EUTROPHICATION:

CHANGES IN ESTUARINE PHYTOPLANKTON PRODUCTIVITY

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THE ESTUARY

Estuaries are individually unique ecosystems, each with specific environmental characteristics. There are, however, some generalizations that can be made describing estuaries overall. Caspers (1967) gives four features applicable to estuaries: 1) limited to rivermouths in tidal seas; 2) saline areas present, their extent dependent on the amount of freshwater runoff; 3) the upper limit of the estuary is defined by the upper limits of tidal influence into freshwater zones; 4) characterized by changeable salinities and instability of environmental factors. Brackish systems have been put into three catagories by a number of workers (cf. Emery, et.al.(1957), Pritchard (1967)) breaking them into positive, inverse and neutral groups. Positive estuaries are river dominated, freshwater runoff exceeding evaporation rate. Inverse estuaries are characterized by rapid evaporation rate, surpassing runoff and precipitation. These are hypersaline the majority of the time. Neutral estuaries have a balance between evaporation and freshwater influx. These classifications, however, are oversimplifications. Pritchard (1967) defines an estuary as a "semi-enclosed coastal body of water which has a free connection with the open sea and within which seawater is measurably diluted with freshwater derived from land drainage." Pritchard's definition restricts the term "estuary" to signify only the so-called "positive estuary". Emery, et.al. (1957) use the term "normal estuary" to be equivalent to positive estuary.

There are four physiographic origins for estuaries:

1) a drowned river valley - the "classic" estuary. Emery (1957) states that most estuaries occupy drowned river mouths, and considers this to be evidence of post-glacial submergence.

2) fiord-type - a glaciated valley (with the characteristic U-shape) with a sill of terminal moraine at the mouth, shallower than the basin on the landward side.

3) bar-built - barrier islands built by current deposition and sedimentation, resulting in an embayment.

4) tectonic-formed - including faulting, or local subsidence.

This paper will be concerned with the drowned river mouth system, because the majority of estuaries in the United States and elsewhere are of this type.

PHYSICAL FACTORS

The control of water mixing and circulation within an embayment is predominately affected by the tides. Periodically, tidal currents mix, to some degree, the fresh and saline waters, exposing shallower portions of the estuarine basin and then flood, re-filling the bay. These currents set up turbulence which stirs up bottom sediments. Often, the action of the tides can be observed upstream, far beyond the upper limit of the salinity gradient(Emery, 1957). Other sources of mixing are freshwater inflow, and wind. It has been shown that freshwater flow acts as breaking waves at the interface of the upper boundary of the saltwater wedge(Pritchard, 1967). Wind may generate small waves, but they are generally quite small, because of the short fetch and shallow bottom, compared to oceanic waves(Emery, 1957).

Water temperatures within an estuary can have seasonal as well as diurnal variation. Shallow waters tend to be colder in winter and warmer in summer. Also, the degree of insolation and air temperature on exposed mudflats can affect water temperature daily. Water temperature varies directly with the distance from the entrance of the estuary. The water at the entrance maintains almost the same temperature as the open ocean, but the farther from the entrance, the greater the temperature differences. Temperatures may vary vertically, with surface water layers being warmed by insolation or cooled by winter air temperature. The greatest annual range of temperature occurs at the surface.

Light intensity and penetration of solar energy in estuarine waters is reduced by absorption and scattering of wavelengths. Water is transparent to wavelengths 450-600 nm(Johnson,1957), however the intensity is further attenuated by coloration in the water (humic acids and/or other stains) and turbidity resultant from suspended particles and sediments (seston). Light intensity is reduced seasonally by river sediment loads and watershed runoff, including silt, sand and mud. The seasonal blooms of phytoplankton populations may even limit their own access to light and limit growth rates by self-shading phenomena. Raymont(1963) and Ruttner(1963) have comparative tables for water transparency (see tables 1 and 2). Because of the turbulence associated with tides and river flow, the suspended particulates will most likely be greater within the confines of the estuary as well as off shore, in the plume of the estuarine/river outflow. Decreasing transparency is

Wavelength, nm :	400	500	600	700	800
Ice (Lunzer Untersee)	96.0	92.0	81.5	55.0	17.0
Distilled water	98.4	99.2	81.0	55.0	11.1
Lake water	33	68	63	31	(10)

TABLE 1: Comparative transparency of waters and ice.
Percent of wavelengths transmitted per meter.
(After Ruttner(1963) from Sauberer(1950).)

