Estuarine Productivity

David L. Correll

Pritchard (1967) defined an *estuary* as "a semi-enclosed coastal body of water which has a free connection with the open sea and within which sea water is measurably diluted by fresh water from land drainage." Estuaries are generally believed to be unusually productive. They have a mean primary production of 1,500 g/m^2/year (dry matter) as compared to only 125 for open ocean, 360 for continental shelf waters, 400 for lakes and streams, and 650 for cultivated land (Whitaker and Likens 1975). Not only are estuaries very productive in the trophic level or biological energy flow sense, but they are productive also by virtue of their essential role as spawning and nursery grounds for many migratory species of marine fish and as feeding and resting areas for many species of water birds (Milne and Dunnet 1972).

In this review I will address the following questions.: Which biota enable estuaries to maintain high productivity? What are the mechanisms by which an estuary is able to maintain the environmental conditions favorable to high productivity?

THE PARTICLE PRODUCERS

Estuaries, like all ecosystems, are dependent on the functions of primary production, primary consumption, predation, and decomposition. However, many of the biota are best described as particle producers and particle consumers (or filter feeders). It is difficult to relate these two groups to the traditional primary producer/primary consumer categories. Thus, for example, bacteria serve several roles other than as decomposers. Bacteria break down higher plant materials and scavenge dissolved and particulate organic matter. In the process, bacteria produce high cell populations (particulates). Bacteria also break down large detrital materials into very fine particles, suitable for utilization by filter feeders. Thus, bacteria also play a role as particle producers.

An attempt to diagram the estuarine energy flow pattern is shown in Fig. 1. Instead of the classical trophic level energy or biomass pyramid, this pyramid is composed of three segments (particle pool, particle consumers, and predators), with areas approximating their energy flow rates. A number of important features are built into the diagram to point out problems in our understanding of estuarine, and perhaps other, food chains. Estuarine vascular plants, in general, are not harvested to any great extent by herbivores, but are subjected to microbial breakdown into suspended and dissolved organic matter, producing microbial cells in the process.

A very dilute but important and rapidly metabolized pool of dissolved organic matter is utilized primarily by bacteria. The pool is also replenished with incompletely assimilated organic matter as food is passed along the pyramid toward its apex. Thus, an oyster filter feeding on particles will release pseudofeces, which when subjected to microbial action will yield some dissolved organic matter, some microbial cells, and some residual particles.

Which Primary Producers Are Most Important?

The primary producers of this system are vascular plants and algae. The vascular plants include submerged plants in the shallow open water areas of the estuary, emergent plants in the tidal marshes, and upland plants on the drainage basin of the estuary. The algae include phytoplankton in the open water basin of the estuary, benthic algal thalli in the shallows, and the algal constituents of the periphyton (a microbial community that coats all underwater surfaces in the marshes and shallows).

What are the relative contributions of each of these groups of primary producers to the energetics and food chains of the estuary? A factor which complicates answering this question is the variability of estuaries morphometrically, meteorologically, chemically, and biologically. However, the energy content of organic matter from upland runoff and from tidal marsh exports is quite modest in comparison to the *in situ* photosynthetic activity in the estuary proper.

In the Rhode River, a subestuary of Chesapeake Bay, phytoplankton produced 2,090 g dry wt/m^2/year, whereas upland runoff released only 6 g dry wt/m^2 of estuary per year (Correll 1975). In the Georgia tidal marshes and the adjacent estuarine waters, recent studies of the δ ^{13}C values for various biota and suspended organic particles indicate that tidal marsh animals are feeding on emergent vascular plant detritus (Haines 1976a). They also indicate that the bulk

