

# The Relationships Among Man's Activities in Watersheds and Estuaries: A Model of Runoff Effects on Patterns of Estuarine Community Metabolism

CHARLES S. HOPKINSON, JR.<sup>1</sup>  
JOSEPH J. VALLINO  
*The Ecosystems Center  
Marine Biological Laboratory  
Woods Hole, Massachusetts 02543*

**ABSTRACT:** Activities of man in rivers and their watersheds have altered enormously the timing, magnitude, and nature of inputs of materials to estuaries. Despite an awareness of large-scale, long-term changes in river-estuarine watersheds, we do not fully understand the consequences to estuarine ecosystems of these activities. Deforestation, urbanization, and agriculturalization have changed the timing and nature of material inputs to estuaries. Conversion of land from forest to almost any other land use promotes overland flow of storm runoff; increases the timing, rate and magnitude of runoff; and increases sediment, organic matter, and inorganic nutrient export. It has been estimated that total organic carbon levels in rivers have increased by a factor of 3-5 over natural levels. Man's activities have also changed the magnitude of particulate organic carbon relative to dissolved organic carbon export and the lability of the organic matter. Historically, rivers and streams had different features than they do today. Two of man's activities that have had pronounced effects on the timing and quality of river water are channelization and damming. Agricultural drainage systems, channelized and deepened streams, and leveeing and prevention of overbank flooding have had the combined effect of increasing the amplitude and rate of storm runoff, increasing sediment load, increasing nutrient delivery downstream, and decreasing riparian wetland productivity. Dams on the other hand have altered natural discharge patterns and altered the downstream transfer of sediments, organic matter, and nutrients. Patterns of estuarine community metabolism are sensitive to variations in the timing, magnitude, and quality of material inputs from watersheds. The autotrophic-heterotrophic nature of an estuary is determined by three primary factors: the ratio of inorganic to organic matter inputs, water residence time, and the overall lability of allochthonous organic matter inputs. A simulation model is used to explore the effects of man's activities in watersheds on the spatial patterns of production and respiration in a generalized estuarine system. Examined are the effects of variations in the ratios of inorganic and organic nitrogen loading, the residence time of water in the estuary, the degradability of allochthonous organic matter, and the ratio of dissolved to particulate organic matter inputs. Simulations suggest that the autotrophic-heterotrophic balance in estuaries is more sensitive to variations in organic matter loading than inorganic nutrient loading. Water residence time and flocculation-sedimentation of organic matter are two physical factors that most effect simulated spatial patterns of metabolism in estuaries.

## Introduction

Environmental change has been occurring at ever increasing rates throughout man's history. The effects of change have always been focused in aquatic systems, especially those at the interface of the land and sea. Effects are experienced most in estuaries not only because the rate of change of man's activities such as urbanization is highest in coastal areas, but also because rivers deliver to estuaries the products of environmental change occurring thousands of kilometers distant.

Activities of man in rivers and their watersheds have altered enormously the timing, magnitude, and nature of inputs of materials to estuaries. Despite an awareness of large-scale, long-term

changes in river-estuarine watersheds, we do not fully understand the consequences to estuarine ecosystems of these activities, such as the conversion from one land use to another, the removal of river floodplains, or the damming of rivers. In this communication we address three questions: What are some of the major activities in watersheds that alter material inputs to rivers? What are the activities of man in river channels and flood plains that alter sediment, organic matter, inorganic nutrient, and water delivery to the coastal zone? and How do changes in the timing and magnitude of material inputs to the coastal zone affect patterns of estuarine ecosystem metabolism?

## Activities in Watersheds

The dependence of man on land and water for life accounts for the close association which has

<sup>1</sup> Corresponding author.

existed between the historic civilizations and the major rivers. The development of various land and water management technologies, such as deforestation, agriculturalization, irrigation, and damming, has contributed to the progress of civilization (Cook 1976). In the process of converting natural land to one of man's landscapes and of using surface waters for development, man has interfered so much with the functioning of watersheds, streams, and rivers, that they now bear little resemblance to those of the past. The major activity on land that directly modifies the nature of watershed runoff into streams and rivers is conversion of land use.

Land use conversion generally proceeds in a regular fashion. Historically the sequence of land use conversion is from natural land (forest or grassland) to community land (urbanization), from natural land to agricultural land (agriculturalization for energy/tree harvest or crop production), agricultural land to additional community land (urbanization), and occasionally from agricultural land back to natural land (abandonment) (Cook 1976; Meade 1982). Each conversion results in a number of environmental changes that disrupt original patterns of water and material output from watersheds to rivers. The changes that ultimately influence the metabolism of estuaries the most are timing and magnitude of water runoff from the land surface, sediment erosion, alteration of organic matter export, and nutrient runoff.

#### TIMING AND MAGNITUDE OF WATER RUNOFF FROM THE LAND SURFACE

The fate of precipitation inputs to a watershed is strongly controlled by the land use composition and the spatial pattern of land uses. Other important controlling variables include climate, topography, and soil characteristics (Dunne and Leopold 1978). There are four major paths that water can follow: overland flow, saturation overland flow, shallow subsurface flow, and groundwater flow. Each of these paths will influence the timing, the total volume, and the chemical composition of the water when it eventually reaches a stream. Along a continuum from lushly vegetated forest to cleared pasture land, to cropland, and finally to high-population-density urban areas, there is a trend toward increased dominance of overland flow and decreased importance of subsurface stormflow. In regions disturbed by man, decreased infiltration capacity is a factor that limits subsurface flow and enhances runoff. On densely vegetated land, subsurface stormflow dominates the hydrograph volumetrically, while in urban areas overland flow dominates the hydrograph.

We present a series of figures to demonstrate the

effect various land uses and land use changes have on the timing and magnitude of water runoff from watersheds. Figure 1a illustrates the spatial pattern of land uses and the water flow paths characteristic of rainstorms of different intensity for a small, Pennsylvania watershed. In the urbanized areas of the watershed, overland flow always dominates, while in cropland areas overland flow only occurs during intense storms.

Figure 1b shows the general relationship between land use and percentage storm runoff. For a 5-cm rainfall, runoff can be as high as 95% for commercial and business land uses and below 1% for natural forest areas. Not only will the amount of storm runoff vary between land uses, the timing and rate of runoff will also change.

The hydrograph in Fig. 1c shows the effect of urbanization on the timing and magnitude of discharge. Urban areas, with their high degree of impervious surfaces are dominated by overland flow. Overland flow facilitates rapid and large percentages of water runoff. Note in Fig. 1c that not only does the water exit the watershed faster following urbanization but the peak rate and volume of runoff is higher as well. Accompanying the increased rate of discharge are higher velocities.