Depth (Meters)	Oceanic Water		Coastal Waters		
	Type I	Type II	Type 1	Type 3	Type 9
0	100	100	100	100	100
1	44.5	42.0	36.9	33.0	17.6
5	30.2	23.4	14.2	9.3	1.0
10	22.2	14.2	5.9	2.7	0.05
50	5.3	0.70	0.02	0.0006	-
100	0.53	0.02	-	-	-

TABLE 2: Percentage amounts of total incident solar energy at various depths for different types of sea water. (After Raymont(1963) modified from Jerlov(1951).)

Type I= clearest ocean water.
Type II= relatively turbid oceanic water (e.g. Red Sea).
Types 1, 3, 9 = coastal waters of increasing turbidity.

attributable to both absorption and scattering of light rays. As water turbidity increases, so too, does the absorption coefficient

Density differences set up a salinity gradient from the estuary mouth to a point somewhere below the limit of tidal influence on the contributing river. Heavier marine water will tend to form a salt or saline wedge as it moves upstream, the lighter freshwater flowing over the saltwater. The deeper portions of an estuary, tidal channels, etc., will have water of a more marine salinity than those shallower regions where water circulation is more likely to mix surface freshwater with the water below. The more stable the halocline, the more likely circulation within the estuary (water column overturn) will be held to a minimum, and phytoplankton will be more likely to remain within the photosynthetic zone for longer periods of time. However, when the estuary is shallow and well mixed, the resulting turbulence can delay the spring bloom, as well as the abundances of populations.