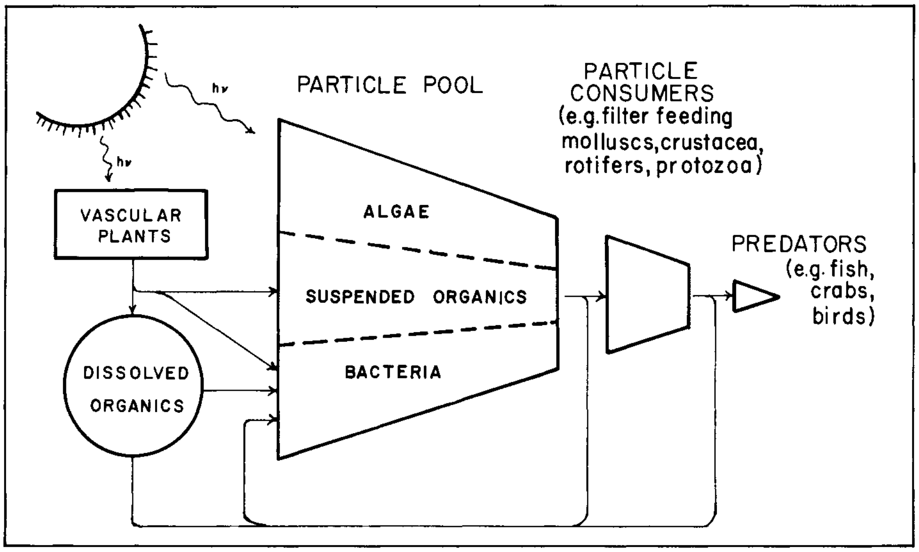

Fig. 1. A schematic representation of the estuarine food web.

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of the suspended organic particles in open estuarine waters is derived from phytoplankton (Haines 1976b).

In two tidal marshes on the York River subestuary of Chesapeake Bay, the export of organic matter was measured directly in monthly, intensive tidal cycle studies. When both tidal flux and chemical composition were measured (Axelrad et al. 1976), these marshes were found to export 227 and 284 g total organic carbon/m^2/year, respectively, to the estuary. In the Patuxent River subestuary of Chesapeake Bay, Heinle and Flemer (1976) found tidal marshes exported only 60 to 135 g dry wt/m^2. Much of this was the result of ice scouring in late winter.

A tidal marsh/mudflat system on the shore of Narragansett Bay was found to export essentially none (less than 1%) of its productivity to Narragansett Bay (Nixon and Oviatt 1973). This system exported only 23.8 g dry wt/m^2 from the tidal marshes to the mudflats and even less to the estuary. Worldwide, estuaries cover between three and four times the area of their associated tidal marshes (Woodwell et al. 1973). Thus, their yield of organic matter to the estuary, per square meter of estuary, is only 25 to 33% of the values quoted above.

These studies indicate that the upland and tidal marsh communities are not as important sources of estuarine organic matter as scientists previously believed them to be. Instead of being very "leaky," these communities have evolved mechanisms to retain and utilize their primary production. This view diverges from a previous one in which the tidal marshes were depicted as providing large amounts of detritus to the estuary and, in effect, were the cause of high estuarine productivity (e.g., Odum and deLaCruz 1967, Teal 1962).

These earlier studies were qualitatively correct; their ballpark estimates for rates of export for organic matter per marsh surface area were reasonable. However, when put in perspective with total estuarine primary productivity, they are a minor contribution. Marine and estuarine fish do use tidal marshes as spawning and nursery grounds and utilize marsh biota. When they return to the estuary, they transport an increment of predator-level biomass, the production of which required approximately 100 times as much primary producer biomass. However, most of the nutrients, carbon, and energy used in their production remained within the tidal marsh community.

If upland drainage and tidal marsh exports are not major sources of energy to the open water basins of estuaries, which sources are important? Undoubtedly, phytoplankton are usually the most important estuarine primary producers in terms of absolute amounts of product. Periphyton, benthic thalloid algae, and submerged vascular plants can only exist in very shallow water in most estuaries, since turbidity limits light penetration to a few meters.

In the Rhode River, periphyton growth rates averaged about 300 g dry wt/m^2/year in favorable shallows as compared to 2,090 for phytoplankton in the estuarine basin (Correll 1975). Submerged vascular plants in the same system are currently not abundant but were of much greater importance as little as 10 years ago (Southwick and Pine 1975). In shallow estuaries, such as Rhode River, these plants carried out in previous times almost as much primary production as phytoplankton do now.[1]

Recent drastic fluctuations and decreases in vascular plant populations have also been reported for the lower Chesapeake (Orth 1976), the Waddenzee (Den Hartog and Polderman 1975), and the Mediterranean coast of France (Peres and Picard 1975). The determination of the causes of this widespread decline in the population of submerged vascular plants is one of the most urgent research problems in the biology of estuaries. In terms of habitat function, these submerged plants form dense beds, which are very important as nursery grounds and protective cover for estuarine animals.

In summary, at the present time the most important primary producers in estuaries seem to be phytoplankton, and submerged vascular plants take an important but secondary role. Periphyton and benthic thalloid algae provide significant amounts of productivity in shallow water areas. In addition, relatively small amounts of organic matter are transferred to the estuary from tidal marshes and uplands.

