ESTUARINE MICROPHYTE PRODUCTIVITY

by

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TABLE OF CONTENTS

TABLE AND FIGURES

INTRODUCTION

An estuary is an interface where mixing of river and sea water occurs, often within the confines of an embayment. The abrupt environmental changes between these two environments pose a multiplicity of stresses to the estuarine biota, placing a premium on the ability to adapt to a wide range of conditions.

Few species have sufficient adaptability to meet these conditions and so estuarine species diversity is low (Odum, 1970). Additionally, estuaries are "young" ecosystems in that pioneer species are always present because constant flushing by fresh water and the tides precludes a successional sequence from going to climax. Such "young," low diversity ecosystems are characterized by large standing crops of short lived species (resulting in short nutrient recycling times), and high primary productivity. Table 1 provides some net primary productivity values for various estuaries and other ecosystems. Microphytic net production plus macrophytic net production is often very high in estuaries, albeit less than tropical rain forests and many agricultural crops.

Table 1. Net Primary Production in Different Ecosystems

		Annual Net Production ($gm\ C/m^2$)	Reference
MARINE	**Estuarine Microphytes**		
	Chesapeake Bay	72 (upper bay) 365 (lower bay)	Flemer, 1970
	St. Margaret's Bay	190	Platt, 1971
	Beaufort Channel	113-225	Williams and Murdoch, 1966
	Departure Bay	200	Stephans et al., 1967
	Estuarine and Neritic Macrophytes		
	Zostera	1500 (maximum)	Mann and Chapman, 1975
	Fucus, Ascophyllum	500-1000	Mann and Chapman, 1975
	Open Ocean Microphytes		
	Sargasso Sea	77 (in 1958) 58 (in 1959)	Menzel and Ryther, 1961
	Oregon Coast	43 (outside of Columbia River plume)	Anderson, 1964
	California Coast	11.03	Cushing, 1971
TERRESTRIAL	S. Thailand Rain Forest	2563	Kira, 1975
	C_3 Alfalfa (37° N)	2670	Loomis and Gerakis, 1975
	C_4 Sugar Cane (21° N)	6030	Burr et al., 1957

Estuarine microphyte productivity on a volumetric basis is usually very high, especially during blooms, however on an areal basis may be comparable to adjacent neritic waters due to the shallowness of the photic zone in estuaries (Ryther, 1963; Williams, 1966).

Estuarine microphytes are represented by both benthic and planktonic forms. In the shallow areas of estuaries the benthic microphytes (primarily motile pennate diatoms in temperate latitudes) receive ample light and are the main contributors to microphyte productivity on an areal basis (Leach, 1970). In deeper parts of estuaries planktonic microphytes are the major primary producers. Often the nanoplankton far outweigh the netplankton in terms of productivity (Williams and Murdoch, 1966; Malone, 1971; Van Valkenburg and Flemer, 1974).

This paper is primarily concerned with the ecology and productivity of estuarine planktonic microphytes. A statement by Provasoli (1958) suggests a perspective on how to view the complex interactions influencing microphyte productivity in estuaries:

> . . . the ecology of algae . . . mainly concerned so far with the effect of the abiotic environment on the organism, is finally aligning itself with the realities of ever changing cyclic systems in which the effect of the abiotic environment on organisms, the effect of organisms on the environment, and the interactions of organisms all contribute to the bio-geochemical cycles.

Keeping Provasoli's statement in mind, I discuss, in the first two parts of this paper, the two main limiting factors to estuarine microphyte productivity: 1) nutrients, and 2) light. Then I discuss the effects of temperature and circulation on estuarine microphyte productivity, and end with a discussion of microphyte seasonal productivity cycles in temperate estuaries.

NUTRIENTS

Nutrients find their way into estuaries via land drainage, from deep ocean water brought into estuaries during periods of upwelling, as regenerated nutrients from the decomposition of animal and plant matter, and very often as industrial and residential waste effluent (Ketchum, 1967).

Of the major nutrients required by all phytoplankton, nitrogen and phosphorus are most often limiting (Parsons and Takahashi, 1973), while diatoms require the additional nutrient, silica. Many other nutrients are used only in trace amounts, but nevertheless are required for growth and are often referred to as micronutrients.

Nitrogen

Nitrogen is required by phytoplankton for the biosynthesis of protein, and both inorganic and organic forms are

present in estuaries. Inorganic forms of nitrogen found in estuaries include molecular nitrogen, nitrate, nitrite, and ammonia. In most non-polluted estuaries the molecular nitrogen is unused due to the absence of nitrogen fixing microphyte blue-green algae. The only form of nitrogen directly incorporable into amino acids by the microphytes is the ammonium ion (Falkowski, 1975), and the reduction of other inorganic forms of nitrogen is therefore required prior to usage in cellular anabolism. Reduction takes place within the cell, after transport across the cell well and plasmalemma, and because reduction requires energy it is of little surprise that ammonia is taken up preferentially (Grant et al., 1967; Corner and Davies, 1971; Bates, 1976). Nitrate and ammonia are often the most abundant forms of nitrogen in estuaries and the rate of their uptake may control how fast blooms develop. It has been demonstrated that nitrate and ammonia uptake rates are functions of light intensity and ambient nitrate and ammonia concentrations.

Nitrogen uptake is against a concentration gradient and therefore it is generally accepted that active transport is the mechanism of uptake (Falkowski, 1975). It has been proposed that simple diffusion of nitrate across the cell membrane occurs because the inducible enzyme nitrate reductase might act to maintain low cellular nitrate con-

centrations thus resulting in a positive concentration gradient. However, large disparities between uptake rates and nitrate reductase activity rates make this theory untenable (Eppley and Rogers, 1970). Recently Falkowski (1975) has found a nitrate activated ATPase located in the plasmalemma that functions in active nitrate uptake in six of seven phytoplankton species studied. He suggests that the direct relationship between light intensity and nitrate uptake might result from the fact that the ATP is being supplied by cyclic photophosphorylation. Bates (1976) provided evidence to support this theory when shade adapted algal cells with more chlorophyll-a per cell than sun adapted cells exhibited greater nitrate uptake velocities.

Once the nitrate is within the cell interior its reduction is mediated by the enzyme nitrate reductase and stimulated by increasing light intensity. The hydrogen donor required for nitrate reduction seems to come either directly from photosynthesis (Hattori, 1962) or indirectly from respiration (Grant and Turner, 1969).

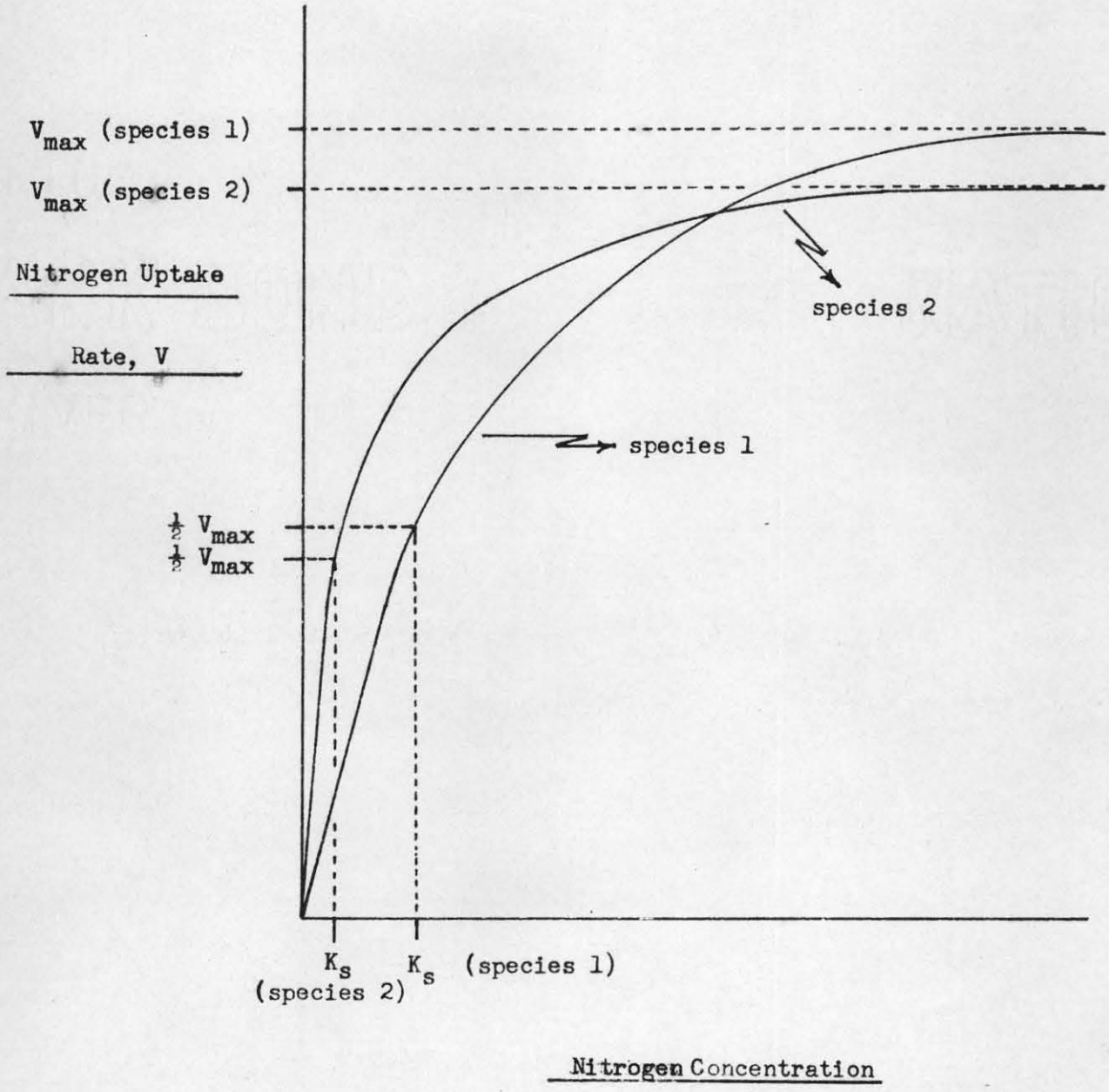
In addition to light intensity, the concentration of nitrate and ammonia influence the rate of their uptake by phytoplankton. Uptake follows Michaelis-Mention enzyme kinetics, i.e., the uptake rate of the nutrient progressively increases at higher nutrient concentrations to a point (V_{max}) where increased nutrient concentration causes

