dark-bottle techniques will result in a maximum rate, since light at the lower wavelengths is inhibiting to bacterial activity in sea water (Zika, 1977). The few studies which have been made certainly demonstrate the importance of bacteria to normal phytoplankton growth through much of the year (Watt & Hayes, 1963; Sen Gupta, 1968; Melnikov & Volostnykh, 1974). The dynamics of this "regenerative" system were described for nitrogen regeneration in Long Island Sound by Harris (1959).

Some workers feel that bacteria act as net conservers, rather than as net regenerators, tying up organic nitrogen and phosphorus in their bodies until they autolyze, or are digested by the protozoans and small metazoans (Pomeroy, 1970). Even if this were the case, however, bacteria are the necessary link between the dissolved organic matter and the regenerated inorganic nutrients; whether the conversion proceeds in one step or several, the number of active bacteria must be a rate-controlling step. Regeneration by means of autolysis will proceed in the absence of protozoans and small metazoans, as evidenced by the early work of von Brand et al. (1937, 1939), and the more recent work of DePinto and Verhoff (1977), among others.

The necessity for bacterial control of productivity through nutrient regeneration should be obvious to any oceanographer who has run nutrient analyses in the open ocean. Except for the period immediately preceding a spring bloom, at least one and sometimes all of the essential inorganic nutrients are in very short supply. The standing crop of phytoplankton is not necessarily approaching zero, however, and in some waters may be quite high. The organisms are not in any sort of resting phase, but are healthy and growing, just as if nutrients were present. In fact, nutrients are available; however, just as fast as they become available they are taken up by phytoplankton. The only conditions under which the regenerated nutrients can accumulate are when phytoplankton growth is limited by some other factor, such as day length, or when regeneration rates are faster than the fastest possible growth rate for the phytoplankton.

The effects of bacterial regeneration can be demonstrated clearly in the metabolism of the *Sargassum* community. The Sargasso Sea is notoriously low in inorganic nutrients, so low that Sargasso surface sea water is often used as the blank for nutrient determinations, and maintains an extremely low standing crop of phytoplankton. Yet the organisms living in the *Sargassum* patches seem to be thriving.

The weed furnishes an excellent surface for bacterial growth, and microbial respiration has been estimated as half the respiration of the entire community (Smith et al., 1973). Reactive phosphate measurements in *Sargassum* patches are as much as six times those of the surrounding surface water (Culliney, 1970). In the local environment of the *Sargassum* patch, at least the phosphate is regenerated faster than it can be absorbed by the community. It would seem that the nitrogen and phosphorus in the surface waters of the Sargasso Sea are present in the wrong form to sustain phytoplankton growth. What are missing are the surfaces necessary for the maintenance of active bacterial populations. Where the surfaces are present, nutrient regeneration can be found. We have habitually commented that the waters of the Sargasso Sea are lovely, blue, and clear because they are so unproductive. Perhaps we should say that they are so unproductive because they are so clear, because the burden of particulate matter normally carried by ocean water has had time enough to settle out, leaving insufficient surface area for proper regeneration of nutrients.

#### “RENEWAL“ VERSUS “REGENERATION“ SYSTEMS

We can consider that there are two major modes of phytoplankton population control in the oceans. The one with which we are most familiar involves the supply of nutrients to the surface waters by the actual addition to these waters of new, nutrient-rich water. The nutrients in this new water have been regenerated somewhere else in the oceans, usually at depth. Because the supply of nutrients to the surface waters is dependent upon the supply of new water, we will call this system of regulation of productivity the “renewal“ system. It is typical of upwelling areas everywhere, and of the temperate and boreal oceans in the period before the spring bloom, when deeper water is brought to the surface by mixing due to the breakdown of summer thermal structure in the water column and to winter storms.

In such renewal systems the inorganic nutrients are characteristically all high, at least at the start of the growing season or upwelling incident, and the characteristic phytoplankton organisms are diatoms. Since the nutrients are supplied from “new“ water, high productivity can occur with little regeneration, and with a rather low particle content, at the start. Obviously, continued high productivity will lead to high particle content as both dissolved and particulate materials are added to the surface layers.