Which Algae Are Most Important?

To determine which algae are most important, the net productivity of various phytoplankton must be considered. Unfortunately, not many publications have data which directly address this topic in estuaries. In the Rhode River, the distribution of biomass or standing crop between eight commonly occurring classes of algae and two categories of abundant but taxonomically ill-defined algae (the microflagellates and the nanoplankton) was complex and constantly changing (Correll et al. 1975). Dinoflagellates usually dominated the biomass, and the sum of the microflagellate and nanoplankton biomass fluctuated between 1 and 36% of the total. These values were determined by direct microscopy of fixed plankton samples taken over an entire year.

Rates of incorporation of ^{14}C-bicarbonate into the cell structure of various phytoplankton species were determined by autoradiography on the same populations (Faust and Correll 1977). The rates of carbon fixation per biomass, at the species level, varied by one to several orders of magnitude within each population studied, and the higher values were consistently associated with the smaller species. Thus, there is a tendency toward overemphasis on the productivity of the larger species when biomass provides the only data available.

In a one-year study of the phytoplankton of Narragansett Bay, cell counts for various species were done by direct microscopy, and carbon fixation was measured for four size fractions, separated by filtration (Durbin et al. 1975). Chain-forming diatoms of sizes over 20 μm dominated the biomass of spring and fall blooms, whereas flagellates dominated the summer populations. Algae of sizes less than 20 μm were the most important primary producers on an annual basis.

In Chesapeake Bay, nanoplankton of less than 10 μm were reported in one study to be responsible for over 90% of the phytoplankton carbon fixation (McCarthy et al. 1974); in another study they accounted for the great majority of cells and 65–75% of the plankton primary production (Van Valkenburg and Flemer 1974). One reason estuarine productivity is normally high is probably the high algal diversity. As physical and chemical environmental conditions shift, which normally occurs continually in the estuary, various sectors of the population have near optimum conditions and respond with high specific productivity rates.

The Relationship Between Algae and Bacteria

A strong relationship between phytoplankton and planktonic bacteria population dynamics has been observed by

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[1] Charles H. Southwick, Department of Pathobiology, Johns Hopkins University, Baltimore, MD, personal communication, May 1975.

several workers. In a one-year study of the Rhode River, algal and bacterial cell numbers had a high positive correlation (Faust and Correll 1976), and the metabolic activity of algal and bacterial cells also were highly correlated (Faust and Correll 1977). Furthermore, the metabolism and biomass of English Channel algae and bacteria have been found closely correlated (Derenbach et al. 1974). A field and laboratory study of the interactions between algal and bacterial populations in the Schlei Fjord indicated selective positive and negative species interactions (Rieper 1976). Ukeles and Bishop (1975) found evidence that bacteria enhanced algal growth in laboratory cultures by releasing stimulatory substances from substrates.

Bacterial particle productivity is important. Derenbach, Le, and Williams (1974) found this heterotrophic particle productivity to be from 1 to 30% as high as the phytoplankton primary production in the English Channel. Faust and I (1976) found bacterial biomass to vary from 2 to over 100% of the phytoplankton biomass present in the Rhode River estuary.

THE PARTICLE CONSUMERS

The particle consumers include benthic mollusks, zooplankton, larval and juvenile fish and invertebrates, adult filter-feeding fish, and certain benthic invertebrates such as bryozoa and polychaetes. Harvests from Chesapeake Bay in 1971 included 13.6 kg fresh weight/ha/year for oysters and clams and 132 kg/ha/year for members of the filter-feeding shad family (Roberts et al. 1975). In the Patuxent River subestuary of Chesapeake Bay, Heinle (1966) estimated copepod productivity to be about 365 kg/ha/year. Of course, very high values of harvest are sometimes found for concentrated shellfish beds, but the fact that they may feed on particulates from a much larger area must be kept in mind.

Milne and Dunnett (1972) reported a total net production of the mussel *Mytilus edulis* at one station in the Ythan estuary, located 20 km north of Aberdeen on the North Sea, to be 400 kg dry wt/ha/year. Walne (1972) reported harvests of benthic mollusks to vary from 300 to 7,800 kg fresh weight/ha/year for a series of United Kingdom estuaries and concluded that a reasonably productive estuary can yield a harvest of about 100–200 kg dry wt/ha/year of mussels. Berrie (1972) reported a production of 50 to 120 kg dry wt/ha/year for bivalves, 75 to 134 for porifera, and 16 to 37 for bryozoans in the River Thames estuary, for a total benthic particle consumer net productivity of 214 to 233 kg dry wt/ha/year.