no further increase in uptake rate (MacIsaac and Dugdale, 1969; Caperon et al., 1971). This hyperbolic function is defined by two parameters: V_{max} - the maximum uptake rate, and K_s - the half saturation constant, which is the nutrient concentration that results in an uptake rate one half of the maximum (see Figure 1).

Estuarine phytoplankton inhabit comparatively nitrogen rich waters most of the year. It has been observed (MacIsaac and Dugdale, 1969; Corner and Davies, 1971), that in such environments, the phytoplankton have higher V_{max} and K_s values (species 1 in Figure 1) than do the plankton in more oligotrophic waters (species 2 in Figure 1). Within estuaries, phytoplankton species having higher V_{max} values for nitrogen tend to predominate when nitrogen levels are non-limiting. The greater uptake rate of these species imparts a competitive advantage over those species with lower V_{max} values. When nitrogen concentrations decrease, for example towards the end of a bloom, the phytoplankton species with lower K_s values are able to obtain nitrogen at a greater rate than species having high K_s values and so they now have the advantage (Dugdale, 1967; Corner and Davies, 1971; Paasche, 1973; Guillard et al., 1973).

Hulburt (1970) might dispute this theory of phytoplankton competition in estuaries. He contends that

Figure 1. Nitrogen Uptake vs. Nitrogen Concentration.



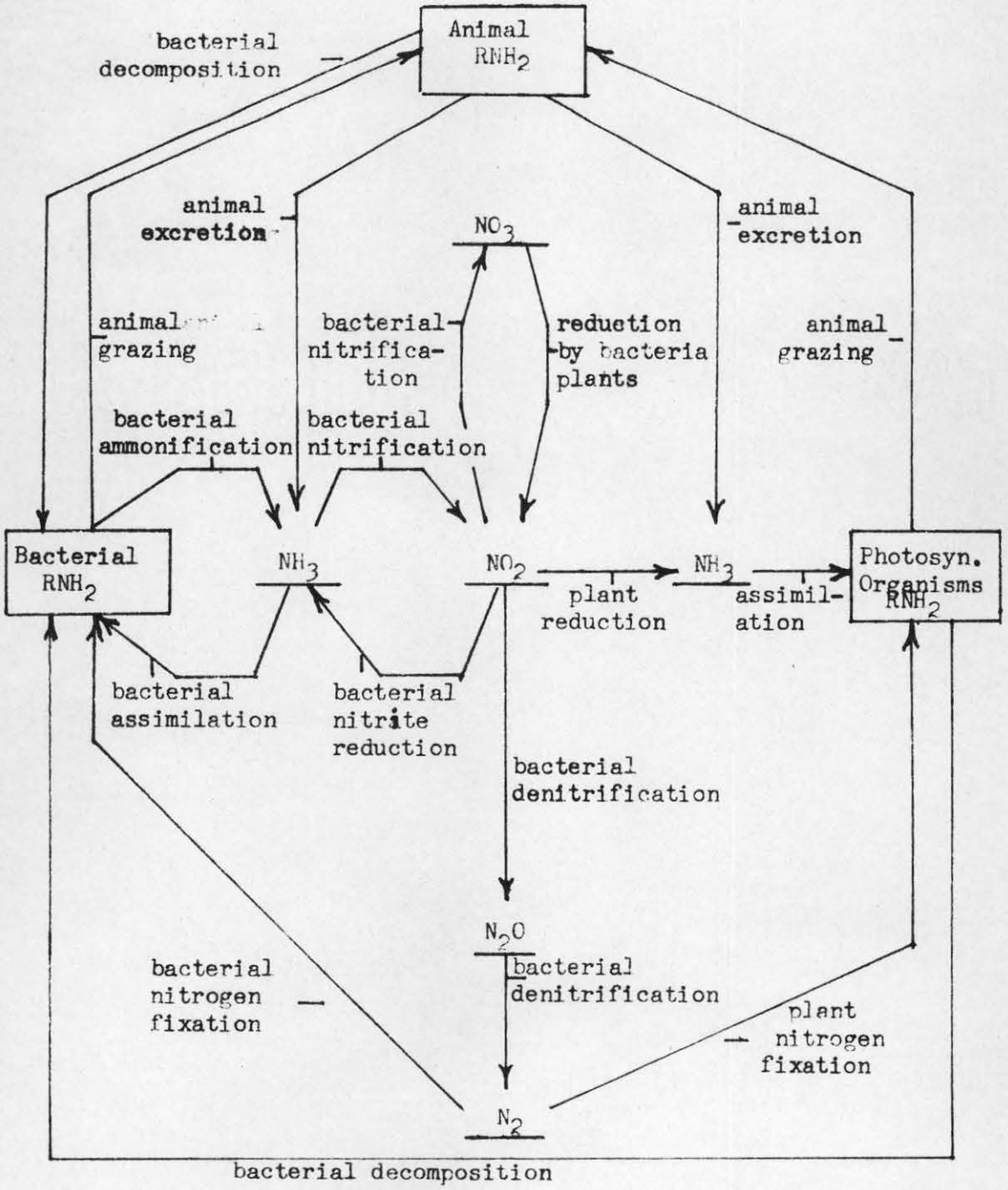
dominance due to competition for nutrients only occurs when cell densities approach 10^9/liter. Only at these densities do the "nutrient spheres" that supply the nutrients to each cell overlap and provide an opportunity for competition to take place. Much more research into phytoplankton competition is needed.

Organic nitrogen is in the form of free amino acids and some heterocyclic compounds such as purine and pyrimidines (Brezonik, 1972). The amino acids are the most important form of organic nitrogen in microphyte nutrition. Wheeler et al. (1974) were able to show usage of amino acids at low concentrations in twenty-five species of marine phytoplankton and the uptake rate was increased by nitrogen starvation. Hobbie et al. (1968) measured dissolved free-amino acid flux rates in the York River Estuary and found them to be an average of 1.3% of the surface rate of primary production (i.e., of carbon fixed).

The Estuarine Nitrogen Cycle

Figure 2 is a diagram showing the physiological origins of inorganic nitrogen in the sea. Estuaries are eutrophic environments because of the addition of terrigenous nitrogen, and therefore both regenerated nitrogen and nitrogen from mineral sources are available for assim-

Figure 2. The Physiological Origins of Inorganic Nitrogen in the Sea (modified from Vaccaro and Ryther, 1959).



ilation. Regenerated nitrogen has three sources, that regenerated within the estuary, that regenerated in the rivers, and that brought into the estuary from the coastal water (Riley, 1967). There is a transfer of nitrogen to higher trophic levels via animal grazing on microphytes and to the bacteria during decomposition.

Zooplankton grazing on phytoplankton recycles the nitrogen locked in phytoplankton biomass because the zooplankton excrete ammonia and soluble organic nitrogen as waste products (Vaccaro and Ryther, 1959; McCarthy, 1972). The large zooplankton populations found in estuaries during and shortly after phytoplankton blooms results in the release of phytoplankton-bound nitrogen which may then be utilized by the remaining phytoplankton and thus perpetuate these blooms (Carpenter et al., 1972).

The suspended organic and inorganic particles in estuaries provide a vast substrate for bacterial decomposition (Nelsen, 1947; Darnell, 1967), which contributes to rapid remineralization of organic nitrogen. Estuarine bottom sediments, which are rich in bacteria and often anoxic, play a major role in nitrogen remineralization (Brezonik, 1972).

Because of the fact that estuaries are nutrient traps --due primarily to long water residence times (Ketchum, 1967)--for inorganic and organic nitrogen, and because con-

ditions are suitable for rapid remineralization of organic nitrogen into inorganic nitrogen, it is not surprising that estuaries have high nitrogen levels. Since young ecosystems like estuaries are inhabited by short-lived organisms, only a small fraction of the total nitrogen is locked up in living matter with the majority of the nitrogen being available for incorporation into biomass. As Riley (1967) points out, much more research into the cycling rates of all nutrients in estuaries is needed before a clear picture of estuarine primary productivity cycles can be realized.