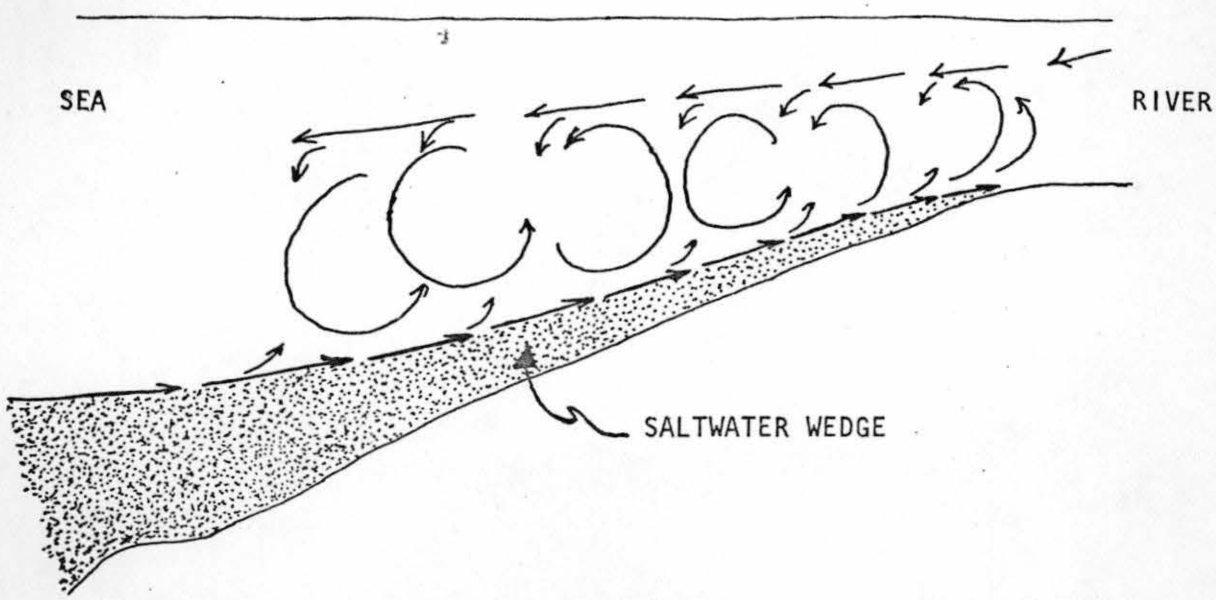

FIGURE 1: Schematic diagram of the salinity gradient and water circulation, showing the mixing of lighter freshwater with heavier seawater. This mode of circulation tends to produce a "nutrient trap", retaining and recirculating nutrients within the estuary.
(Redrawn from Odum(1959).)

CHEMICAL FACTORS

Salinity varies diurnally and seasonally in most estuaries. Any one location within an estuary can have a greater or lesser salinity than an adjacent spot. Daily, salinity may vary with high and low tides from nearly pure marine water to entirely freshwater. Seasonally, an estuary can take on hypersaline characteristics in the summer when evaporation exceeds precipitation, or freshwater inflow, while in the winter, brackish and freshwater characteristics predominate.

Seawater is a buffered system, pH being maintained between 8.0 and 8.3 . Moore(1958) suggests pH may not be significant as a limiting factor in such a buffered system, where pH is relatively stable. Moore(1958) cites Bachrach and Lucciardi(1932) as having found diatoms able to grow between 6.0 and 9.0, with an optimum at 9.0. Higher pH tolerance for littoral Ulva spp. has been shown to be 10.0, the level raised in tide pools by its own photosynthetic activity. Fogg(1965) mentions that pH may be affected by preferential absorption of nutrients in a culture medium. When ammonium ion is present as the nitrogen source, preferential uptake by the algae will result in the medium becoming too acid to support growth. With the absorption of nitrate, pH tends toward alkalinity, but generally culture media are well buffered.

When CO_2 is limiting, pH may rise as high as 11.0, as photosynthesis uses up all available CO_2. In such a case, growth stops. As far as estuaries are concerned, being neither totally saline nor freshwater, nor a closed culture, I suggest that the extension of seawater and subsequent mixing with freshwater may extend the marine buffer system and stablize pH within the estuary. There may be diurnal changes and local "pockets" where photosynthetic activity alters pH to extreme acidity or alkalinity, but the estuary as a whole will remain stable. Cupp(1943) states that diatoms are not limited in growth by pH.

Nutrients enter an estuary from a number of sources: 1) coastal marine waters; 2) river and land (watershed) drainage; 3) the mixing of estuarine bottom sediments and settled nutrients in the water column. The estuary acts as a "nutrient trap" (see Figure 1, Odum(1958)), where subsurface countercurrents -- higher density seawater flowing along the bottom, pick up nutrients as they flow into the estuary -- mix with the surface layers of freshwater. Nutrients are retained and recirculated further by oscillating tides and tidal currents. River and drainage contributions are leached nutrients carried from the soil by precipitation as suspended particles or dissolved in solution to the estuary. On an ocean-wide basis(Ketchum,1967) river nutrient contribution is only a small part of the total required for all marine productivity. Odum's(1958) description of an estuary as a "nutrient trap" is applicable to the estuary with a marked density gradient. In the mixed estuary, with no density gradient (Ketchum, 1951), Riley, 1967) there is increased drainage with resultant flushing rate increase.

Nutrient sources within the aquatic ecosystem Likens(1972) include: 1) available nutrients, dissolved in water, as suspended particles, or on the exchange interface of bottom sediments; 2) organic matter in living or dead organisms, feces, detritus, etc.; 3) primary or secondary minerals in sediments and suspended particles. Organisms take up available nutrients and minerals, grow, reproduce and die, their remains settle to the bottom, where bacteria and benthic consumers gradually (or rapidly, in some cases) break down the detritus into more utilizable forms to be recycled and mixed into water circulation.