Overland flow becomes an important process on lands following clear-cutting. As shown in Fig. 1d, water export from an experimentally clear-cut watershed in Hubbard Brook Valley in New Hampshire increased 26–41% over the pre-cut conditions (Bormann and Likens 1982). Volume and rate of runoff remained high for over a decade following the clear-cut. Streamflow decreased markedly during the first 4 yr of revegetation, largely due to increases in transpiration.

Processes that increase surface runoff reduce infiltration capacity, surface detention, and depression storage. These processes include reduction of vegetation and construction of impervious surfaces. They are the two main processes associated with deforestation, agriculturalization, and urbanization. The net effect of these processes is to increase the importance of overland flow, to increase the volume and rate of runoff discharge, and to decrease the interval between when rainfall enters the watershed and runoff exits. By reducing groundwater flow, an additional effect is to reduce groundwater recharge, which supplies streamflow during dry times of the year. Thus streamflow can cease entirely. Land uses that produce overland flow also yield sediment, plant nutrients, and organic matter: parameters having significant downstream ecological impacts.

#### LAND USE EFFECTS ON SEDIMENT EROSION FROM WATERSHEDS

Prior to widespread deforestation of land for agricultural use 2,000–4,000 years ago, sediment ero-

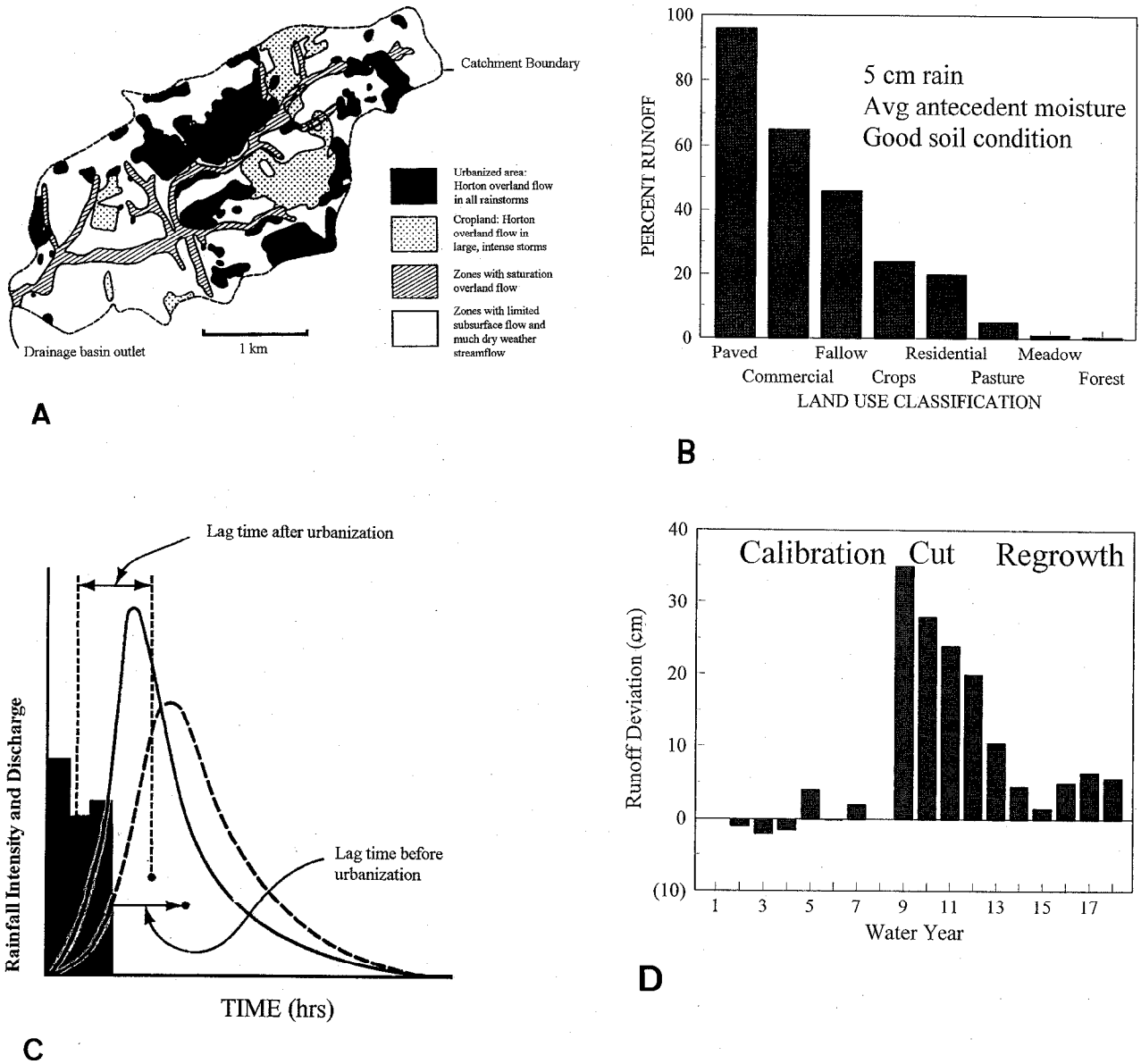


Fig. 1. The effects of various land uses and land use changes on the timing and magnitude of water runoff from watersheds. Reprinted courtesy of W. H. Freeman and Co. and Springer-Verlag. a. The spatial pattern of runoff-producing areas in a catchment in Pennsylvania. Note that land use changes will cause changes in the spatial pattern of runoff processes. From Dunne and Leopold (1978) b. Runoff percentages for various land use categories. Curves were constructed from tables in the United States Soil Conservation Service (1972) and Dunne and Leopold (1978) that describe soils receiving good management and having average infiltration capacities. c. The effect of urbanization on the timing and magnitude of storm runoff. From Dunne and Leopold (1978). d. Deviations of annual streamflow between reference and clear-cut forests in Hubbard Brook New Hampshire. From Bormann and Likens (1981).

sion was minor and the riverine load of sediment was markedly less than today (Meade 1982). In North America, soil erosion increased by more than a factor of 10 when settlers cleared forests, broke the soil, and planted crops. Sediment runoff into coastal systems is of interest for two primary reasons: suspended sediments reduce light availability for primary production and yields of organ-

ic carbon from watersheds are closely correlated with sediment yields.