Phosphorus

Microphytes utilize phosphorus as a component of nucleic acids and as high energy compounds within the cell. It is a required nutrient, and both organic and inorganic phosphorus are present in estuarine water in dissolved, colloidal, and particulate forms (Kramer et al., 1972).

Dissolved inorganic phosphorus as orthophosphate, and dissolved organic phosphorus are used by marine microphytes (Chu, 1946). However, phosphatase enzymes are required for dissolved organic phosphorus utilization by phytoplankton, and the synthesis of these enzymes is stimulated only by low orthophosphate levels (Chu, 1946; Kuenzler and

Perras, 1965; Perry, 1976), a condition unlikely in estuaries much of the year. When orthophosphate is depleted, phytoplankton continue to grow, suggesting that they have the ability to store orthophosphate (Pomeroy et al., 1963; Corner and Davies, 1971).

Phosphate uptake by microphytes is hyperbolic with respect to external and internal phosphate concentrations, and is described by Michaelis-Menton enzyme kinetics (Rhee, 1973). Rhee (1973) postulates that the inhibition of phosphate uptake at high phosphate concentrations (which he observed for the freshwater green alga Scenedesmus sp.) is due to the inactivation of uptake sites as the internal phosphate store accumulates. An internal phosphate store--probably inorganic polyphosphate (Harold, 1966)--attaches to the enzyme-substrate complex after transport across the cell membrane, thus inactivating it and making it unavailable for further transport. The inhibition of phosphate uptake with increasing cellular concentrations of polyphosphate was not observed by Perry (1976) for Thalassiosira pseudonana.

The larger nitrate and ammonia half saturation constants (K_s) observed in microphytes under eutrophic conditions over those observed under oligotrophic conditions (MacIsaac and Dugdale, 1969; Corner and Davies, 1971) has not been conclusively established for phosphorus. For

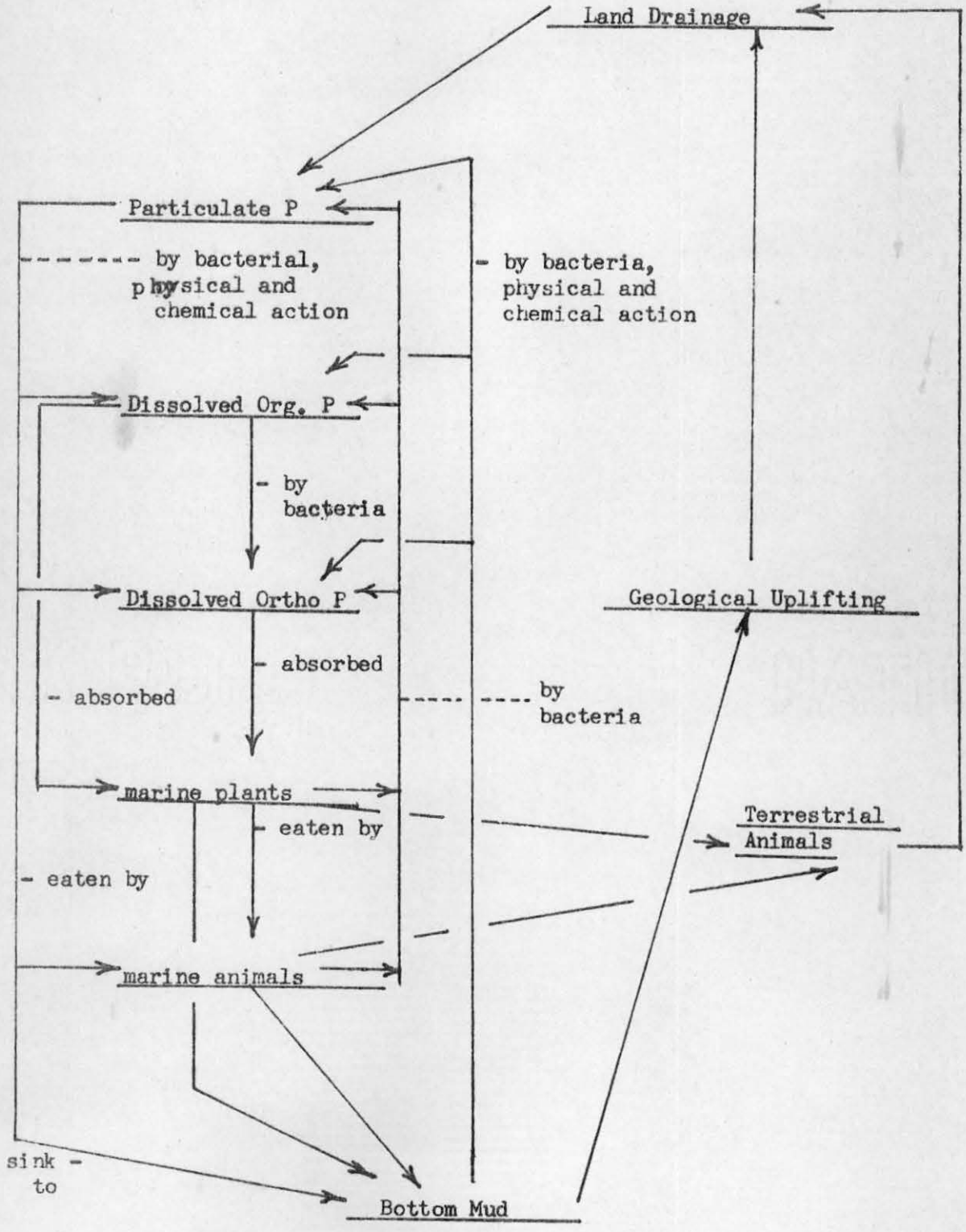
example, Perry (1976) found no significant difference in K_s values between two clones of Thalassiosira pseudonana, one neritic and the other oceanic. However, he did find that the maximal uptake rate of phosphate (V_{max}) increased in phosphate-limited cultures over that in non-phosphate-limited cultures.

The Estuarine Phosphorus Cycle

The marine phosphorus cycle is illustrated in Figure 3. It is important to again note that estuaries benefit from terrigenous phosphorus input in addition to regenerated phosphorus.

One of the major differences between the oceanic and estuarine phosphorus cycles is the role of bottom mud in acting as a phosphorus sink. As dead matter sinks down through the water column in the ocean organic and inorganic phosphorus is released by the process of decomposition. These nutrients are lost in the deep ocean water and bottom sediments, however, they may later be brought to the photic zone during upwelling or destruction of the seasonal thermocline. The phosphorus exchange rate between the ocean floor and water in the photic zone is very low. Estuarine sediments are subject to frequent resuspension and consequently there is much more phosphorus exchange between the sediments and the overlying water. Jitts

Figure 3. The Marine Phosphorus Cycle (from Chu , 1946).



(1959) studied phosphate exchange between the muds and the overlying water of the Swan River, Derth, Estuary and the Georges River Estuary. He found that the impact of well oxygenated fresh water caused the estuarine mud to adsorb phosphate. This caused a depletion in the phosphate content of the water. The fact that Jitts (1959) found an inverse relationship between phosphate adsorption and particle size suggests some kind of surface activity. This view is further supported by the observation that decreased phosphate adsorption occurs in silts high in organic content, probably because the organic matter tends to bind together the silt particles, thus decreasing surface area.

Pomery et al. (1965) studied the Doboy Sound in Georgia and established that phosphate adsorption was in two phases: a non-biological fast uptake phase involving ion exchange, and a slower biological phase in which microorganisms mediated phosphate exchange between the sediments and the interstitial water. They concluded that the degree of adsorption and exchange is determined by the depth of water circulation within the sediments.

Phosphate precipitation and its subsequent loss to the sediments is promoted by high levels of Iron III in the oxidized sediments of well mixed estuaries (Jitts, 1959). As long as oxidizing conditions prevail insoluble ferric phosphates remain highly concentrated in the sediments.

When reducing conditions occur ferric iron is reduced to ferrous iron with the subsequent liberation of the phosphate ion.

Bray et al. (1973) found that the upper 20 cm of Chesapeake Bay bottom sediments contain ten times more phosphate than the overlying water column. Pomeroy et al. (1965) claim that during estuarine microphyte blooms, depletion of dissolved phosphate in the water column is correlated with the release of phosphate from the sediments and thus may perpetuate these blooms. The nature of the phosphate equilibrium between sediments and overlying water is not clear. It would seem that the oxidizing conditions and high iron content found in most estuaries would make the release of phosphate from the sediments nearly impossible. The high concentrations of phosphate in estuarine sediments makes disturbance of these sediments a source of massive phosphorus input into estuarine waters (Pomery et al., 1965; Bray et al., 1973), especially if Iron III is unavailable for phosphorus precipitation.

Pomeroy et al. (1963) have shown that zooplankton excrete phosphorus in organic and inorganic forms. Martin (1968) demonstrated phosphorus excretion by zooplankton in Narragansett Bay during times when phytoplankton were scarce, due to the oxidation of phosphate containing lipid storage products which accrued during periods of food

abundance. The excretion of phosphorus compounds by zooplankton is part of the recycling of phosphorus from the water to the phytoplankton, to the zooplankton via grazing, and finally back to the water as zooplankton excretory products.