These are comparisons of harvest and "production" numbers; harvest by man probably never exceeds half of production in open estuaries. When Milne and Dunnett (1972) analyzed the utilization of mussel net productivity in the Ythan estuary, they found man harvested only 34%, while birds harvested the rest. The net productivity of particle consumers in Chesapeake Bay is probably about 150 to 300 kg dry wt/ha/year, whereas some estuaries in the United Kingdom have net productivities of perhaps double these figures.

How do these particle consumer productivities compare with particle production rates? In the Rhode River estuary, phytoplankton production (2,090 g dry wt/m^2/year) plus bacterial particle production (e.g., 10% of algal) plus upland runoff and tidal marsh "leakage" (approximately 100 g dry wt/m^2/year) plus particulates from submerged vascular plants (approximately 200 g dry wt/m^2/year) total 2.6 kg dry wt/m^2/year or 26,000 kg/ha/year. This is about 100 times our estimate for Chesapeake Bay particle consumer productivity.

However, the Rhode River is probably more productive than most open parts of Chesapeake Bay by a factor of at least two. Furthermore, there is an overlap between particle producer and consumer categories. For example, copepods are particle consumers, which are, in turn, consumed by particle consumers like ctenophores (Roberts et al. 1975) or menhaden (McHugh 1967).

THE PREDATORS

The most clearcut predators in estuaries are aquatic birds, some of the finfish, and some species of crabs. Of course, most predatory species are really somewhat omnivorous, especially under duress. In their study of the Ythan estuary, Milne and Dunnet (1972) conducted an extensive predator investigation and found 53 species of bird and 22 species of fish predators. They found that of the net production of mussels, eider consumed 21%; oyster catchers, 13%; and gulls, 16%. They reported the following average annual biomass of predators (in kg fresh wt/ha): redshank, 0.3; turnstone, 0.04; shelduck, 0.5; eider, 10; flounder, 125; gobies, 3. These standing crops of predator total about 14 kg dry wt/ha. Net productivity values were probably of the same magnitude as the average annual standing crops.

In Chesapeake Bay in 1971 (Roberts et al. 1975), nonfilter-feeding finfish harvests were 8.2 kg fresh wt/ha, and blue crabs *(Callinectes sapidus)* were 32 kg fresh wt/ha, for a total commercial harvest of about 4 kg dry wt/ha/year. These values must be revised upward to 8-12 to adjust from harvest to net production, and they do not include the production of waterfowl, herons, etc.

Berrie (1972) reported predatory fish gross production (bleak and roach) in the River Thames estuary to be 120 kg dry wt/ha/year. Most of this production was by fish of less than one year age, with less than 1% of the population weighing over 20 g fresh weight. The production of fish over one year old was 36 kg dry wt/ha/year.

No careful, quantitative bird predation studies have been reported for the River Thames or Chesapeake Bay. Thus, estuarine predator net productivity seems to vary from 10 to possibly as much as 50 kg dry wt/ha/year.

MECHANISMS FOR MAINTAINING HIGH PRODUCTIVITY

If, normally, most (80–90%) of the photosynthate is due to the *in situ* primary production of phytoplankton and submerged vascular plants, what are the conditions that allow such high *in situ* primary productivity? One factor is the presence of favorable levels and suitable ratios of all the necessary plant growth nutrients. The seawater that mixes into the estuary to create brackish conditions contains more than adequate levels of such plant nutrients as calcium, magnesium, sulfur, potassium, and trace elements. Normally, fixed nitrogen and phosphorus are the two limiting nutrient factors in seawater. Runoff from estuarine watersheds is relatively rich in these two nutrients and creates a gradient from high to low concentrations as one moves toward the sea (Correll 1975, Pomeroy et al. 1972, Rochford 1951).