The major factors controlling rates of sediment erosion from watersheds include land use, vegetative cover, topographic steepness, soil type, precipitation intensity and duration, and agricultural conservation practices (Wischmeier and Smith 1978). Land use, vegetative cover, and conserva-

tion practices are processes directly under human control. There are order of magnitude differences in sediment yields from various land uses and vegetative covers. The sediment yield factor, an important parameter in the universal soil loss equation, increases from 0.001 for medium age forest stands, to 0.05 for well-maintained grazed pasture land, to 0.3 for agricultural land devoted to row crops with minor conservation practices (Wischmeier and Smith 1978). Figure 2a shows the relation between sediment yield and percentage cropland in a watershed for two unglaciated regions in the eastern United States. The greater the percentage of cropland the greater sediment runoff will be. Regional differences are mostly a consequence of the type of farming, the soil depth and condition, farming practices, and variations in topography. Sediment erosion from urban land is high during the transition phase when homes, shopping centers, and roads are being constructed but decreases when lawns are planted and roads are paved (Wolman 1967).

The historical record of sedimentation in lakes or river deltas provides a glimpse of past patterns of deforestation. Milliman et al. (1987) related major events in the Yellow River drainage basin during the past 2,300 years to data on historic rates of sedimentation in intertidal and marine sediments. The estimated annual load, which is a proxy for sediment erosion, cycled up and down in relation to the intensity of agricultural usage, the conversion to pasture land, and the abandonment and reforestation of agricultural land (Table 1). Prior to 200 B.C. the river was channeled, the loess plateau was mostly forested, and little sediment was lost by channel overflow. The annual load was estimated to be <35% of present levels. Heavy agricultural activity up to A.D. 60 resulted in substantial increases in sediment loss, approximately 80% of modern loss. Following the Mongol invasion, much of the steppes returned to grazing pastures and sediment loss decreased to perhaps 50% of modern loss. Since A.D. 600 heavy agricultural usage has resulted in extensive erosion of the loess plateau: an estimated annual sediment loss of  $1.2 \times 10^6$  tonnes. Similar observations have been made for Black Sea watersheds where historic patterns of erosion are closely related to temporal patterns of deforestation (Fig. 2b). Erosion was low and uniform from 800 B.C. until after the first centuries A.D., then the general rate increased and became highly variable (Tamm 1991).

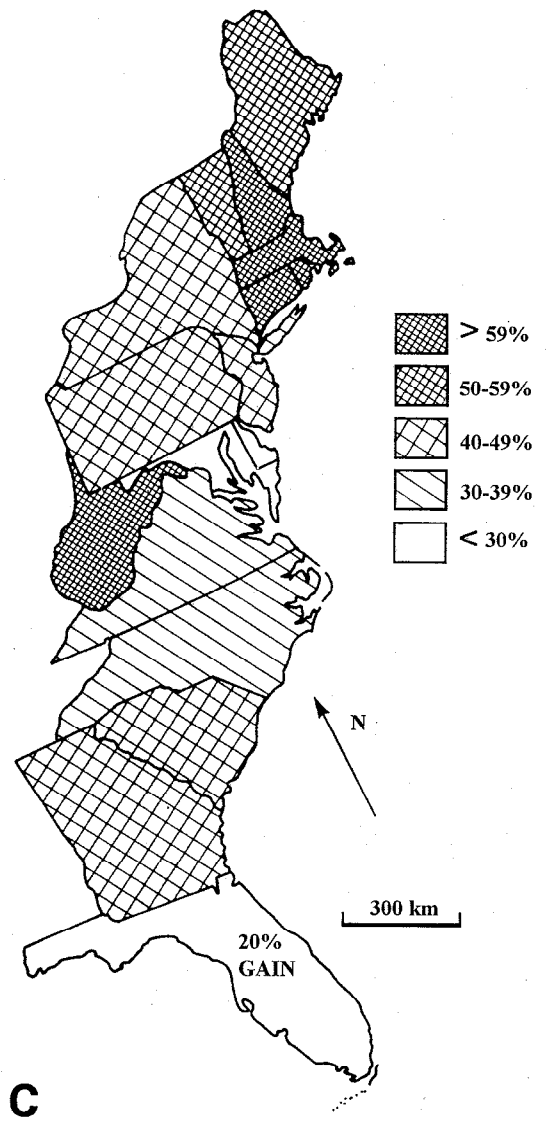
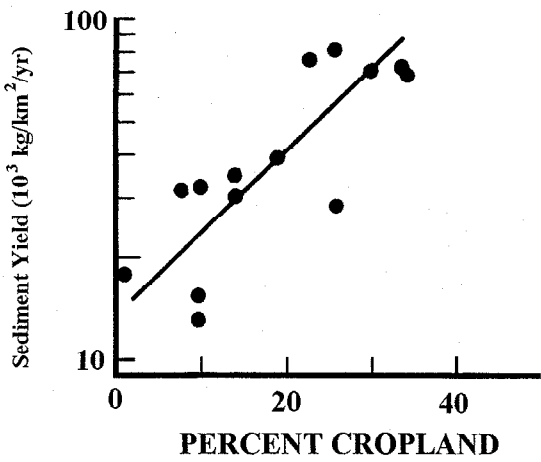
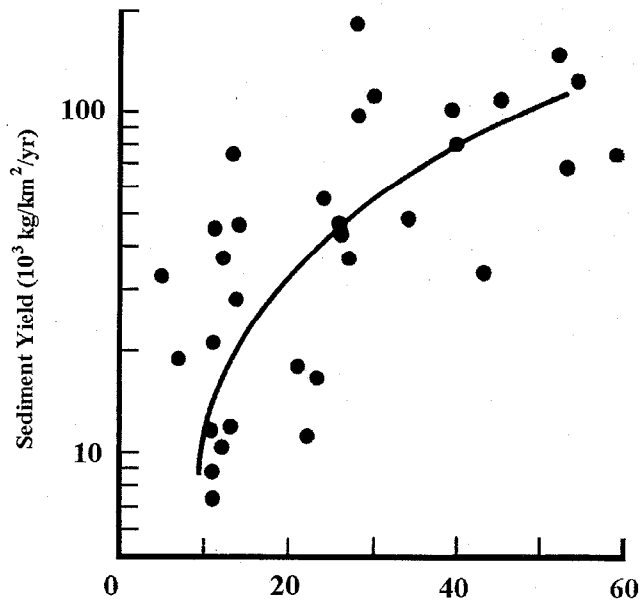
Deforestation is an important process that continues around the globe. While there are disagreements on the actual rate of tropical forest conversion, deforestation rates are substantial. Estimates published by the Food and Agriculture Organiza-

tion of the United Nations amount to  $1.13 \times 10^6$  km<sup>2</sup> yr<sup>-1</sup> for all tropical regions (Tamm 1991; Dixon et al. 1994). On a global basis, Dixon et al. (1994) estimate deforestation to be proceeding at the rate of  $15.4 \times 10^6$  ha yr<sup>-1</sup>. There are regional discrepancies to the overall global trend. Some portions of the more developed countries of the world are actually experiencing marked decreases in the areal extent of cropland (Fig. 2c) (Meade 1982; Dixon et al. 1994). While some of the decrease represents conversion to urban land, the majority is due to abandonment and reforestation.