The exchange of phosphate between bottom sediments and the overlying water, the rapid remineralization of organic phosphate due to the high concentration of bacteria, the rapid hydrolysis of organic phosphorus, and the input of phosphorus via river input, combine to make phosphorus levels in estuaries high throughout the year.

Silica

Diatoms take up silicon in the form of ortho-silicic acid and deposit it in their frustules as hydrated amorphous silica. In temperate regions where diatoms are abundant (Parsons and Takahashi, 1973), silicon can limit diatom populations (Carritt and Goodgal, 1954; Guillard et al., 1973; Thomas and Dodson, 1975).

In natural waters silica occurs in three forms, as a particulate, a colloidal polymer, and as a monomer. Silica will dissolve in natural water up to a concentration determined by the solubility product of the monomer, and subsequent solubilization of the particulate will result in a colloidal polymer being formed. The polymer can depoly-

merize if the concentration of the monomer falls below saturation. River-sea water mixing within estuaries causes increased depolymerization of the colloid. As Okamoto et al. (1957) point out, this is due to the fact that sea water is not saturated with monomeric silicate and when the colloidal riverine silicate encounters these unsaturated conditions depolymerization results.

The behavior of silica in the estuarine environment has been studied by a number of authors (Bien et al., 1958; Stefansson and Richards, 1963; Liss and Spencer, 1970; Wollast and DeBroeu, 1971; Liss and Pointon, 1973; Sholkovitz, 1976). Ambiguity as to whether silica is removed by abiological processes (i.e., flocculation) remains. Boyle et al. (1974) have shown that the studies of Bien et al. (1958), Liss and Spencer (1971), and Wollast and DeBroeu (1971) may be in error and actually show little or no abiological removal. The superior method recently developed by Sholkovitz (1976) to test the behavior of ions in solution as they move through the estuary has shown little abiological removal of silica in four Scottish estuaries (3-6% of the river borne silica). He attributes this to the fact that silica does not form a complex with humic acids as do many trace metals, and thus is not removed when the humic acid-ion complex is flocculated.

The diatom population in an estuary may take up such

large amounts of silicate that growth becomes silicate limited. Platt and Subba Rao (1970) determined average silicate uptake rates during a diatom bloom in St. Margaret's Bay, Nova Scotia, during the exponential and stationary phases of the bloom. The mean value, derived from the slopes of the regressions of bloom age and silica concentration, was 15.3 mg--at $Si/m^2/day$.

Estuarine diatoms have higher silica concentrations per cell than do oceanic forms and the uptake of silicate by the estuarine diatoms is greater at high silicate concentrations than by oceanic forms. Guillard et al. (1973) showed that an estuarine clone of Thalassiosira pseudonana (from Moriches Bay, New York) had a half saturation constant for silicate 5.15 times that of a clone from the Sargasso Sea, and that each clone apparently increased the amount of silica per cell when initial silica concentrations were increased. These authors also found that the maximum growth rate of the estuarine clone was 2.9-4.4 doublings per day (95% confidence limits), while the clone from the Sargasso Sea had a maximum growth rate of 2.0-2.3 doublings per day.

The slow regeneration of silica from estuarine sediments by simple diffusion of interstitial water rich in silicate (from frustule dissolution) into the estuarine water column (Liss and Spencer, 1970; Wollast

and DeBroeu, 1971) combined with high silicate uptake rates by estuarine diatoms can quickly deplete available silica. The low silicate concentration subsequent to a diatom bloom can lead to the emergence of microphytes not requiring silicate or those able to reproduce faster under low silicate concentrations (Guillard et al., 1973; Paasche, 1973; Thomas and Dodson, 1975). This is assuming that other nutrients are in adequate supply.

Micronutrients and Growth Factors

Micronutrients are those elements essential to microphytic growth but needed only in small quantities while growth factors enhance growth but are not required by all microphytes.

Biotin, thiamine (vitamin B_1), and cobalamin (vitamin B_{12}) are generally considered to be growth factors (Provasoli, 1963). Many estuarine microphyte species are auxotrophs for one, two, or all of these (Vishniac and Riley, 1961). Much of the data on growth factors comes from the development of algal culture media, and the bulk of the field work has been on cobalamin. Therefore, cobalamin will be briefly discussed here.

Cobalamin is produced by free living bacteria, and by those living epiphytically on macroalgae (Karlstrom et al., 1960; Curl, 1962), as well as by non-auxotrophic algae

through exudation and release upon decay. Because of the very low requirement for cobalamin by cobalamin auxotrophs --each 10^{-9} grams supports 800,000 cells of the euryhaline species Monochrysis lutheri (Droop, 1957)--cobalamin seems never to be limiting in estuaries (Droop, 1957). All of the auxotrophic diatoms of the Sargasso Sea are absent during the period of low cobalamin concentration and only occur when cobalamin levels are $0.06\text{-}0.1 \times 10^{-9}$ grams (Menzel and Spaeth, 1962). This is evidence for the ability of low cobalamin levels to limit oceanic cobalamin auxotrophs.

Fe, Mn, Cu, Zn, Mo, Co, B, Na, and Cl are required by microphytes as micronutrients. The transport of these micronutrients to the oceans via estuaries is by ions in solution, ions in the crystal lattice of sediments, ions adsorbed onto the surface of sediments, and ions associated with organic matter (Kharkar et al., 1968).

Most micronutrients are non-limiting in estuaries and in neritic waters. However, the availability of the trace metal micronutrients are important, and so the role of organic chelators is important.

Organic Chelators in Estuaries

Humic acids (fulvic, humic, and hymatomelonic acids) are natural chelators derived from soil and marsh leachates,

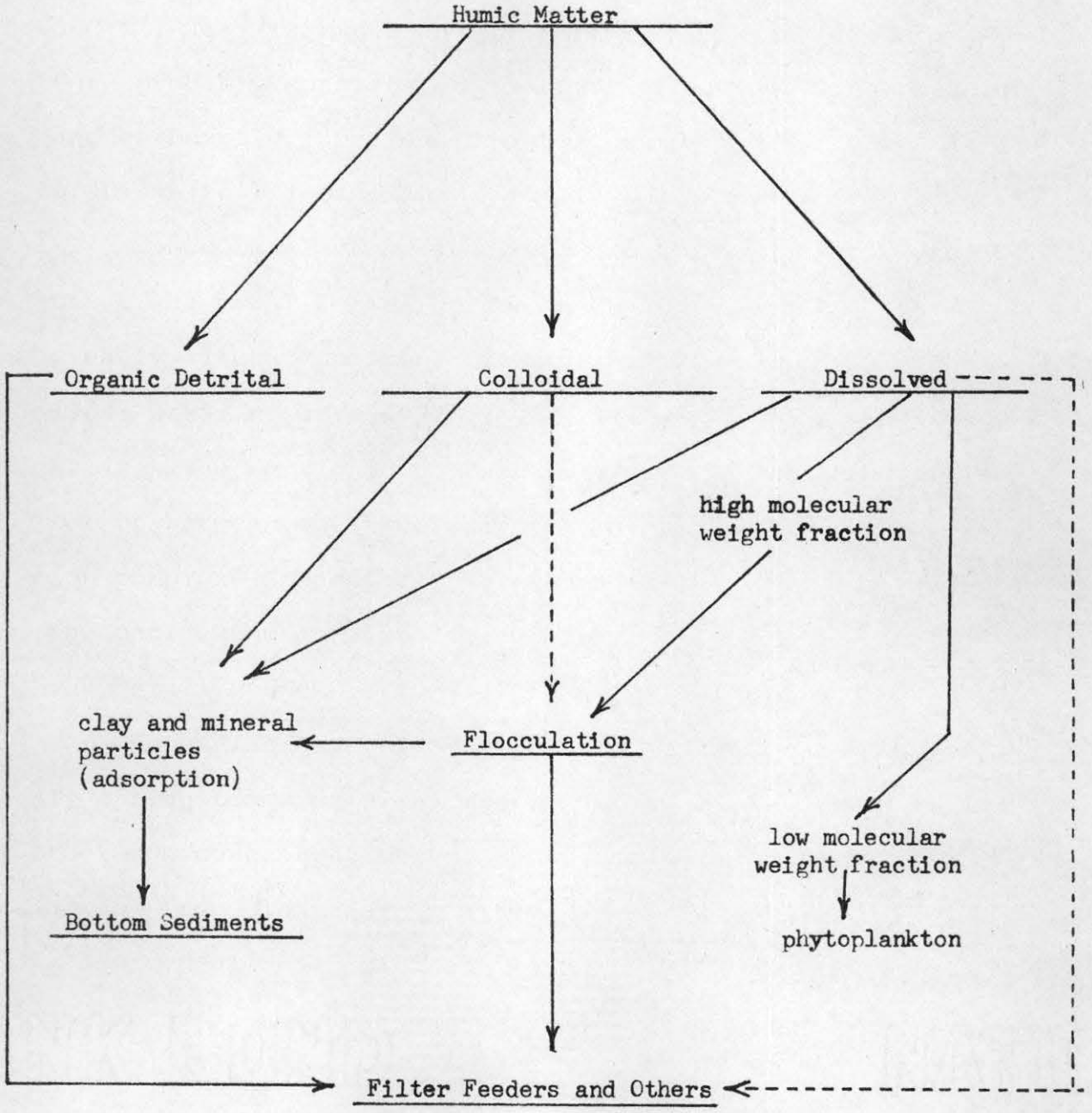
plant decomposition products, and exudates of brown algae (Prakash, 1971; Sieburth and Jensen, 1968). The composition of these natural organic chelators is varied and have the empirical formula of C(50-60%), O(30-40%), H(4-6%), and N(1-4%) (Tschapek and Wasowski, 1976), and their structure probably consists of an aromatic nucleus with phenolic and carboxylic functional groups in a polyanionic configuration (Phillips, 1972).