What, then, prevents these plankton and their high nutrient contents from being flushed out to sea? The plankton are gradually flushed down the estuary; at the same time, they tend to settle toward the bottom. They carry a large proportion of the nitrogen and phosphorus, which they have assimilated in the surface waters, along with them to the bot-

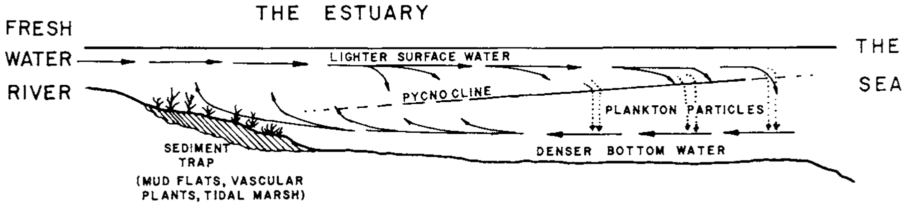

Fig. 2. Schematic diagram of nutrient conserving and modulating mechanisms in estuaries, including the two-layered salt-wedge; plankton circulation pattern; the sediment trap; the tidal marsh, vascular plant "nutrient pump"; and deep bottom sediment modulators.

tom. Typical estuaries maintain a "salt wedge" of intruding seawater on the bottom (Fig. 2), producing a surface flow of fresher water and a counterflow of more brackish, heavier water (Bowden 1967). These layers are separated by density variations due to both salt concentration and temperature differences. Estuarine ecologists believe this countercurrent of more brackish water is largely responsible for nutrient "trapping" or conservation in estuaries (Ketchum 1967, Odum 1971). Both living and dead particulates, which settle through the pycnocline or zone of maximum vertical density differential into the countercurrent, are carried upestuary along with their nutrient contents.

Another factor in this transport is the fact that the countercurrent layer tends to become anaerobic, especially near the bottom in warm weather. When this happens, high levels of nutrients, especially phosphorus, are solubilized from the bottom sediments. As the countercurrent moves upestuary, it gradually mixes into the upper layer through the action of turbulence induced by wind, tides, and friction between the opposing currents.

Some biota use the countercurrent to disperse their progeny and to avoid, to some extent, being swept out to sea. Examples are the blue crab and croaker, which spawn at the mouth of Chesapeake Bay (Cronin and Mansueti 1971). Moreover, phytoplankton are sometimes carried upestuary in the countercurrent and repopulate the upper estuary.

At times, when nutrients are high in upper estuary surface waters, they tend to be taken up rapidly in tidal marshes, mudflats, and bottom sediments (Correll et al. 1975). At times of low nutrient concentrations in estuarine surface water, a net release of nutrients occurs (Gardner 1975). Overall, in the long term, very little nutrient is trapped or released from these reservoirs; in the short term, however they act as nutrient filters or modulators (Axelrad et al. 1976, Bender and Correll 1974). The marshes also tend to trap particulate nitrogen and phosphorus, convert them to orthophosphate, ammonia, dissolved organic phosphorus, and nitrogen, which are then exported back to the open waters of the estuary (Axelrad et al. 1976).

Estuaries are measurably diluted by land runoff, which delivers high concentrations of mineral particulates derived from land erosion. The Rhode River estuary receives about 1.2 metric tons per ha of estuary of mineral particulates per year from land runoff (Correll et al. 1976). When a freshwater river flows into an estuary, the current velocity drops, the pH and ionic composition of the water are altered, and all but the fine clay fraction of the mineral particulates are deposited in a rather short distance. This zone is called the sediment trap (Fig. 2). In Rhode River, the sediments are deposited in this zone at an average rate of about 11 tons per ha/year. In general, this process sequentially produces tidal mudflats, low tidal marshes, high tidal marshes, and finally fast land. The sediments that are deposited and the organic matter and nutrients that are carried with them form very rich bottom sediments, since they resulted from topsoil erosion on the watershed.

At the tidal-mudflat stage of sedimentation, these areas can support large populations of submerged vascular plants. These plants are believed to have the capability of acting as nutrient "pumps" between surface water and bottom sediments. Thus, on the one hand, they can take up nutrients from the sediments and lose them to the water via death and decomposition, leaching from leaves, herbivorous activity, or perhaps by direct excretion. On the other hand, their leaves can take up nutrients directly from the water, at least under some conditions, and translocate them to their roots. Dense eelgrass (*Zostera marina*) beds in the Izembek Lagoon of Alaska take up phosphorus from bottom sediments at the rate of 166 mgP/m^2/day and excrete it into the tidal waters as orthophosphate at the rate of 62 mgP/m^2/day (McRoy and Barsdate 1970, McRoy et al. 1972). This eelgrass nutrient pump activity brought about significant diel fluctuations in overlying surface water and sediment interstitial water phosphorus concentrations.

Thus, estuaries maintain high productivity by maintaining high nutrient levels in bottom sediments and water column. This is done by nutrient/plankton trapping via the "salt wedge" countercurrent and the nutrient-modulating actions of tidal marshes, bottom sediments, and submerged vascular plants.

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