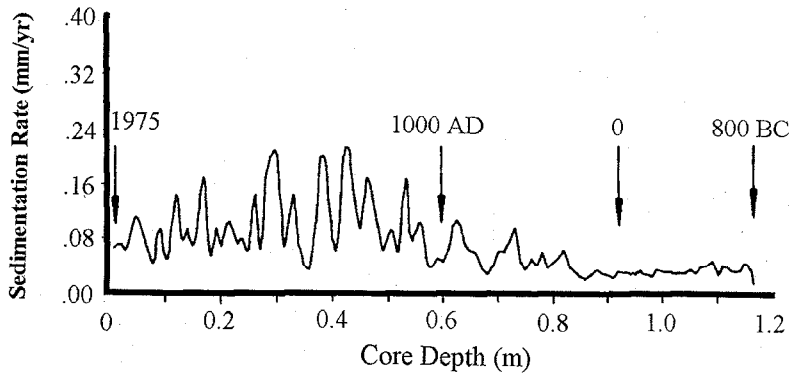
#### THE RELATIONSHIP BETWEEN LAND USE, SEDIMENT YIELD, AND ORGANIC CARBON RUNOFF

Most major rivers are heterotrophic with respiration exceeding primary production (Kempe 1984). The organic matter fueling the heterotrophy originates from allochthonous inputs from river drainage basins and from sewage. It has been estimated that total organic carbon levels in rivers and export to the sea has increased by a factor of 3–5 over natural levels and rates (Meybeck 1992). To predict future levels of heterotrophy, it is necessary to identify the sources of the organic matter and the processes controlling its input. In contrast to an extensive body of knowledge concerning water and sediment runoff processes on land, considerably less research has been devoted to organic matter. Most of the information comes from ecosystem research conducted in temperate forest watersheds of the northern hemisphere and from sporadic, nonsystematic monitoring of organic matter concentrations in the lower portions of major rivers. Frequently organic matter and land use relations are inferred from riverine concentrations of organic matter taken far downstream.

Organic carbon appears to be strongly related to patterns of sediment erosion and land use. As sediment erosion increases, as measured by total suspended solids (TSS) concentration in rivers, there is a curvilinear decrease in percent particulate organic carbon (POC) and a curvilinear increase in POC concentration (Fig. 3a) (Ittekkot and Laane 1991). Strong relationships have also been found between the dissolved organic carbon to particulate organic carbon (DOC:POC) ratio and TSS (Fig. 3b). For rivers with low TSS, the ratio averages about 10.2:1 and decreases with logarithmically increasing TSS concentrations to about 1:1 (Ittekkot and Laane 1991). These relations suggest that in forested or well-vegetated watersheds, carbon export is low and primarily in a dissolved form. As sediment erosion increases, POC export is enhanced more than DOC export. With increasing erosional power, the relative importance of the



**A**



**B**

TABLE 1. Historic patterns of land use and land loss in the Yellow River over the past 2,300 years. From Milliman et al. 1987.

Years	Event	Estimated Percentage of Modern Load	Estimated Annual Load ( $\times 10^9$ t)	Land Lost Over Time Interval ( $\times 10^9$ t)
A.D. 600–present	Heavy agricultural usage: extensive erosion of loess plateau	100	1.2	1,656
A.D. 50–A.D. 600	Mongol invasion; steppes return to grazing pastures	50	0.6	324
200 B.C.–A.D. 60	Agricultural use, with many river channels diverting silt to the ocean	80	1.0	250
340 B.C.–200 B.C.	River channeled; loess plateau mostly forested; relatively little sediment lost by channel overflow	35	0.4	59
				Total 2,290

various sources changes from DOC, to POC associated with fine, easily eroded soils, to coarser soils with lower carbon contents. This shift is also reflected in the decreasing percentage of POC as a component of TSS.

Howarth et al. (1991) showed a solid relationship between land use and both DOC and POC concentrations in runoff. DOC concentrations are lowest in forest runoff ( $1.4 \text{ mg l}^{-1}$ ) and highest in agricultural runoff ( $6.9 \text{ mg l}^{-1}$ ). Total organic carbon export followed the same pattern: urban export being high but lower than that from agricultural areas ( $6.3 \text{ g C m}^{-2} \text{ yr}^{-1}$ ,  $3.2 \text{ g C m}^{-2} \text{ yr}^{-1}$ , and  $0.14 \text{ g C m}^{-2} \text{ yr}^{-1}$  for agriculture, urban, and forest). Groundwater DOC concentrations are generally lower than DOC in surface runoff because decomposition lowers DOC during the long groundwater residence time. The ratio of DOC to POC is generally highest in runoff from forested watersheds and decreases as the percentage of agricultural land increases (Schlesinger and Melack 1981). This reflects the enhanced power to export particulate material from watersheds having substantial overland flow potential.

Considering whole river systems from around the globe, there are robust patterns between annual total organic carbon load of rivers and both annual river discharge and river drainage area (Schlesinger and Melack 1981). The slope of the TOC-discharge relation indicates that the average concentration of carbon exported from land is  $10 \text{ mg l}^{-1}$ , and the slope of the TOC-drainage area relation indicates that the mean denudation rate is  $7.2 \text{ g C m}^{-2} \text{ yr}^{-1}$ . This estimate of denudation rate is substantially higher than Howarth et al.'s

(1991) estimate for the Hudson River watershed, perhaps reflecting the fact that the Hudson River system was formerly glaciated. Meade (1982) found rates of sediment erosion from formerly glaciated watersheds were generally lower. Interestingly, Schlesinger and Melack (1981) found no difference in denudation rates between tropical, temperate, or boreal regions. Basically, watersheds with great relief and high runoff showed large losses of organic carbon regardless of region or glacial history. Discrepancies between studies reflect two things. One, the database for these studies is really quite small. Two, frequently the studies are conducted at totally different scales. Schlesinger and Melack (1981) were looking at rivers from all regions of the world, while Meade (1982) conducted his study in one region, the eastern United States temperate forest zone.