Trace metal chelation occurs when the chelator and the trace metal form a molecular ring structure which greatly alters the properties of the metal ion (Johnston, 1964; Desai et al., 1972). The chelator effectively solubilizes the particulate trace metal and an equilibrium is set up between the free trace metal ions and the celator-ion complex (Spencer, 1957). Microphytes either metabolize the entire complex liberating the metal ions, or use the very small concentrations of free metal ions.

Estuaries have high humic acid concentrations especially during times of high river discharge. In addition to the high concentrations of terrigenous humic acids, humic acids from plant decomposition products and algal exudates also accumulates. High concentration of these natural chelators assure an abundant supply of trace metals in forms usable by the microphyte populations.

Figure 4 shows the fate of terrigenous humic matter

Figure 4. Fate of Terrigenous Humic Matter in Inshore Water (from Prakash, 1971).



in estuarine waters. Input is primarily through fresh water drainage. Periods of heavy rainfall that result in soil erosion can literally inundate an estuary with humic substances (Phillips, 1972). During such periods estuarine waters often appear slightly yellow and this has led to calling humic substances "gelbstoff." Prakash (1971) points out that red tides are often preceded by heavy rain. The humic acid chelators introduced when the rains cause massive soil erosion keep trace metals abundant which, along with increased vitamin concentration from the soil, helps maintain the exponential growth of the dino-flagellates.

Flocculation and adsorption are probably the major means of removal of humic acids in estuaries (Sholkovitz, 1976). When the chelator-ion complex is flocculated the trace metal is lost to the sediments and this process partially accounts for the non-conservative behavior of many trace metals in estuaries (Sholkovitz, 1976; Eckert and Sholkovitz, 1976). Sholkovitz (1976) studied four Scottish estuaries supplied by rivers which drained peat soils and were therefore high in humic acids. Ninety-eight-115% of the Fe, 10-70% of the Al, and 90-100% of the Mn were removed from the river water due to the flocculation of the humic acid-ion complex. Values of greater than 100% were obtained when the concentration of the

element in the flocculant exceeded that of the river water. This is possible when sea water contributes to flocculant composition.

The low molecular weight fraction of humic acids, between 700 and 1500, stimulates algal growth more than the high molecular weight fraction (Prakash, 1971). The low weight fractions are of terrigenous origin rather than from plant exudates, and therefore tend to predominate in estuaries during high river flow.

High trace metal input into estuaries from rivers and their availability made possible by the chelating action of humic acids are the reasons why microphytic growth is rarely limited by the micronutrients in estuaries, even though large amounts of the trace metals are removed by flocculation and adsorption.

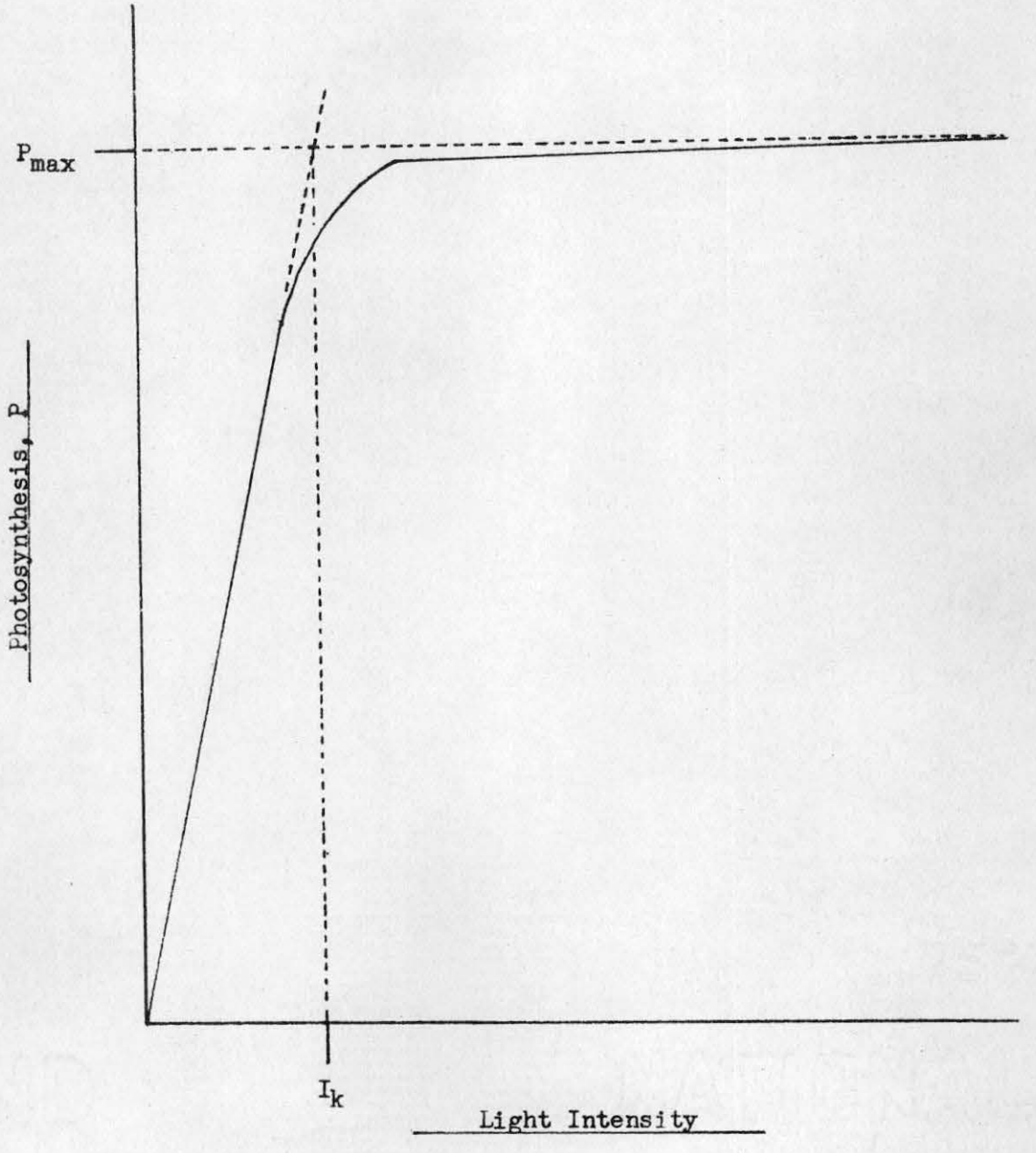
LIGHT

Energy provided by photons striking chlorophyll molecules and accessory pigment molecules causes electrons in P680 chlorophyll-a to escape and enter a cytochrome containing electron transport chain to phosphorylate ADP molecules. Further excitation of these electrons occurs in photosystem I and after passage down another electron transport chain are united with NADP(plus) to form NADPH. Both ATP and NADPH are used in the dark reaction to

synthesize sugar from carbon dioxide.

The rate of photosynthesis varies with light intensity as illustrated in Figure 5. The initial slope of the function is determined by the photochemical reactions of photosynthesis (photosystems II and I). If the slope is steep then photosynthetic activity is high, if the slope is shallow photosynthetic activity is low. P_{max}, the maximum photosynthetic rate, is a function of the enzymatic dependent reactions occurring during the dark reaction, assuming that all requisite substances necessary for the dark reaction to take place are in adequate supply (e.g., CO_2) (Parsons and Takahashi, 1973; Steemann Nielsen, 1974). The value of P_{max} is therefore dependent upon the concentration of the enzymes mediating the reactions and the temperature at which the reactions take place. The intersection of a line at P_{max} and a line tangent to the initial part of the photosynthesis versus light intensity curve determines a light intensity I_k, an important parameter which reveals information about the adaptations of an algal species. A shade adapted algal species will generally have a low I_k value relative to a sun adapted species because its photosynthetic rate is greater at low light levels when measured on a per cell basis. Under these low light conditions the shade adapted alga is more efficient than the sun adapted alga in terms of carbon

Figure 5. Photosynthesis vs. Light Intensity.



fixed per cell per quanta of light because it contains a higher concentration of chlorophyll. At high light intensities the sun adapted species fixes more carbon than the shade adapted species when measured on a per unit dry weight basis (i.e., its P_{max} is greater) because the concentrations of enzymes used in the dark reaction are higher. Thus tropical species adapted to high light intensities tend to have higher I_k values than do temperate species (Strickland, 1958). By computing I_k values from Ryther's (1956) data, it is evident that his mixed culture of dinoflagellates had an I_k value of over twice that of a mixed culture of diatoms. This is further evidence for the adaptation of phytoplankton to their natural environments.