BIOLOGICAL FACTORS

Primary producers in any aquatic ecosystem include phytoplankton, periphyta and macrophyta. The periphyta include benthic sessile diatoms and epiphytes. Macrophyta are higher plants rooted in the substrate, generally below the water line, with their leaves on or above the surface of the water. This way they have the best of both worlds -- roots in the rich bottom muds, and photosynthetic organs in full sunlight. This paper is concerned only with the phytoplankton segment of aquatic primary production.

Phytoplankton in the estuarine environment are predominately of marine origin(Patrick, 1967). Neritic phytoplankters are brought into the estuary by tides, currents and wind action. The phytoplankton community may be divided between nannoplankton and "net plankton". Nannoplankton include diatoms, dinoflagellates, coccolithophores, silicoflagellates, and small, naked green flagellates and nonmotile photosynthetic cells smaller than 10μ. The nannoplankton normally pass through the finest nets. They generally belong to the plant groups Chrysophyceae, Chlorophyceae and Cryptophyceae (Raymont, 1963). The larger net plankton include diatoms, dinoflagellates, larger coccolithophores and some colonial species which, together, may clog nets, whereas, if they were individual, they would flow through the net meshes. Raymont(1963) reports that though diatoms and dinoflagellates are in all seas, diatoms are the important primary producers in higher latitudes, especially polar regions. Diatoms are the dominant primary producers in boreal (subarctic) areas. They have been studied physiologically and in productivity studies more than most groups in the temperate seas off the United States for that reason -- their abundance. There is more literature about diatom nutrition than most groups; however, with eutrophication, the phytoplankton community changes to other groups of algae more capable of handling the new higher nutrient levels and changes in light availability.

Diatom nutrient requirements as listed in Lewin(1962) include Si, N, P, K, Mg, O, H, C, S, B, Mn and Ca. Mo, Co, Fe and I are required in trace amounts. If given a choice of nitrogen sources, ammonium ion will be taken up by most diatoms before either nitrate or nitrite (Cupp, 1943, Eppley and Rogers, 1970) and will be taken up until the concentration is depleted to within 1 to 0.5μM. Nitrate is a close second followed by nitrite(Eppley and Rogers,1970). In Cupp(1943), she states that Harvey(1940) reports that urea, uric acid and possibly certain amino acids may be used by diatoms as alternate nitrogen sources. McCarthy(1972) studied urea uptake by marine phytoplankton, and concluded that with saturation constants of urea and ammonium ion being similar in the marine environment, marine phytoplankters should be capable of utilizing urea. Once taken up into the cell, however, the ability to utilize urea depends on the presence or absence of particular biochemical processes within the cell (McCarthy, 1972). Ryther and Dunstan (1971) mention the classic "duck farm studies" in Great South Bay and Moriches Bay on Long Island Ryther(1954). Nitrogenous compounds were monitored, including nitrate, nitrite, ammonium ion and uric acid -- the nitrogenous excretory product of ducks. It was found that there was no trace of any of the above nitrogen forms except in the tributaries where the duck farms dumped their effluent. Ryther(1954) tentatively concluded that nitrogen was rapidly assimilated in any and all forms by the algae.

Other phytoplankton, such as dinoflagellates, may prefer their nitrogen in the form of amines and amino acids over nitrate ion (Moore, 1958).

Aquatic phosphorus takes three forms(Ruttner, 1963): 1) dissolved organic 2) particulate (in suspension); and 3) dissolved inorganic phosphorus. Since phosphorus is a nutrient that is present in such small amount in most aquatic environments, especially the freshwater environment, many phytoplankton have developed methods to store phosphorus above and beyond structural and functional needs (Ruttner, 1963). It has been shown(Einsele, 1940, in Ruttner, 1963) in fertilization experiments that plankton algae were able to accumulate more than 10 times as much phosphorus as they normally contained; they will store phosphorus in excess of actual needs, given a large enough supply. This has also been established physiologically by many workers, in careful culture experiments, and by use of radioactively labelled phosphorus (P^{32}). However, even with such normally low levels of phosphorus, its rate of turnover from its uptake to subsequential release back into the "open" system plays an important part in overall phosphorus utilization. Watt and Hayes(1963, in Fogg,1965) have estimated turnover times for dissolved inorganic phosphorus as 1.5 days, particulate phosphorus as 2.0 days and dissolved organic phosphorus as 0.5 days in inshore waters off Halifax, Nova Scotia. Other workers have given the turnover cycling rate for dissolved organic phosphorus as low as 60 seconds(Ruttner,1963). Moore(1958) suggests that though some organic phosphorus compounds can be utilized by algae, most of it is broken down to phosphate ion by bacterial action and is later used by the algae(Blinks, in E.M.Smith(1951),in Moore,1958).