The relative degradability of organic matter runoff from land is an important parameter that can influence patterns of metabolism in receiving waters, including estuaries. Estimates of organic matter lability range from 10% to 75% (Richey et al. 1990). Lability is often based on the chemical composition of the organic matter in rivers, long after it has run off land. Thus extrapolation to the lability of the material when it first ran off the land is difficult. Ittekkot and Laane (1991) determined lability on the basis of carbohydrate and protein content of the total carbon sampled in a river. Figure 3c illustrates the relationship between the percentage of organic carbon that is labile and the TSS concentration. As the suspended solids concentration increases, the labile percentage decreases. The labile fraction shows regional differences (Ittekkot 1988), presum-

Fig. 2. The effects of various land uses on sediment erosion from watersheds. Reprinted courtesy of J. Geology and John Wiley and Sons. a. Relations between sediment yield and percent cropland in two river basins of the eastern United States. Top—Potomac River. Bottom—Susquehanna River. From Meade (1982). b. Rates of sedimentation in a sediment core from the Black Sea are attributed to historic changes in land use in the watershed over the past 2,800 years. From Tamm (1991). c. Decrease in the area of cropland in the eastern United States between 1944 and 1969 as a percent of 1944 cropland area. From Meade (1982).

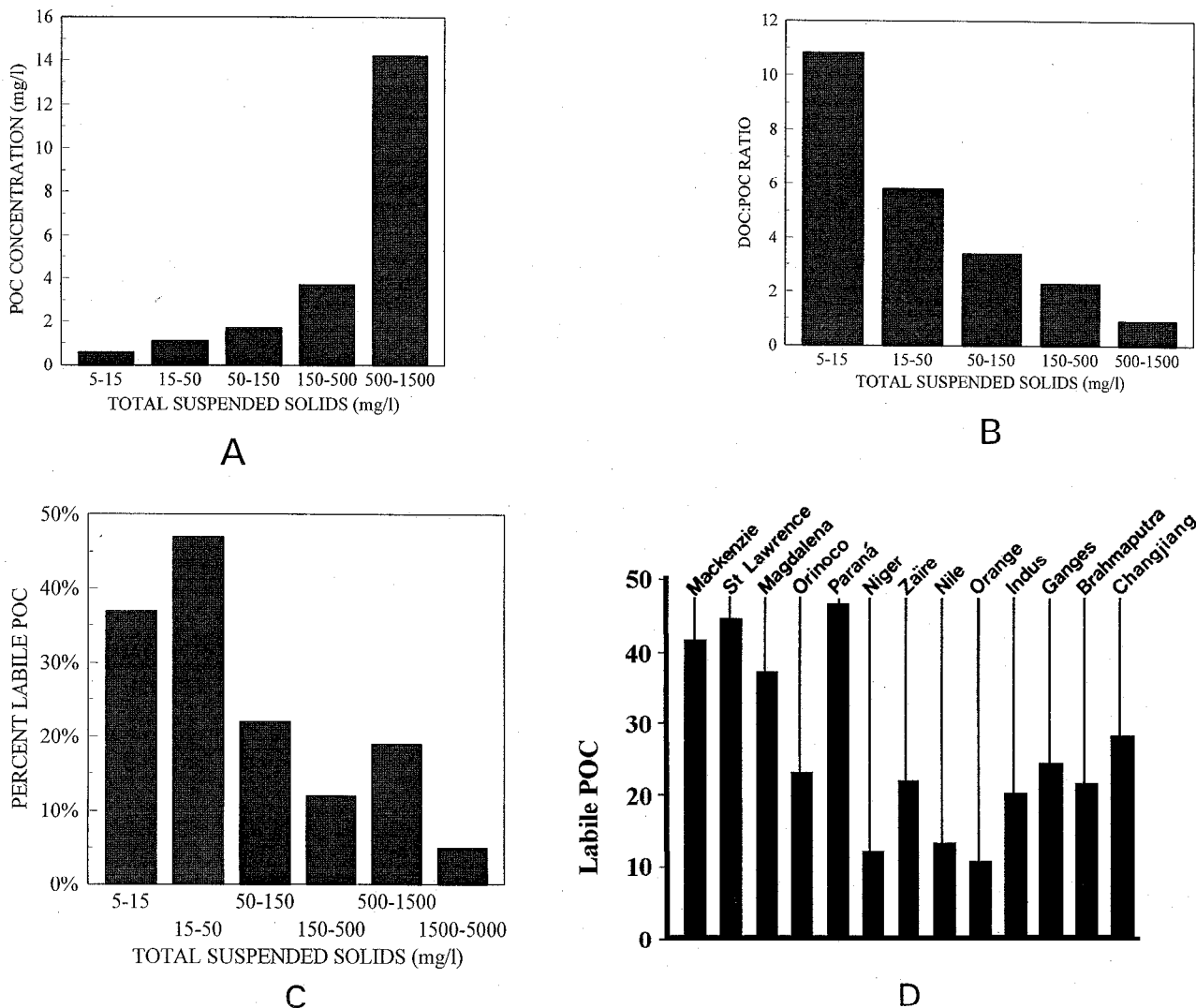


Fig. 3. The relationship between total suspended solids load (TSS) of rivers and riverine organic carbon. From Ittekkot and Laane (1991). Reprinted courtesy John Wiley and Sons. a. Mean concentration of particulate organic carbon in world rivers expressed as concentrations per liter in different ranges of concentration of suspended matter. b. Relationship between the ratio of dissolved and particulate organic carbon and TSS. c. Relationship between TSS and the percentage of total organic carbon load that is relatively degradable. d. Labile particulate organic carbon composition of some major world rivers.

ably reflecting a temperature effect on organic matter decomposition. Temperate region rivers (e.g., Mackenzie, St. Lawrence, Paraná) have relatively high labile POC fractions while tropical and subtropical rivers (e.g., Brahmaputra, Ganges, Zaire) have a much lower labile fraction, 40% versus 20% (Fig. 3d). This pattern has been interpreted to indicate that most of the labile organic carbon has already been decomposed in tropical areas due to higher temperatures. This conclusion is supported by the lower organic matter C:N ratios hence more humified organic matter in the warmer tropical rivers.

To better predict the effects of changing land use

patterns on organic matter export from watersheds, an assessment of organic matter sources and organic matter degradability is essential. Systematic investigations of organic matter runoff from various land uses in all regions of the world, coupled with actual measurements of metabolism and decomposition of the material prior to mixing with autochthonous sources of organic matter in rivers would be of great benefit.