Many species of algae have the ability, within limits, to vary the amount of chlorophyll in their chloroplasts, the shape of their chloroplasts, and the amounts of enzymes governing the dark reaction, all in response to changing light intensities (Brown and Richardson, 1968; Parsons and Takahashi, 1973; Jerlov, 1974). For example, an alga that is adapted to low light levels and is suddenly subjected to high light levels may decrease the size of its chloroplasts and the amount of chlorophyll in its chloroplasts to prevent photooxidation of its photosynthetic elements (Steemann Nielsen, 1952). Cartenoids seem to channel excess light energy absorbed by the pigments but

not used in photosynthesis into harmless pathways as another means to prevent photooxidation during times of high light intensity. These changes affect the shape of the photosynthesis versus light intensity curve. Steemann Nielsen (1974) has shown Chlorella vulgaris to have a higher initial rate of photosynthesis and a lower P_{max} when grown under low light conditions, as compared to a low initial photosynthetic rate and high P_{max} when grown under high light conditions when photosynthesis is measured on a per unit dry weight basis. This indicates that photosynthetic pigments and enzymes increase in concentration when an alga adapts to higher light intensities.

Sun and shade adapted algal populations are separated in time and space by their limited range of adaptability to varying light conditions. In a well mixed estuary little light adaptation occurs due to the short length of time a cell is at a particular light intensity. This contrasts with the open ocean in high latitudes where the seasonal thermocline effectively maintains stable algal populations throughout the photic zone (Steemann Nielsen, 1974).

Light in Estuaries

The amount of light available for photosynthesis by microphytes is governed by the season, the composition of

the atmosphere, the state of the water surface, and the composition of the water itself. How the season affects the amount of light will be discussed in a later section.

The amount of solar radiation reaching the sea surface depends on atmospheric conditions. Scattering and absorption from dust particles, water vapor, and ozone are the main attenuators in the atmosphere (Robinson, 1966; Parsons and Takahashi, 1973). Latitudinal variations in weather patterns significantly influence how much light is attenuated prior to penetrating the water surface.

The light reaching the water surface is either transmitted or reflected and generally the rougher the surface conditions the greater the reflection. This may not be true, however, when the sun is low on the horizon, in which case rough conditions may result in an increase in transmission because the angle of incidence decreases (Cox, 1974). In small estuaries calm conditions usually prevail because wind fetch is insufficient to generate large waves. However, in very large estuaries like Chesapeake Bay, wind fetch is sufficient to produce large waves and their height is limited by depth and wind duration.

Much more important than light reflection by waves in estuaries is the increased turbidity caused by the resuspension of estuarine silts due to the scouring effect of the waves. This increased turbidity greatly increases

the attenuation of the light transmitted through the air-water interface. This light is absorbed selectively according to the equation: $I_d = I_o e^{-kd}$ where I_d is radiant energy at depth d, I_o the radiant energy at the surface, and k the extinction coefficient. The extinction coefficient varies with wavelength and the amount of suspended matter in the water. In estuaries where high turbidities prevail, blue light is scattered and red light is transmitted maximally (Strickland, 1958; Parsons and Takahashi, 1973), i.e., particulates cause short wavelength scattering. Particulates have relatively little effect upon wavelengths greater than 600 nm other than shading effects (Strickland, 1958).

Horizontal variations in turbidity causes horizontal variations in light penetration (Nash, 1947; Postma, 1967). The source of turbidity are sediments from the rivers, the sea, and the estuary itself. The degree of turbidity depends on the state of the tide, tidal height, and river flow (Perkins, 1974). Generally turbidity maximums occur at the fresh-salt water mixing zone where flocculation occurs (Postma, 1967) and at this point light penetration can be minimal. The degree of turbidity has definite effects on phytoplankton productivity by governing the amount and quality of light available for photosynthesis (Perkins, 1974).

Yellow organic matter (humic substances) is a major cause of light absorbance in the blue and ultraviolet regions of the spectrum (Quasim et al., 1968; Kirk, 1976). High concentrations of yellow organic matter in estuarine waters can therefore limit microphyte productivity by light attenuation. The green algae, the diatoms, and the dino-flagellates all have both chlorophyll-a and the carotenoid beta-carotene which have absorbance peaks in the blue region and therefore photosynthesis by these groups can be severely limited by high concentrations of yellow organic matter.

TEMPERATURE

Temperature variation within estuaries is greater than that of the open ocean because estuaries are semi-enclosed, shallow systems that react comparatively rapidly to changes in insolation, sea temperature, and river temperature. For example, the water overlying estuarine mud flats can increase in temperature rapidly because the heat absorbed by the mud is readily transferred to the water (Nelson, 1947). The most rapid water temperature changes occur when the surface to volume ratio is great (Nash, 1947). In such shallow systems periods of upwelling bringing cold water to the surface can significantly reduce estuarine water temperature where tidal exchange is great (Perkins,

1974).

The susceptibility of estuaries to rapid temperature fluctuations affects the microphyte productivity. Temperature affects the maximum photosynthetic rate (P_{max}) of microphytes by controlling the rate of the enzymatic reactions occurring during the dark reaction (Parsons and Takahashi, 1973; Jerlov and Steemann Nielsen, 1974). However, temperature will only be important if light is saturating and nutrients are in adequate supply. These effects are revealed when photosynthetic Q_{10} values of two or more occur. Q_{10} values close to one indicate independence of P_{max} on temperature and either light, nutrients, or both are limiting. Seasonal variation in light intensity (in temperate areas) and nutrient availability may therefore play a role in determining when temperature affects the maximum photosynthetic rate. Williams and Murdoch (1966) found photosynthetic Q_{10} values ranging from 2.3-2.5 in the Beaufort channel and the authors concluded that temperature controls the photosynthetic rate in the channel throughout the year. That temperature has little or no effect on photosynthetic rate in oceanic waters has been attributed by Kirk (1976) to the low nutrient concentrations of oceanic waters. He contrasted this with the temperature regulation in estuaries which often have non-limiting nutrient concentrations.

Williams and Murdoch (1966) have suggested that high temperatures may effect nutrient regeneration rates by increasing the rate of decomposition by bacteria. If temperature dependent nutrient regeneration rates occur then this might help explain the summer peak of productivity found in many estuaries (Ryther, 1963; Williams, 1966). Thus far there has been little work done on the relationship between temperature and nutrient regeneration rates.

ESTUARINE CIRCULATION

Estuarine circulation patterns result from the interactions of tides, winds, river flow, Coriolis force, and the morphology of the estuary. The type of circulation and how vigorous it is influence microphyte numbers and species composition as well as influencing light penetration and nutrient retention. The following is a brief discussion of estuarine circulation types and how they affect microphyte productivity.

The type A estuary is vertically stratified with respect to salinity. The denser sea water lies in a wedge along the bottom, conforming to the progressive decrease in depth upstream. The salt wedge never reaches sea level height because the fresh water flowing over the wedge causes friction at the interface of the two water masses, thus reducing the maximum height. Type A estuaries are

characterized by large fresh water inflows, small tidal ranges, and large depth to width ratios. The only mixing of the two water masses is by advection at their interface.

Type B estuaries are also stratified but less so than type A estuaries. The slight mixing occurs because river flow is less and the tidal range greater than in type A estuaries.

Type C estuaries are non-stratified, well mixed systems with large tidal ranges, small river inflows, and small depth to width ratios. Coriolis force acts to produce a lateral salinity gradient.

A lateral salinity gradient is non-existent in the vertically homogeneous type D estuary. The complete mixing which occurs in type D estuaries is due to large tidal ranges, high tidal velocities, and small river inflows. These conditions often result in tidal overmixing such as that which occurs in Coos Bay, Oregon (Burt and Queen, 1957). Here, during ebb tide the estuary is vertically homogeneous and because the flood tide velocity often exceeds six knots, the more saline water flows over the less saline low tide water, which remains fairly stationary because of friction with the bottom. Eventually, upstream, or when flood tide velocities decrease, the density inversion breaks down and complete mixing of the water masses occurs.

The theoretical framework of how estuarine circulation patterns influence plankton populations was developed by Ketchum (1954) and the author was unable to find recent literature addressing this subject. What follows, then, is an iteration of Ketchum's ideas and some of the author's own observations.