Vitamins and other organic compounds influence phytoplankton rates of growth or "increase" as Fogg(1965) prefers to call them. Such organic growth factors may, themselves, be limiting. Thiamine, vitamin B_{12}, and biotin(Droop,1962b, and Provasoli,1963, in Fogg,1965) have been shown to be nutrients required by many phytoplankters.

Generally speaking, phytoplankton nutritional requirements are very much similar to those of terrestrial plants, with the exception of silica for diatom frustules, and perhaps some of the B vitamins (e.g. B_{12}). Over-fertilization, in a sense, may cause high enough concentrations of nutrients which exceed optimum levels, resulting in toxic conditions for some phytoplankton groups. For example, certain high levels of ammonium ion are toxic to specific diatoms(P. Donaghay,pers. comm.). Such toxic conditions tend to promote a shift from the indigenous or native algal groups unable to cope with an overdose of nutrients to those species either tolerant or able to adapt to the new regime; species that can effectively utilize the newer high nutrient concentrations and/or grow and reproduce under such conditions. The population changes to one characterized by phytoplankton that are able to thrive, more or less, effectively, and cope in an environment with self-shading, concentrations of metabolites, antibiotics and growth promoters encountered in overcrowded "bloom" conditions.

A concept important in understanding phytoplankton ecology is that of "physiological state" Raymont 1963). Essentially, physiological state of any one group of diatoms is directly affected by their environmental history. If grown under a specific light, temperature and nutrient regime, this will affect future optimum growth, reproduction and assimilatory rates and tolerances.

LIMITING NUTRIENTS

The concept of limiting nutrients began with agricultural research dealing with crop yield. Liebig's Law or the law of minimums, as it was called, is a principle whereupon nutrients must be available at a critical minimum level at which a plant can continue to grow and produce to its fullest capacity. Below this level, the organism will be unable to function at its peak. Trace elements, required in only minute amounts e.g. boron, and copper, were found to be the major limiting nutrients (Odum, 1958).

With the addition of increased amounts of nutrients *via* applied fertilizers, it must be remembered that by not increasing all the required nutrients, upsetting the ratio of those normally available, one or more may instead be limiting. The controversy concerning limit'ng nutrients be it carbon, nitrogen or phosphorus has not been solved, except for specific cases. Phosphates and nitrates have been held as the culprits for eutrophication of lakes, streams, and inshore marine waters. Limitations on the amounts of available phosphates used in making detergents have been established as a method of nutrient management.

Schindler(1971) attempted to determine if carbon was limiting in a Canadian Shield lake. He assumed phosphorus was limiting, and in the course of the experiment fertilized the lake. Before the addition of nitrogen and phosphorus to the lake, the initial CO_2 level was lower than after fertilization. It was assumed that carbon was not limiting, as the primary production had increased without the addition of any carbon source. Schindler(1971) decided that CO_2 was available from the air. He suggests that, although both nitrogen and phosphorus were added to the oligotrophic lake to increase primary productivity, phosphorus is the primary limiting nutrient based on evidence from tube experiments, where those tubes not fertilized with phosphorus showed no response or increase. The tube experiments were done within the previously fertilized lake.