In the case of the spring blooms, the inorganic nutrients are consumed in a relatively short period, and the system shifts from a renewal to a regenerative mode. In upwelling regions, the area and duration of upwelling are indeterminate. Instead of a large regional ascent of deeper water to the surface, the upwelling seems to occur in small areas over short periods of time (see, for example, Jones, 1972). Thus we would expect that in nominally upwelling areas there would be some regions where the dominant mode of productivity would be regenerative. Even during upwelling incidents, at some distance down-current from the point of upwelling the mode should shift from renewal to regeneration; a similar shift should occur in the area of upwelling some short time after the cessation of the off-shore wind.



The regenerative mode, the more common mode over most of the oceans, is marked by low nutrient content. At least one of the inorganic nutrients should be close to zero. Also, while organic nitrogen and phosphorus can be regenerated to the inorganic forms in situ in the surface waters, most of the regeneration of silicate from the particulate to the dissolved state takes place deeper in the water column, since this regeneration requires re-solution of diatom tests. These tests drop through the surface layer and out of the euphotic zone after the death of the organisms, and the dissolved silicate is not brought back into the surface layer until the system again enters the renewal mode. Because of this lack of silicate, we would expect regeneration systems to be dominated by  $\mu$ -flagellates, dinoflagellates, or blue-green algae. Typically, a shift from renewal to regenerative mode also involves a shift from diatoms to dinoflagellates.

An almost classic demonstration of the shifts in mode occurred in a recent cruise off the coast of Peru, the Joint II cruise of the Coastal Upwelling Ecosystems Analysis program (Barber, personal communication). On this cruise, a normal upwelling incident, involving the transport of high-nitrate water to the surface, resulted in a normal (for this area) diatom bloom. When the offshore winds slackened and the upwelling ended, the nitrate went essentially to zero, the silicate dropped sharply, and a dinoflagellate bloom began. With the resumption of the offshore winds the silicate and nitrate again rose sharply and the diatom bloom resumed.

In another incident, the upwelled water was drawn from an anoxic layer at about 100 m depth. This layer lacked both nitrate and nitrite. The system, although technically a renewal system, shared some of the features of a regenerative system in the lack of nitrate, and was dominated by dinoflagellates. It would be interesting to know the form in which nitrogen was present in this incident; if it were present as organic nitrogen, then a high POC should also have been present, to permit rapid regeneration once the water parcel had reached the surface.

While it is relatively easy to make a quick and dirty estimate of the potential productivity of a renewal system, since the nutrients are normally supplied in a great excess of the amount which can be used immediately by the resident population, it is much more difficult to estimate the productivity of a regenerative system. Since the nutrients are normally regenerated at a rate well within the uptake rate of the dominant phytoplankton organisms, there may appear to be no nutrients whatsoever in the system. Furthermore, the increase in zooplankton brought about by incidents of renewal, as in spring blooms, may ensure that the standing crop of phytoplankton is kept low. It is difficult to distinguish between a regenerative system which is just ticking over and one which is turning over furiously, if the only measurements available are of standing crops. We must measure turnover rates, or, if these measurements are not feasible, we must look to the content of the higher trophic levels.

I would propose that we distinguish between these possibilities by examining the particle content of the water. If my analysis is correct, it is not possible to have a high regeneration rate without a high particle count. An even better technique would be to measure only those bacteria present on particles. A variant of the ATP

measurement, using a coarse filtration, might be a key to the productivity of regenerative systems.

The regenerative process must be to some extent autocatalytic. At very low particle counts, and therefore at low rates of regeneration, the nutrients supplied may only be sufficient for the maintenance of the population, and not for growth. Above a threshold value, the growth of phytoplankton populations should supply enough new particulate matter to ensure increased regeneration. This could result in a system with positive feedback, leading eventually to a plankton bloom. This is probably what occurs in spring blooms and in upwelling areas, when the system shifts from the renewal to the regenerative mode; the particulate content of the water, after some period in the renewal mode, is great enough to sustain a dinoflagellate bloom in the regenerative mode.