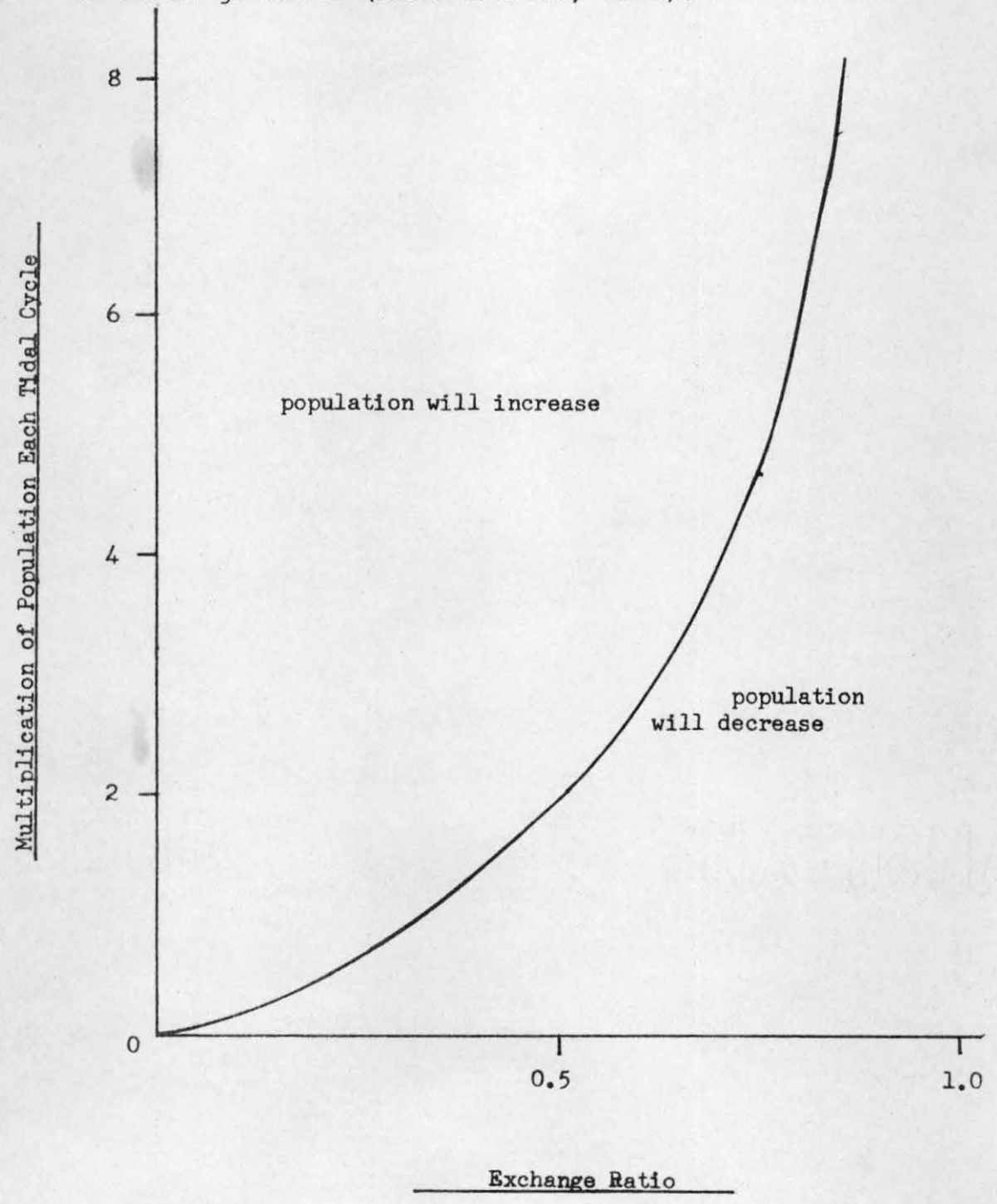
The microphyte populations in estuaries are either endemic (i.e., without recruits from either the river or the sea) or augmented with recruits. The nature of the microphyte populations depends to a large extent upon the exchange ratio of the estuary (Ketchum, 1954), defined as the fraction of the high tide volume permanently replaced each tidal cycle. This value is a function of the tidal range and the water depth. Each part of the estuary has a unique exchange ratio owing to varying tidal amplitudes and water depths throughout the estuary, and the exchange ratio for the estuary as a whole is obtained by integrating the individual exchange ratios. Estuaries with large exchange ratios tend to have microphyte populations similar to the adjacent ocean waters (i.e., a high level of recruitment from the ocean) while those with small exchange ratios tend to have endemic populations (Ketchum, 1954; Ryther, 1954; Perkins, 1974). However, it seems likely that in estuaries with high overall exchange ratios, there occur pockets where exchange is low and endemic populations

might be established.

Endemic populations must have a reproductive rate that balances losses occurring from circulation, death, and grazing by zooplankton. Figure 6 from Ketchum (1954) shows what multiplication rate must be maintained to balance losses due to circulation alone. The curve would be shifted to the left if losses due to death and grazing were taken into account. The curve is probably strictly applicable only to type C and D estuaries because the microphyte populations tend to be evenly distributed throughout the water column due to vigorous mixing. However, in stratified estuaries endemic populations which inhabit the less stable uppermost layer would have to reproduce faster than indicated in Figure 6 because this layer is more rapidly lost from the estuary than the exchange ratio would indicate. Those endemic populations inhabiting the lower more saline layer need not reproduce to the degree indicated by Figure 6 because this layer is not lost to the sea at the rate the upper layer is, and in fact type A estuaries often have a countercurrent within the salt wedge which carries suspended material upstream.

Non-endemic estuarine microphyte populations, (i.e., those that receive recruits from outside of the estuary) are termed temporary autochthonous, and are made up of two components. The estuarine component consists of the

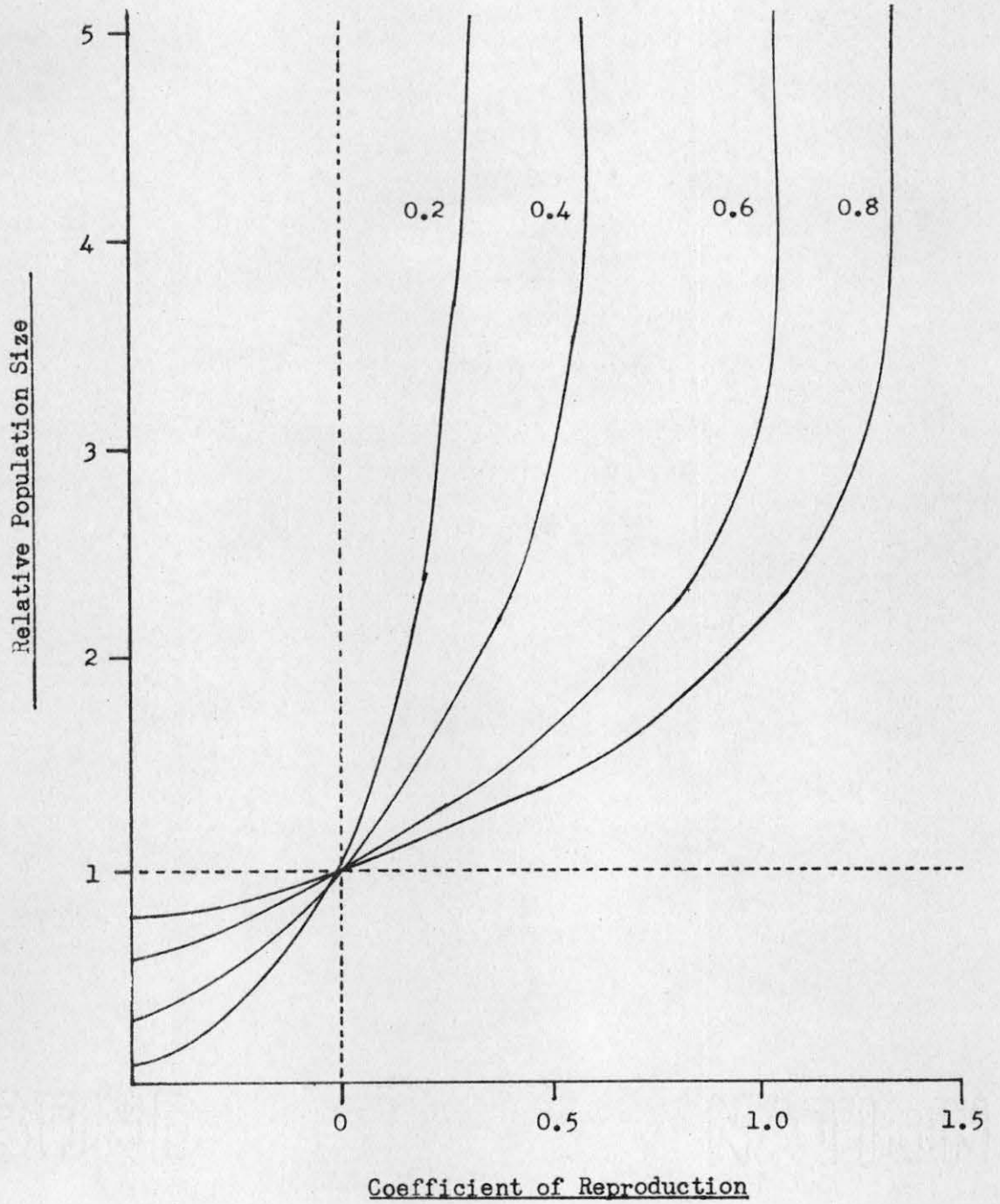
Figure 6. Multiplication of Population Required to Maintain Steady State, Endemic Population as a Function of Exchange Ratio (from Ketchum, 1954).



population pool inhabiting the estuary, and the recruit component is the segment of the population being carried into the estuary by the tides or by river flow. The recruit population then augments the already present estuarine component of the population. If the reproductive rate of the estuarine component is zero then its population level will be equal to the level of augmentation by the recruits. Any positive reproductive rate by the estuarine component will result in a steady increase in the estuarine population pool. Even when the reproductive rate of the estuarine component is negative a steady state estuarine population results due to continuous recruit augmentation, albeit lower than with a positive or zero reproductive rate.