#### THE RELATIONSHIP BETWEEN LAND USE AND INORGANIC NUTRIENT RUNOFF FROM WATERSHEDS

One of the results of man's activities on the Earth's surface is a marked increase of nutrient lev-

els, particularly nitrogen and phosphorus, in all aquatic systems (Vollenweider 1968; van Bennekon and Salomons 1981). Due to the worldwide phenomenon of nutrient-induced eutrophication, considerable research has been devoted to understanding the causative processes. First efforts were focused on easily identifiable point sources of nutrients, such as sewage and industrial discharges, while later and present-day efforts are more geared toward quantifying nonpoint source inputs, such as diffuse inputs from agricultural lands.

A striking relationship exists between land use and mean total nitrogen and phosphorus export. Omernik (1976), summarizing information from 473 subwatersheds in the eastern United States (Fig. 4a), showed that forest land has the lowest export of N and P, followed by urban and agricultural land covers. N export is roughly twice as high from agricultural watersheds ( $982 \text{ kg km}^{-2} \text{ yr}^{-1}$ ) than from forested watersheds. This relationship has also been observed in European watersheds (Kempe et al. 1991).

Man has a profound influence on nutrient loading to streams. Figure 4b shows an increase in concentration for both N and P as a function of the population density normalized to the water discharge (Wollast 1983). This relationship suggests that the pristine concentration of inorganic N was  $5 \mu\text{M}$ , that the present concentration is  $52 \mu\text{M}$ , and that the contribution per individual is  $500 \text{ moles person}^{-1} \text{ yr}^{-1}$ . On a worldwide basis these contributions are probably high, as the data is biased toward rivers in industrialized regions. However, the general form of the relation is undoubtedly sound.

Alteration of land use has a great effect on nutrient export from the land. Nutrient export increased markedly following an experimental forest clear-cut in the Hubbard Brook experimental forest in New Hampshire (Fig. 4c). Nitrate concentrations increased spectacularly, from a weighted concentration of  $0.9 \text{ mg l}^{-1}$  prior to cutting to  $53 \text{ mg l}^{-1}$  two years later (Likens and Bormann 1975). Whereas nitrate N is normally conserved in the undisturbed forest, much nitrate is flushed from the deforested system presumably due to mobilization from decomposing organic matter and enhanced rates of microbial nitrification. Annual net export of nitrate also increased considerably, exceeding  $500 \text{ kg ha}^{-1}$  two years after the clear-cut. In general, strong linear relationships have been demonstrated for the concentration of inorganic nutrients in streamwater and the degree to which land has been cleared for agriculture (Fig. 4d).

Runoff of inorganic nutrients from land surfaces is a major factor contributing to eutrophication in aquatic systems. The two primary sources of nutri-

ents are urban and agricultural lands (Omernik 1976). The higher the density of these two activities in watersheds, the higher the export of N and P to streams, rivers, and ultimately, estuaries (Fig. 4e). Effective control of nutrient runoff will require concerted efforts at reducing inputs from these two land uses (Slaymaker 1982).

#### Activities in River Channels and Flood Plains

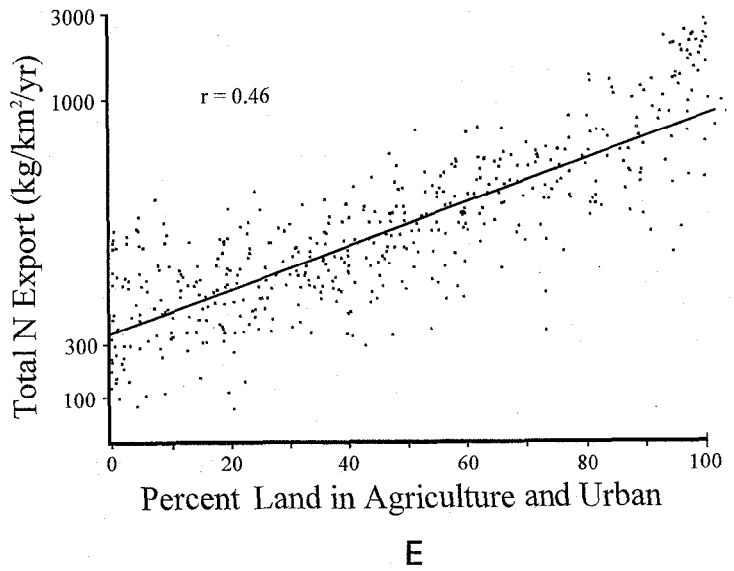
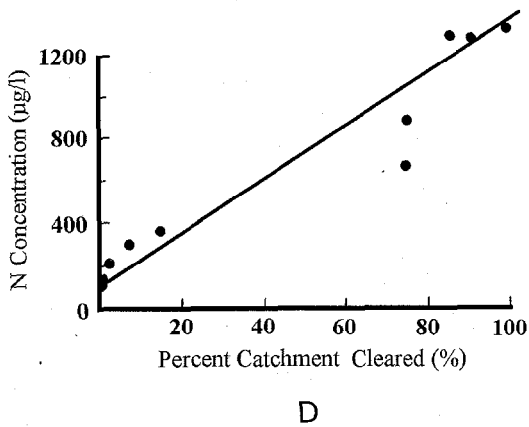
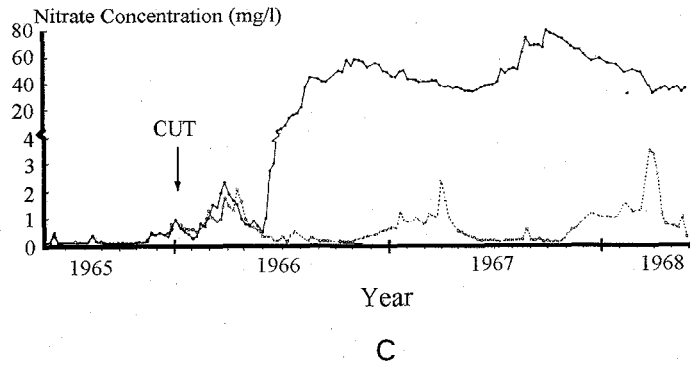
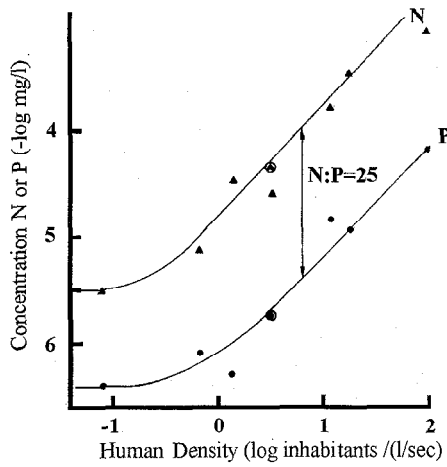
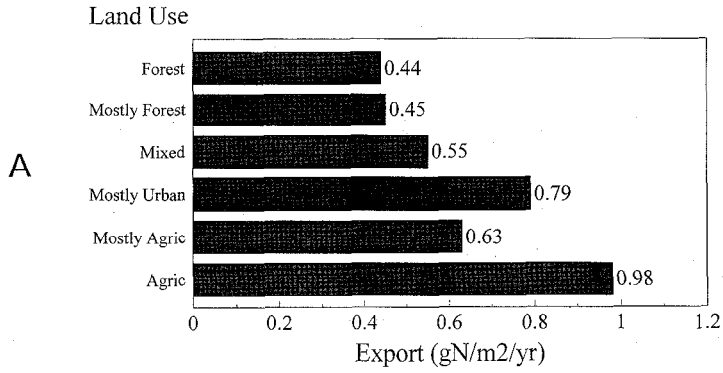
Historically, streams and rivers had different features than they do today. Rivers often had extensive flood plains, backwater areas, riparian wetlands, many woody snags, and debris dams (Sedell and Froggett 1984, Naiman 1986). Waters were previously much clearer, with light often reaching the bottom of smaller systems. Large amounts of organic matter were sequestered in the watershed and sediment output was less than a tenth of what it is today (Naiman 1986).

