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Mechanisms Maintaining High Productivity in Georgia Estuaries

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Abstract

The results of studies of the extensive, unpolluted estuaries at Sapelo Island, Georgia indicate that the following factors are responsible for high productivity: (1) ebb and flow water movements resulting from tidal action, (2) abundant supplies of nutrients, (3) rapid regeneration and conservation of nutrients due to activity of microorganisms and filter feeders, (4) three types of primary production units (marsh grass, benthic algae, and phytoplankton) which insure maximum utilization of light at all seasons, and (5) year-around production with successive crops. These factors are discussed and illustrated by data obtained by various workers at the University of Georgia Marine Institute, Sapelo Island.

INTRODUCTION

ESTUARIES ALONG THE GEORGIA COAST are characterized by a five- to seven-mile-wide complex of water, salt marsh, and small hammocks or islands that lies between the mainland and the sea islands. The salt marsh is irrigated by water moving within a network of sounds, tidal rivers, and tidal creeks. The water is shallow, being for the most part less than 10 meters in depth, and turbid due to suspended detrital material and inorganic solids.

Investigations of these extensive, unpolluted estuaries near Sapelo Island, Georgia, have been continuing since the founding of The University of Georgia Marine Institute in 1953. The Institute is operated with the generous financial support of Richard J. Reynolds through the Sapelo Island Research Foundation. Additional funds have been provided by The University of Georgia, the National Science Foundation, and the Atomic Energy Commission.

This paper is based primarily on the results of studies at Sapelo Island by full-time resident staff members and by staff members and graduate students from the University of Georgia and other campuses. The role of tidal marshes in estuarine production has been considered previously by Odum (1961).

One inevitable conclusion can be drawn from the results of these investigations. It is that these estuaries are among the most productive natural ecosystems in the world. We now estimate that the primary productivity is 2,000 g of dry organic matter/m²/year or 10 tons of dry organic matter per acre per year

(Odum, 1961). In comparison, this rate of production is of the same order of magnitude as yields obtained from intensively cultivated crops such as rice and sugar cane. Therefore, we ask the question: "Why are these estuaries so productive?"

The productivity of estuaries, as well as the productivity of most ecosystems, is essentially dependent on the rate of primary productivity within the system or, in other words, on the amount of organic material formed as the result of photosynthesis. Thus, just as man is ultimately dependent on green plants for his food supply, so are all other heterotrophic organisms dependent on this source of energy. Therefore, the high productivity of estuaries is really a function of the rate of plant growth.

What we will consider today are five factors enabling a high rate of plant growth and consequently high productivity to be maintained.

RESULTS

Three Primary Production Units

The first factor considered is that organic material is being synthesized by three types of primary production units. These are *Spartina alterniflora,* (cord grass), benthic or "mud" algae, and phytoplankton. Each of these production units occupies a different zone within the estuary so that available light and nutrients are utilized efficiently. *Spartina* is a rooted aquatic plant growing in the intertidal zone; "mud" algae, primarily diatoms, are also found in the intertidal zone on the mud; and phytoplankton are the microscopic plants suspended in the water. Mud algae and *Spartina* photosynthesize at low tide when the intertidal zone is not covered by water. Therefore, carbon is fixed during the daylight hours over the entire estuary which includes both salt marsh and water.

Spartina, in terms of amount of organic material fixed and surface area covered, is the most important primary producer accounting for two-thirds to three-fourths of the primary production in the estuary while the mud algae contribute one-fourth to one-third. Previously, the contribution of phytoplankton was considered to be less than ten per cent.

However, recent studies by one of us (CLS) have shown that the phytoplankton may be much more important. On three days in August, the net rate of primary production by phytoplankton averaged 0.25 g $C/m^2/hr$ (Figure 1). Assuming that this rate was maintained for only 10 hours each day and that the organic material produced was 50 per cent carbon, the amount of dry organic material produced was 5.0 $g/m^2/day$. At this rate, the annual phytoplankton production would be 9 tons dry organic matter/acre.