Figure 7 illustrates the relative population size of the estuarine segment of a non-endemic population versus the coefficient of reproduction of the estuarine component for various exchange ratios. All of the curves intersect at a coefficient of reproduction of zero and a relative population size of one which indicates that the estuarine component population size is the same as the augmenting recruit population being introduced during each tidal cycle. When the coefficient of reproduction of the estuarine component is positive, higher population levels occur in low exchange ratio estuaries than in high exchange ratio estuaries. High exchange ratio estuaries with negative estuarine

Figure 7. Population Size vs. Coefficient of Reproduction for Various Exchange Ratios (from Ketchum, 1954).



component reproductive rates will have higher population levels than in low exchange ratio estuaries because the estuarine component population is present in the high exchange ratio estuary for a shorter period of time and consequently is not so greatly depleted by death.

Estuarine circulation patterns greatly affect the location and the magnitude of turbidity maximums, and thus influence light penetration and photosynthesis. Turbidity maximums will be much more pronounced in stratified estuaries than in well mixed estuaries.

The magnitude of the turbidity maximum depends on the amount of suspended sediment in both the river and the sea, the sediment size, and the strength of the estuarine circulation (Postma, 1967). In stratified estuaries suspended particles in river water may sink into the denser salt wedge and be carried away from the sea by the countercurrent. Vertical mixing can resuspend the particle in the outflowing fresh water. A particle can make a number of these transits before being deposited in the estuary or out at sea (Postma, 1967). This results in an area of maximum turbidity. As Postma (1967) points out, only limited particle sizes will contribute to the turbidity maximum, smaller particles are promptly carried down the estuary in the fresh water layer and larger particles quickly settle out and are not resuspended. The same process applies to particles of marine

origin carried up the estuary in the salt wedge counter-current.

Decreased river flow such as that found in type C and D estuaries suppresses the magnitude of the turbidity maximum because there is no stratification. In such systems flocculation probably removes much of the sediment near the head of the estuary and relatively clear water is found downstream of this zone of flocculation. However, if the estuary is shallow with a strong tidal flow resuspension of sediments occurs, especially at the estuary mouth. Williams and Murdoch (1966) found just such a situation in the Beaufort Channel, and because of the high turbidities productivity on an areal basis was no greater than that found in adjacent neritic waters, even though the productivity at the surface of the estuary was quite high. Strong tidal flow was the reason for high turbidities in the estuarine waters near Sapelo Island, Georgia (Ragotzkie, 1959).

Phytoplankton in the upper layer of stratified estuaries receive light unattenuated by the turbidity maximum. The phytoplankton living in the salt wedge are most likely shade adapted in order to overcome the decreased light levels found there. In many instances, the salt wedge may be well below the compensation point and no net production occurs.

Estuarine circulation patterns influence nutrient

levels. Estuaries with small exchange ratios and long water residence times tend to concentrate nutrients more than estuaries with large exchange ratios and short water residence times. Extreme eutrophication can result if large amounts of sewage are being dumped into the estuary.

Stratified estuaries tend to lose river borne nutrients quickly; however, nutrients may be trapped at the salt-fresh water interface. This occurs when decaying matter is circulated up and down the estuary between the salt wedge in the same way that sediment particles cause the turbidity maximum. Mineralization of organic matter takes place during these transits.

Type C and D estuaries with little river inflow probably rely on nutrients brought by the sea for enrichment and if neritic waters are low in nutrients, such estuaries may be relatively impoverished.

SEASONALITY

Estuaries characteristically have periods of maximal productivity corresponding to periods of reduced limitation by nutrients and light. The following is a generalization of the seasonal cycle of microphyte productivity in temperate estuaries with cognizance that such a generalization is not universally applicable and that the complex interactions of many factors which dictate nutrient and light levels are

still rather poorly understood.

Maximum radiation in the northern hemisphere occurs in December. Minimum radiation occurs during December and June for the two hemispheres, respectively. Monthly variation in solar radiation increases with increasing latitude, both north and south (Kondratyev, 1969). Low estuarine microhpyte productivity values are observed from mid-fall to mid-winter (Riley, 1967) due to the low light levels, and during this period nutrient levels tend to increase because their regeneration exceeds their utilization. The vernal increase in light triggers a spring diatom bloom in many estuaries (Riley, 1967) that may occur anytime from mid-winter to mid-spring. This spring bloom was observed by Mandelli et al. (1970) in the waters of Long Island, New York (40° 30' N), by Stephens et al. (1967) in Departure Bay, British Columbia (49° 35' N), by Platt (1971) in St. Margaret's Bay, Nova Scotia (44° 35' N), and by Pratt (1965) in Narragansett Bay, Rhode Island (41° 38' N). Pratt (1965) and Martin (1965) both contend that the spring bloom of diatoms in Narragansett Bay is triggered by the release of zooplankton grazing pressure, and not by the high vernal light intensities, although this is certainly a requisite.

Spring blooms were absent from Chesapeake Bay (39° N) (Flemer, 1970) and the Beaufort Channel (45° 34' N) (Williams and Murdoch, 1966; Williams, 1966). There was a summer

productivity maximum at these two locations. In the Beaufort Channel there was a high degree of correlation between productivity and water temperature, which is attributed to the postulated increased rate of nutrient regeneration with increasing temperature. The dominant summer forms are the dinoflagellates (Riley, 1967) due primarily to the warmer water temperature.

The cessation of the spring or summer bloom is caused by one or more of the following factors: grazing by zooplankton, depletion of nutrients, or self-regulation due to increased turbidity when cell densities are very high (Riley, 1967). Little documentation of this latter cause can be found. Grazing by zooplankton is probably not as important in terminating estuarine phytoplankton blooms as it is in terminating oceanic phytoplankton blooms (Heinrich, 1962) because the zooplankton are less diverse in estuaries which leads to less stable populations. Williams (1966) concluded that zooplankton grazing was unimportant in controlling the summer phytoplankton bloom in the Beaufort Channel. Heinrich (1962) has shown that in neritic waters the zooplankton bloom lags well behind the phytoplankton bloom, which contrasts with the coincident blooms of oceanic phtyoplankton and zooplankton. Martin (1965) has shown this zooplankton lag in Narragansett Bay. However, Riley (1946) contends that the often inverse relationship between phyto-

plankton and zooplankton abundance is evidence for grazing, there being a lag in exponential growth of the zooplankton upon encountering the rich phytoplankton food source.

The most often observed causal factor terminating spring or summer microphyte blooms is the depletion of one or more nutrients (Riley, 1967). Certainly light levels are high enough during these periods to allow vigorous growth. Spring bloom cessation in Narragansett Bay is caused by the depletion of nitrate and silica (Pratt, 1965). Riley (1967) suggests that the spring diatom bloom in Long Island Sound is terminated by nutrient depletion.

Short, small blooms in autumn are observed in the waters off Long Island (Mandelli et al., 1970), in Narragansett Bay (Pratt, 1965), in Chesapeake Bay (Flemer, 1970). Fairly high productivity levels were observed by Platt (1971) in St. Margaret's Bay. Riley (1967) attributes autumn blooms in temperate estuaries to a slight increase in nutrients due to their greater regeneration rates at the time of the seasonal temperature peak. Riley (1967) found that the autumn bloom in Long Island Sound is caused by a slight increase in nitrate levels and the stability of the water column, which maintains the nutrients and the phytoplankton in the photic zone. The termination of autumn blooms must be due in part to declining light levels.

In summary, estuarine phytoplankton productivity peaks are observed in either spring or summer, and often small blooms develop in autumn. Each estuary is unique and discovering how conditions interact to create blooms necessitates an understanding of the estuarine hydrography--including the turbidity regime, nutrient cycles and supplies, temperature regime, and influence of the continental shelf waters on these variables.

CONCLUSIONS

This paper has reviewed the control of estuarine microphyte productivity by nutrient and light levels. The cycles of nitrogen and phosphorus were reviewed, as well as the role of natural chelators in making available essential trace metals to the microphytes. The role of temperature in primary productivity was discussed, as were estuarine circulation and its effect on nutrient and light levels. Finally, the seasonal cycle of phytoplankton productivity in temperate estuaries was reviewed.

The complex interactions of the many variables influencing microphyte productivity levels in estuaries is still poorly understood. Much more research in a variety of disciplines is required and the following reflects the author's opinion of the important areas needing study:

Physiology

*nutrient uptake mechanisms by microphytes. While some information on inorganic nitrogen uptake is available, not as much has been done on phosphorus uptake or organic nitrogen uptake.

*phytoplankton exudates and zooplankton excretion products --what kind, their levels, their importance.

*the role of organic nutrients in microphyte production.

Ecology

*nutrient cycles.

**the role of benthic invertebrates in nutrient cycles.

**the role of temperature in nutrient cycling rates.

**elucidating other variables controlling cycling rates.

*the role of both zooplankton and benthic organisms in controlling estuarine microphyte population levels.

*the nature of phytoplankton competition.

**more on nutrient uptake rates relating to competition.

*factors influencing microphyte succession in estuaries.

Geology

*sediments and their role in adsorption of nutrients.

*the behavior (conservative or non-conservative) of solutes entering estuaries.

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