Two of man's activities have had pronounced effects on the timing, magnitude, and quality of water coursing between watersheds and the coastal zone: channelization and damming. Included in the channelization activity are loss of primary streams associated with urbanization, channel straightening and enlarging, leveeing, loss of flood plains, and loss of backwater areas and riparian wetlands. These activities have dramatically altered the timing and magnitude of water discharge, the trapping of sediments, the accumulation of organic matter, and the conversion of inorganic nutrients to organic forms.

Urbanization has resulted in the virtual elimination of primary and secondary order streams that under normal conditions keep both sediment and runoff distributed among many small channels, each of which plays its part in delaying movement of flood peaks, providing channel storage and slowing the average speed at which water is delivered to larger systems (Dunne and Leopold 1978). In the United States, under federal and state legislation, Herculean efforts have been devoted to promoting land drainage and reducing flood damage. Efforts by the Corps of Engineers, the Bureau of Land Reclamation, and the Tennessee Valley Authority have totally altered 1,000s of miles of streams and rivers in the United States. Levees and floodwalls line over 8,300 miles of streams (Dunne and Leopold 1978) and there have been over 5,000 miles of "channel improvements." The Soil Conservation Service has "improved" thousands of miles of other streams. These efforts do not include dams. In spite of these efforts, flood damage continues to increase. The use of flood-prone land continues to rise faster than attempts to reduce flood damages.



Total N Export vs Land Use



In natural river systems, already low rates of sediment erosion from land were further lowered through efficient sediment trapping on river floodplains and riparian wetlands during floods (Brinson et al. 1981). Riparian wetlands have been reported to trap 2–40 kg P ha<sup>-1</sup> yr<sup>-1</sup> (Mitsch et al. 1979; Yarbrow 1983). Riparian wetlands and flood plains are net accumulators of inorganic nutrients via biomass production and organic matter accumulation in sediments (Wharton et al. 1982). Inorganic nutrient inputs to these systems are taken up in biomass, immobilized, and exported in an organic form (Conner and Day 1976; Day et al. 1977; Brinson et al. 1984; Elder 1985). Agricultural drainage systems, channelized and deepened streams, leveeing, and prevention of overbank flooding have had the combined effect of increasing the amplitude and rate of storm runoff, increasing sediment load, increasing nutrient delivery downstream, and decreasing riparian wetland productivity (Hopkinson and Day 1980a,b). An example of the effect of channelization on a daily river hydrograph is presented in Fig. 5a. Channelization of the Kissimmee River has greatly increased the amplitude of water discharge and completely altered the seasonal pattern of water level (Fig. 5a). Day-to-day variations in discharge now often approach levels of variation only seen on a seasonal basis prior to channelization.

Damming is the other major activity of man that has forever changed the character of river systems. On a global basis, river flow regulation was a minor activity until about the mid 1800s. Dams greatly alter the timing of water discharge downstream as well as the quantity of sediment delivery, and organic and inorganic nutrient export. While the general effect of dams is to regulate and smooth out the discharge hydrograph, there are cases where, due to diel variations in urban electrical power demand, the frequency of discharge variation increases.

Dams are extremely effective water flow regulators. The Colorado River is one of the most heavily regulated rivers in the world, water being stored for human consumption, irrigation and power generation. Whereas it has been estimated that flow averaged 600 m<sup>-3</sup> s<sup>-1</sup> prior to flow regulation, many channels in the river delta presently have no

flow. In the Volta River the annual variation in high and low flow exceeded a factor of 10<sup>3</sup> prior to the construction of the Akosombo Dam (Fig. 5b); however, it is regulated now at a constant discharge of 1150 m<sup>3</sup> s<sup>-1</sup> (Petr 1986).

Trapping of sediments behind dams approaches 100% efficiency. Prior to the construction of the High Aswan Dam in Egypt, 10 × 10<sup>6</sup> tons of sediment were deposited annually in flood plains along the Nile River and the remaining 93% was transported to the Nile Delta. As seen in Fig. 5c, following dam closure, 98% of sediments are retained within the reservoir (Shalash 1982). The removal of sediment from the river has altered estuarine circulation patterns (Sharaf-El-Din 1977), increased coastal subsidence (Stanley 1988), increased deltaic land loss (Burelli 1992; Stanley and Ware 1992) and reduced commercial fisheries yield (Wadia 1982).

It may be thought that dams serve the same function as floodplains and riparian wetlands in how they influence the dynamics of water, sediments, nutrients, and organic matter. However, the accumulation of sediments in reservoirs behind dams does not promote deltaic building at the coast nor is vegetation growth on floodplains or riparian forests enhanced. Due to the increased residence time of water in reservoirs behind dams, organic matter decomposition has time to proceed and perhaps even be augmented through UV radiation. Primary production of phytoplankton is promoted in these systems because of enhanced water clarity, increased surface area receiving solar radiation, and an enhancement of inorganic nutrient supply via organic matter decomposition. Unlike riparian forests, which export relatively recalcitrant, humic-rich organic matter, reservoirs probably export a highly degradable form of organic matter as phytodetritus. Thus dam-built reservoirs affect downstream ecosystems quite differently than do river flood plains and riparian forests.