The annual estimate is probably too high for two reasons. First, a daily rate of 5.0 gm is probably not maintained during cooler portions of the year. But additional measurements for last summer, using both carbon-14 and oxygen methods, indicate that the 5-gm estimate may be typical of production during summer months. Second, measurements so far have been made in only one tidal creek which is but a small fraction of the total area of the estuary. Thus even though the local intensity of production by phytoplankton is high, the amount of production may not be so great when the estuary as a whole is considered. On the other hand, phytoplankton may yet be especially important as a primary producer because the surface area of water exposed to sunlight is increased in the marsh at high tide.

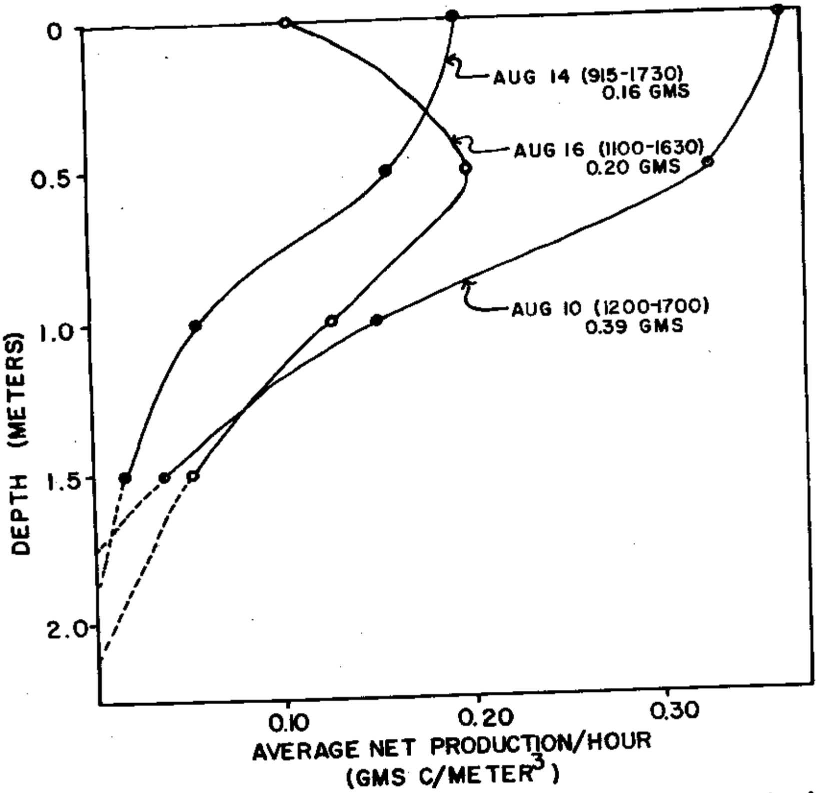

FIGURE 1. Net rate of carbon fixation determined by the oxygen method using a photosynthetic quotient of 1.25. Amount indicated for each date is the net rate of fixation/m^2/hr determined from the area under each of the three photosynthetic profiles.

The surface area at high tide may be from four to five times greater than the area at low tide (Ragotzkie and Bryson, 1955). Phytoplankton production in this water could contribute greatly to the total primary production of the estuary if it is as great as that found in the tidal creeks. As can be seen in Figure 1, most of the carbon is fixed in the upper meter of water.

Tidal Action

Tidal action is the second factor contributing to high productivity that we will consider. We have just noted that it may be an important factor in maintaining high productivity by increasing the surface area under which phytoplankton photosynthesis can occur.