At any given time, not all of the particles produced by autotrophic growth will be available as sites for bacterial growth. Some particles, especially those containing diatom tests, will quickly sink through the euphotic zone; other particles will be ingested by the various grazing organisms, and the undigested remains released as fecal pellets, which will also sink quickly through the euphotic zone. Thus, in regions or periods of low inorganic particulate content the losses from sinking and grazing may prevent microbial regeneration from reaching the threshold value needed for autocatalytic growth of the phytoplankton populations. The threshold value must be relatively high; otherwise, the phytoplankton would exist in a state of perpetual bloom. Alternatively, the rate of loss of particulate matter to the deeper water must be great enough so that bloom conditions, even when attained, cannot be sustained without the addition of some new water.

The autocatalytic process should also have upper limits. The absolute amount of nitrogen and phosphorus in the system will determine the maximum standing crop of phytoplankton, while the temperature of the water will determine the maximum rate of bacterial metabolism. The absolute maximum standing crop of phytoplankton would occur with a bacterial regeneration rate very much faster than the phytoplankton growth rate, so that all of the available nutrients would at all times be bound up in living phytoplankton; I doubt that this condition is ever achieved, but perhaps we should look for it. Also, as the phytoplankton population becomes dense, the turbidity of the water will limit further photosynthesis. Similarly, if the particles are derived from some non-biological source, such as another Krakatoa, the addition of particles should enhance regeneration rates, and therefore productivity, up to the point where the particle density interferes with photosynthesis by interfering with light transmission through the water. In oceanic waters the most reliable simple index to the productivity of an area may be the Secchi disk reading, when properly interpreted.

#### IMPLICATIONS OF PARTICULATE CONTROL OF PRODUCTIVITY

A new explanation for a well-described natural phenomenon is of little value unless it can be tested, either by the prediction of hitherto unexplained effects or by

the generation of laboratory or field experiments. Let us consider the implications of the control of productivity in the regenerative mode through particle concentrations.

### GENERATION OF "RED TIDES"

One of the more vexing problems in the study of phytoplankton population growth has been the occurrence of "Red Tides", the massive dinoflagellate blooms. In northern waters, these are definitely regenerative systems, occurring after the spring diatom blooms, when the water has warmed enough to permit high rates of bacterial regeneration. Theory would predict that the blooms should take place in waters with low standing crops of nutrients, but with high particulate content. Thus they should be expected in coastal waters with some turbidity, and should occur as the surface waters warm in the early summer, raising the rates of bacterial metabolism. It is not surprising that these blooms are common in the turbid Bay of Fundy, and little known along the Atlantic coast of Nova Scotia, where the water is generally low in particulate matter. However, if man's activities along this coastline continue to raise the turbidity of the normally clear water, we should expect to see dinoflagellate blooms spread to these waters, also.

There have been many investigations of these Red Tides in the waters of the Gulf of Mexico, and particularly along the Gulf coast of Florida, where the toxins released by the dinoflagellates kill food fish, and the combined unpleasantness of piles of dead fish along the tide line on the beaches and the "Red Tide hack" induced by volatile organic materials emanating from the blooms acts as a deterrent to tourism. Most of the early work on the genesis of Red Tides looked for the causes in terms of the supply of inorganic nutrients. Thus, Smith (1948) proposed that rock phosphate on the sea floor acted as a source of nutrients for the plankton bloom. Since central Florida is a source of phosphate minerals for industry, it is not surprising that many investigators considered that the blooms were started by a mixture of nutrient-rich river water and oceanic water containing the dinoflagellates. However, it was shown fairly early that little phosphate was contributed by Florida's rivers (Graham et al., 1954). In fact, as long as simple utilization of inorganic nutrients, without bacterial regeneration, was the only mechanism considered, the productivity of these blooms could not be explained (Holmes et al., 1967). In order to gain enough nutrients from the water column, a depth of water would have to be scavenged far in excess of the normal daily migration of these organisms.