Ryther and Dunstan(1971) who studied nutrient levels of the New York Bight and adjacent area (including Great South Bay and Moriches Bay) found nitrogen to be the limiting nutrient. As they took samples farther from the Hudson River mouth region, nitrate levels dropped markedly, while phosphates remained more or less the same. In an earlier study (Ryther, 1954) algal populations in Great South Bay and Moriches Bay were nitrogen limited, the nitrogen having been previously consumed or depleted by algae growing upstream in the tributaries adjacent to the duck farms' waste outfalls. This seems to be similar to the data from the New York Bight. In both cases, nitrogen levels drop with distance from the source of the nutrient input.

Phosphate levels are in excess of those of nitrogen. The P:N ratio is upset. Their comparison of Skeletonema costatum takes water samples from the already enriched waters of the bight and then further enriches these samples with phosphate and nitrate, respectively, plus an "unenriched" sample, shows that for these samples, nitrate sources (in this case ammonium ion) could increase the the growth of S. costatum. They suggest that the "normal" N:P ratio of 10:1 or 15:1 was upset by the overabundance of phosphorus and that therefore nitrogen became the limiting factor in the absolute sense

Droop(1973) proposes that nutrient limitation should be approached by examining relationships and interrelationships/interactions of all nutrients in the system and correlating these with specific growth rates in steady state systems. Three points should be kept in mind when examining nutrient limitation: 1) uptake is directly dependant on external substrate concentration; 2) growth depends on internal substrate concentration; and 3) in a steady state system, rate of uptake (for a particular species, and in the absence of significant excretion) is the product of specific growth rate and internal substrate concentration. Fuhs(1969) found that external phosphorus concentration was one of the factors determining the uptake rate of phosphorus and consequently the internal or bound phosphorus per cell. Internal phosphorus content of the cell directly affects cell composition; any change of the phosphorus levels within the cell alters the distribution of intracellular phosphorus as far as its utilization--structural, functional and storage, as represented by acid-insoluble, acid-soluble and lipid fractions. With external phosphorus supplies restricted, storage fractions within the cell would first be affected, with little effect on growth rate. Continued depletion of the cell's phosphorus would affect the functional fractions, sharply decreasing growth. Further depletion would leave only essential structural fractions involved with cell integrity. No phosphorus would be available for the synthesis of additional structural components (Fuhs, 1969). Just as Likens(1972) admonished workers to examine the aquatic ecosystem as a whole, so must the nutrient system externally and internally be examined. Phytoplankters behave differently from species to species, and in cases from locale to locale, therefore, the individual nutritional behavior of a species should be considered from the perspective of simultaneous internal and external environmental nutrient needs and interactions.

EUTROPHICATION

Eutrophication is the nutrient enrichment of aquatic ecosystems. It should not be considered equivalent to the term "pollution"(Likens,1972), which is determined by the presence of industrial wastes, heavy metals, polychlorinated biphenyls (PCB's) and other chlorinated hydrocarbons. There are two divisions of eutrophic succession: 1) natural, which is slow, perhaps cyclical and may proceed with a geologic time clock; and 2) cultural, accelerated by man's activities, and attitudes, e.g. believing lakes and estuaries to have unlimited capacity to absorb sewage and industrial wastes dumped into them. Margalef(1968) examines the accepted concept of eutrophication and presents a different viewpoint. The classic stance is based on the gradual geologic succession of lake to bog to meadow and finally to forest. Margalef (1968) on the other hand, sees the eutrophic state from an energy standpoint, and considers it to be less "mature" than the oligotrophic counterpart. The eutrophic system is in a constant rate of flux, and no energy equilibrium has been reached toward stability within the system. He approaches the problem of maturity vs eutrophication from an information theory or cybernetics perspective and attempts to get a new look at an old (?) problem. With eutrophic conditions (in lakes) increased nutrient input upsets the established equilibrium leading to increased nutrient levels in solution and causing anaerobic conditions in the hypolimnion. He asserts, based on these effects, that the oligotrophic state is more stable and therefore more mature from an energy point of view.

The estuary is a system naturally high in nutrients. Phytoplankton, zooplankton and larval forms of many animal groups find a good place to live and grow within embayments. Because of the natural "nutrient trap" effect present in estuaries, nutrients sewage effluents, heavy metals, PCB's, chlorinated hydrocarbons and agricultural fertilizers (washed from farmlands into the river drainage) are all equally trapped.