The tidal amplitude at Sapelo Island has a mean range of 6.8 feet and varies from 4.5 to 10.5 feet. The resulting tidal action produces ebb and flood water movements that alternately drain and flood the salt marsh. Water movements are important because, other factors being equal, flowing water is more productive than standing water. The flooding and draining of the marsh are important in that this is the means of transporting material in and out of the marsh. We know for instance that only about five per cent of *Spartina* is consumed "on the stalk" (Smalley, 1959) so that the fate of most of the grass is transformation into detrital material by microorganisms. This detritus is transported by water in the estuary so that it may be utilized by various types of filter feeders. Currents produced by tidal action also maintain particulate material containing nutrients in suspension and transport the material within the estuary.

Abundant Supplies of Nutrients

The third factor contributing to high productivity is abundant supplies of nutrients. A high rate of photosynthesis can be maintained because nutrient supplies are abundant. Photosynthesis by algae is probably limited by factors other than nutrients. Light is undoubtedly an important factor in the extremely turbid waters. If nutrients are limiting any of the primary producers, they are limiting at a very high level of production.

Richard Williams, a graduate student from Harvard University, has been studying the ecology of mud diatoms. He has found that nutrients do not limit growth in the presence of natural water and substrate. Under experimental conditions, in the absence of the mud, growth of the diatoms can be increased by addition of nitrogen to the estuarine water. This also points to the importance of the mud and its associated biota as a source of nutrients. Nitrogen being limiting in the water agrees with results of nutrient enrichment experiments with phytoplankton by one of us (CLS) in that nitrogen addition stimulates growth under the conditions of these experiments.[1]

The abundant nutrient supplies in the estuary are not carried in by fresh-water runoff from the land. Dr. L. R. Pomeroy (personal communication) has measured the phosphorus concentrations of the inflowing Altamaha River and of the estuarine waters. The Altamaha carries only about 0.1 μg atoms per liter of dissolved inorganic phosphorus while the concentration in the estuarine water is 10 to 40 times greater. The estuarine water also has greater quantities of other forms of phosphorus and has a higher concentration of phosphorus than the coastal waters.

Conservation and Rapid Turnover of Nutrients

The fourth factor maintaining high productivity is that, in addition to being abundant, nutrients are not limiting because of their rapid turnover and their conservation in the estuary.

The high concentration of nutrients is not due to stratification which does not occur in our Georgia estuaries. Nutrients, however, may be "trapped" by the vertical mixing of waters of different salinities. Pomeroy (1960) has studied the rate of turnover of phosphorus and has concluded that it is more important in maintaining productivity than the actual concentration. A high rate of turnover means that a single atom of the nutrient can be utilized by organisms many times while a low rate of turnover means that much more nutrient is needed for the same amount of utilization to be realized.

Kuenzler (1961) has shown that the common horse mussel *(Modiolus demissus)*, which is abundant in the marsh, plays an important role in the phosphorus cycle. The mussel is a filter feeder, filtering particulate material from the water and sedimenting most of the particulate material as pseudofeces.

[1]Experiments in which nutrients are added to bottles containing natural estuarine water so that the effect of the nutrients on photosynthetic C^{14} uptake can be determined.

Nutrients and organic material in the pseudofeces remain in the marsh where they are available for estuarine production. Thus the mussel is an important biological agent in the biogeochemical cycling of phosphorus.

Year-Around Production

The final factor contributing to high productivity in estuaries which we will consider is year-around production with successive crops. The marsh grass produces two crops a year. The mud algae maintain a constant rate of production throughout the year in a rather unique manner. During the summer the greatest production takes place when the algae are covered by water, and during the winter the greatest production occurs when the sediments are exposed to direct sunlight (Pomeroy, 1959). Phytoplankton also produces organic matter throughout the year, but at present we have only limited data on the yearly cycle.

DISCUSSION

Data have been presented indicating that estuaries are highly productive. However, this high productivity is based for the most part on the amount of energy fixed in organic material by photosynthetic plants. Unfortunately, this does not tell us anything concerning the fate of this energy. In other words, how much of it is utilized by various components within the ecosystem? It does place an upper limit or indicates the potential for production because the energy flow through the system is governed by the amount of energy fixed during photosynthesis.