The physical conditions necessary for the formation of a bloom, which include calm weather and the formation of a cell of low-salinity water, were outlined by Slobodkin (1953), and have since been demonstrated by other investigators (Ragotzkie & Pomeroy, 1957; Iizuka & Komaki, 1974). These conditions seem to be necessary but not sufficient; a Red Tide does not begin every time the weather is right. It has been suggested that a second necessary condition is the presence of humic acids, which can act as growth stimulants for some dinoflagellates (Prakash & Rashid, 1968; Martin et al., 1971).

The main disadvantages of the concept of humates as growth promoters are first, the amount which would be needed to sustain a bloom, and second, the well-demonstrated sedimentation of humates in estuaries. I would propose, instead, that Red Tides are regenerative blooms, triggered by an addition of particulate matter to a bolus of water created by the mixture of sea water with excessive runoff, usually in a confined estuary such as Charlotte Harbor, Florida. Humic materials from the river systems may be related to Red Tides through two mechanisms; they may be indicators of turbid runoff caused by exceptionally heavy rains, and, since they are themselves particulate, they may be ejected from the estuaries along with the runoff, before they have had time to sediment in the estuary. I suspect it is their particulate nature rather than their chemical composition which is important in the instigation of a dinoflagellate bloom. It might be worth looking for any association between the recent Red Tides and the dredge and fill land developments along the Florida coasts.

Once the particulate content of a low-salinity cell exceeds the threshold value for autocatalytic growth, the bloom should proceed inexorably, until storm winds break up the cell and disperse the particulate matter. When a Red Tide has truly started, the only remedy, as Slobodkin once suggested, lies in prayer. However, if we can define the necessary conditions, we may be able to ensure that these conditions do not often occur. The Red Tides are not necessarily obnoxious; only certain of the dinoflagellate species release toxins, and in many parts of the oceans the dinoflagellates are just as welcome to the rest of the food chain as are diatoms. However, several of the more common species are difficult neighbors, and should not be encouraged.

#### PRODUCTIVITY AND PARTICULATE MATTER: DIRECT EVIDENCE

For the most part, it is difficult to secure any direct evidence linking particulate matter and productivity in the open ocean. It is difficult to distinguish cause from effect when the sampling period is as short as the typical oceanographic cruise or as episodic as even the best of seasonal samplings must be. The best kind of evidence would be a time series, extending over many years, and comparing the productivity in a single area over years of high and low particle count. This kind of long-term experiment has not been run, partly because no one has seen the need for it, and partly because the year-to-year variability in particulate matter in the open ocean is not likely to be great. Regional and seasonal variations seem to be much greater than the year-to-year variations. I must add, however, that we have not really looked for the year-to-year variations, and have tended to lump together and average values taken in the same season over several years, where we have had such data available.

Year-to-year variations can be large enough to show measurable effects in estuaries, where land runoff will vary greatly with the amount of precipitation. This effect may be particularly well marked in northern river systems, where large

amounts of sediment are brought down with the spring meltwaters. We have not yet taken such a series of productivity and particulate measurements in any northern estuary. We do have something almost equivalent in the fisheries statistics from the Gulf of St. Lawrence. Yearly catch statistics furnish an estimate of population size at the age when a year-class enters the fishery. While we do not have measurements of the particulate content of the Gulf waters for the proper years, we do have good runoff statistics for the St. Lawrence. The Gulf is small enough to be affected by runoff from St. Lawrence, and yet big enough for the fish to spend their entire lives there. In four commercially important species taken in the Gulf, correlations have been found between catch size and land runoff during the first year of growth (Sutcliffe, 1972). This work should be followed by annual measurements of productivity and particle number in these waters, to determine whether the correlation holds at the level of primary productivity, and whether predictions of size of year class, and therefore the enforcement of fishing regulations, can be based on such a measurement.