As far as diatoms are affected by nutrient levels, they will, with time, adapt to change with the increases. There are intraspecies variations. Taking the same species from estuarine, nearshore, offshore locales, putting each, separately, under the same steady state conditions, each one will behave differently, with different growth rates and uptake rates, based on their past genetic history (Guillard, 1963). Eppley and Thomas(1969) compared nearshore and oceanic diatom (*Asterionella japonica* and *Chaetoceros gracilis*) nitrogen uptake rates. They found that the coastal *A. japonica* had higher K_s values (for either uptake or growth) than *C. gracilis*, of the open sea. The neritic diatom took more substrate (nitrate in this case) to reach half saturation (K_s= half saturation constant) than did the oceanic diatom. Their data (Eppley and Thomas, 1969) suggest that the neritic diatom would have more efficient uptake at high nutrient levels and the oceanic diatom would have more efficient uptake at low nutrient levels, as they would need to do in their natural environment.

Patrick(1967) sees overall changes of species present -- changes in whole phytoplankton populations growing within the estuary. Diversity decreases with eutrophication. Numbers of individuals tend to increase, where numbers of species incapable of surviving the new nutrient regime and increased turbidity and self-shading drop to those species that can thrive and grow fast enough to win a place in the sun, as it were, by sheer numbers. With eutrophication the phytoplankton population may change entire phylum groups (Patrick, 1967), (e.g. to blue green algae). The algae that will be the dominant group will have the highest growth rate under the new conditions. High growth rate leads to high numbers, provided there is no grazing pressure.

A eutrophic estuary may have a phytoplankton population that is smaller than would be expected for the nutrients available. The question arises, why isn't the nutrient level dropping, or the population growing? There are two reasons for this: 1) grazing pressure may keep diatom populations down to a minimum; 2) toxins (Rohde, 1948, in Fogg, 1965) may keep phytoplankton numbers down. If the reverse is true, where the water is thick with phytoplankton, this may represent forms adapted to high nutrient supply -- these may have outgrown and displaced the native populations. In these cases, perhaps the secondary consumers (grazers) have not been introduced rapidly enough to begin to graze on the primary producers available. The new "eutrophic" species aren't being grazed because the grazers are not available. The primary production becomes "wasted energy", the trophic cycle being short-circuited, since it will mainly go to bacteria until adapted zooplankton or bottom feeders become available.

Nutrient management (tertiary sewage treatment and pollution control) has been suggested and even put into effect as the solution towards solving the eutrophication problem (Jaworski, Lear, Jr., & Villa, Jr., 1972). Studies of the effects of sewage effluents on river phytoplankton (Wager & Schumacher, 1970) found the number of species remained the same downstream from the outfall, but total numbers of organisms had increased, the increase being most pronounced for the greens and blue greens, and the least for the diatoms. The numbers of taxa were typical for productive waters, but not of heavily polluted waters. Should nutrient levels be lowered to pre-eutrophic levels through nutrient management, the phytoplankton populations would gradually shift back to those with more efficient uptake at lower nutrient levels.

CONCLUSION

Estuaries are normally high in nutrients. Past environmental conditions (light, temperature and nutrient levels) affect the physiological state of marine phytoplankton, directly by influencing their abilities to grow and/or adapt to new conditions. Intraspecies variations

result through the adaptation of diatoms to environmental conditions. If estuarine eutrophication proceeds slowly enough, diatom species will adapt to those higher nutrient levels and increased turbidity and self-shading. The diatoms and other algal groups which will succeed in competition for light and space, in a region of overcrowded blooms, will be those that can out-race all the others numerically, those with the highest growth rate. Eutrophic conditions will promote a shift in the species present to those that have more efficient uptake (and therefore faster growth rate) at increased nutrient levels. When measures are put into effect to control the progress of eutrophication (through management of nutrient excesses) the phytoplankton populations will gradually return to species able to efficiently uptake nutrients at the lower levels or concentrations.

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