We will be able to determine the energy flow and production of the animals in the estuary when more is known about the food habits and energy requirements of the animals and when more is known about the fate of organic material produced during photosynthesis. To do this we will have to learn more about detrital material, as it seems that much of the production is channeled through this type of organic matter.

Several generalizations can be made from what we have already learned. The first of these is concerned with basic research. Even though investigators at Sapelo Island have been free to pursue their own research interests, their results have had practical applications. These practical applications, however, are sometimes difficult to predict in advance.

The second generalization is that the estuarine complex consisting of salt marsh and water should be considered as a single unit. It is the interaction between the salt marsh and the water that makes the estuaries so fertile. We are often asked: "Of what value is the salt marsh?" or "What can be done with all that wasted land?" We can now answer that the salt marsh supplies food for aquatic organisms and that the shrimp and other seafood we eat may well have ultimately been nourished by *Spartina*.

We have seen that nature has produced in the estuary an efficient means of maintaining high productivity. The estuary is fertilized and produces large quantities of organic material without any help from man. Therefore, the third generalization is that we should concentrate our efforts on the utilization of this resource, not on altering it, so that we may harvest more efficiently what is produced naturally. To do this will require more study of estuaries and a change in our way of thinking.

Dr. Odum, in this regard, has proposed that estuarine conservation districts be established so that the production of estuaries can be utilized more efficiently (Odum, 1961).

LITERATURE CITED

KUENZLER, E. J.
1961. Phosphorus budget of a mussel population. Limnol. Oceanog. *6:* 400-415.

ODUM, E. P.
1961. The role of tidal marshes in estuarine production. N.Y. State Conservationist.

RAGOTZKIE, R. A. AND R. A. BRYSON
1955. Hydrography of the Duplin River, Sapelo Island, Georgia. Bull. Mar. Sci. Gulf and Caribbean. *5:* 297-314.

POMEROY, L. R.
1959. Algal productivity in Georgia salt marshes. Limnol. Oceanog. *4:* 386-397.
1960. Residence time of dissolved phosphate in natural waters. Science. *131:* 1731-1732.

SMALLEY, A. E.
1959. The growth cycle of *Spartina* and its relation to the insect populations in the marsh. Proc. Salt Marsh Conf., Mar. Inst., Univ. Georgia. p. 96-100.

Effects of Turbidity on Some Larval and Adult Bivalves

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Abstract

The article is devoted to an analysis of the experiments on effects of turbidity upon larval and adult bivalves. Studies of the American oyster, **Crassostrea virginica,** the larvae of the same species, and of **Venus mercenaria** are emphasized although several other species are also considered. Turbidity was caused by several substances, including natural silt and the clay-like substance, kaolin. Exposures of adult mollusks lasted from three hours to several weeks. Larvae of oysters and clams were grown in different concentrations of turbidity for periods as long as two weeks. Very small quantities of silt, etc., sometimes stimulated normal activities of adult and larval mollusks. This may be due to absorption by particles of suspended materials of toxic substances present in the water and to slight mechanical stimulation of the gills of adults. However, concentrations as small as 0.1 of one gram per liter of water significantly reduced the rate of water pumping and strongly affected the character of shell movements of the adults. Different turbidity-creating substances, when present in the water in the same concentrations, affected the experimental animals in a different degree. Different species of mollusks, their eggs and larvae were affected to different degrees by the same concentrations of the same turbidity-creating substances. Results suggested extension of the studies to sizes and shapes of suspended particles and to determining whether effects are mechanical or chemical. Data indicated that lamellibranchs feed most effectively in relatively clear water.

INTRODUCTION

SINCE OYSTERS, CLAMS, AND MUSSELS are widely distributed and constitute important fisheries, various aspects of their biology have been extensively studied. Baughman's (1947) bibliography of oysters, alone, contains references to thousands of articles devoted to the biology and ecology of these mollusks. Since the appearance of Baughman's review, many new articles have been