#### EXPERIMENTS ON INCREASING PRODUCTIVITY

It has long been recognized that the highly productive regions of the oceans are either offshore banks or upwelling regions. It does not seem feasible to increase the productivity of either of these types of regions, although proposals have been made from time to time to use the excess heat from nuclear power generation to create artificial upwelling. While this idea seems plausible, the effect would be purely local, and probably unimportant in terms of worldwide productivity. As long as we think of oceanic productivity only in terms of these two highly productive but greatly limited systems, we must be pessimistic about any large increase in utilization of oceanic productivity for food (Ryther, 1959).

However, for the most part the oceans are regenerative, rather than renewal systems. In a regenerative system, productivity is largely limited by rates of regeneration of nutrients, and therefore by bacterial metabolism. Since the rate of metabolism in bacteria is strongly temperature-dependent, it is not likely that we can do much to increase the metabolic rate per organism. We may be able to increase the number of active organisms by supplying them with more sites for activity, in the form of particulate matter.

I would propose an experiment, to be run in some low-productivity region of the ocean, such as the Sargasso Sea, the North Pacific Gyre, or the Tongue of the Ocean in the Bahamas. A portion of the ocean should be marked off with drogues, and a phytoplankton and zooplankton census taken both inside and outside the test area. The test area should then be seeded with particles having a neutral buoyancy, and the populations both inside and outside the test area should be followed for some period. I would predict that the test area should show an increase in standing crop of phytoplankton, at least until the local herbivores got the message, and that the dominant phytoplankton types would be dinoflagellates. Whether we could actually trigger a Red Tide would depend on the weather, since

increased turbulence could disperse our local collection of particles, and upon whether we could exceed the threshold level for autocatalytic growth.

### THE PROBLEM OF POLLUTION

In our investigations of the effects of pollution on life in the oceans, we have been concerned with the effects of pollutants on phytoplankton (Musser et al., 1972; Fisher et al., 1973; Fisher, 1975), although considerable work has also been done on organisms in the higher trophic levels, such as fish (MacGregor, 1974) and bottom invertebrates (Odum et al., 1969). While phytoplankton are most susceptible to materials in solution, the chlorinated hydrocarbons, such as DDT and the PCB's, as well as the petroleum derivatives, appear to be present largely as part of the particulate fraction (Risebrough et al., 1968; Pfister et al., 1969; Cox, 1971; Poirrier et al., 1972; Bidleman & Olney, 1974; Khan, 1974; Pierce et al., 1974; Seki et al., 1974; Hughes & McKenzie, 1975; Scura & McClure, 1975). This might seem fortunate for the overall economy of the ocean, since it reduces the concentration of pollutant in solution, and seemingly transfers the point of entry into the food chain to the higher trophic levels, thereby cutting down the possibility of biological amplification.

However, if one of the pollutants which adsorbs on particulate matter should be bactericidal or even only bacteriostatic, the immediate effect would be a reduction in productivity in the regenerative systems, which is to say in almost all of the oceans. The toxic material would be applied directly to the point of maximum sensitivity; even low concentrations per unit volume could result in high concentrations on the surfaces of particles. We do not know whether any of the common pollutants are in fact injurious to marine bacteria, since the proper kinds of tests have not been run. The usual microbiological test procedure, based on colony growth or turbidity in inoculated enriched media, does not answer the question we are asking about the effect of the material on the health of the whole bacterial community.

I would suggest a test based on the quantity which really interests us, the regeneration rate. Let us determine a regeneration rate for a given parcel of sea water, in the laboratory in the dark, and then add to the parcel a known quantity of particulate matter coated with the material to be tested. Any decrease in rate of regeneration would be an immediate indication of possible trouble. We might already be suffering from this kind of trouble; several investigators have speculated in private conversations that the overall productivity of the open ocean may have decreased over the last ten years, although they have attributed this possible decrease to changes in climatic patterns. Work already mentioned has demonstrated that pollutants can achieve worldwide distribution in a very short period, by aerial transport. We must be careful, indeed, that some new product of the chemist's ingenuity is not distributed throughout the oceans before we discover its toxicity to marine bacteria.

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