### Effects of Allochthonous Material Inputs on Patterns of Estuarine Metabolism

#### A CONCEPTUAL MODEL

A diagrammatic model of an estuarine ecosystem synthesizes our ideas on the effects of water-

←  
Fig. 4. The relationship between land use and inorganic nitrogen runoff from watersheds. Reprinted courtesy of the United States Environmental Protection Agency, Springer-Verlag, and John Wiley. a. Relationships between land use and stream exports of total nitrogen. From Omernik (1976). b. Relationship between human density on the watershed and the concentration of N and P in runoff water. From Wollast (1983). c. Stormwater concentrations of NO<sub>3</sub><sup>-</sup> in a forested and a clear-cut forest. The upper solid line is the clear-cut forest. From Likens and Bormann (1975). d. The relationship between the percentage of watersheds that have been cleared for agriculture and inorganic nitrogen concentration in streamwater running off land surface. From Attiwill (1991). e. The relationship between agricultural and urban land uses as a percentage of total watershed area and inorganic nitrogen export of the total watershed. From Omernik (1976).

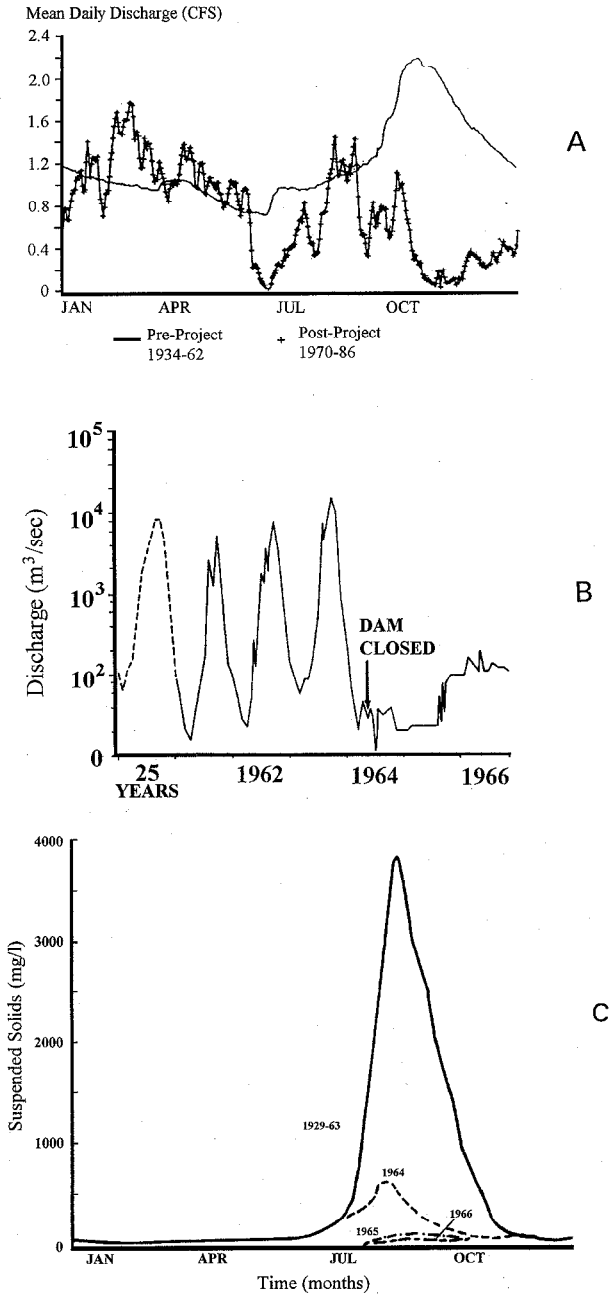


Fig. 5. The effects of channelization and damming on water and sediment discharge from rivers. Reprinted courtesy W. Junk Publishers. a. Effect of channelizing the Kissimmee River on temporal patterns of mean daily discharge. Curve with crosses is a 16-yr average following channelization and the other curve is a 18-yr average immediately prior to channelization. b. Effect of the Okosombo Dam on Volta River discharge. From Petr (1986). c. The effect of the High Aswan Dam on downstream suspended solids concentration in the Nile River. Note that within a 3-yr period following dam closure, approximately 98% of sediment inputs to the Aswan reservoir are trapped. From Shalash (1982).

shed inputs to estuaries (Fig. 6). The purpose of the model is to illustrate how organic matter and inorganic nutrient inputs control production, respiration, net community metabolism, and the autotrophic-heterotrophic nature of an estuarine system. As conceptualized, the estuarine ecosystem is bounded by the land and sea, exchanging inorganic nutrients and organic matter with each. Inputs from land are conceptualized as being controlled by the rate of water input and the concentrations of organic matter and inorganic nutrients in the water. Inputs from the sea are viewed as being controlled by tidal mixing and the concentration gradient between estuary and ocean. As conceptualized, the estuarine ecosystem is highly simplified and lumped into seven compartments: autotrophs, benthic and pelagic heterotrophs, organic detritus in the water column and sediments, and inorganic nutrients in water and sediments. Ecosystem processes modeled are gross and net primary production, autotrophic respiration, heterotrophic assimilation of organic matter and autotrophic grazing, sedimentation, organic matter decomposition, nutrient remineralization, burial, and denitrification. Primary production is controlled primarily by inorganic nitrogen availability, but light availability is also an important control (as modified by suspended solids concentration).

A series of equations describes the processes constituting net community metabolism. Net community production is the balance between gross production (GP) and total community respiration (TCR). In nutrient currency, it is equivalent to nutrient immobilization minus nutrient regeneration. Net community metabolism can be further defined by the following equation:

$$\text{Import} + \text{Gross Production} = \Sigma \text{Respiration} + \text{Burial} + \text{Export}$$

For an ecosystem to be net autotrophic, gross production must exceed the sum of autotrophic respiration, heterotrophic respiration, and benthic respiration. The ratio of gross production to total respiration is  $>1$  in an autotrophic system; gross production - total respiration is positive. In autotrophic systems there is a net uptake of inorganic nutrients and a net increase in organic nutrients.

For an ecosystem to be net heterotrophic, the ratio of gross production to total respiration is  $<1$  and gross production - total respiration is negative. In contrast to autotrophic systems, in heterotrophic systems there is a net accumulation or export of inorganic nutrients and a net consumption or import of organic nutrients.

Important controlling variables include the ratio of C to N in allochthonous organic matter, the relative degradability of allochthonous organic mat-

## GENERALIZED ESTUARINE MODEL

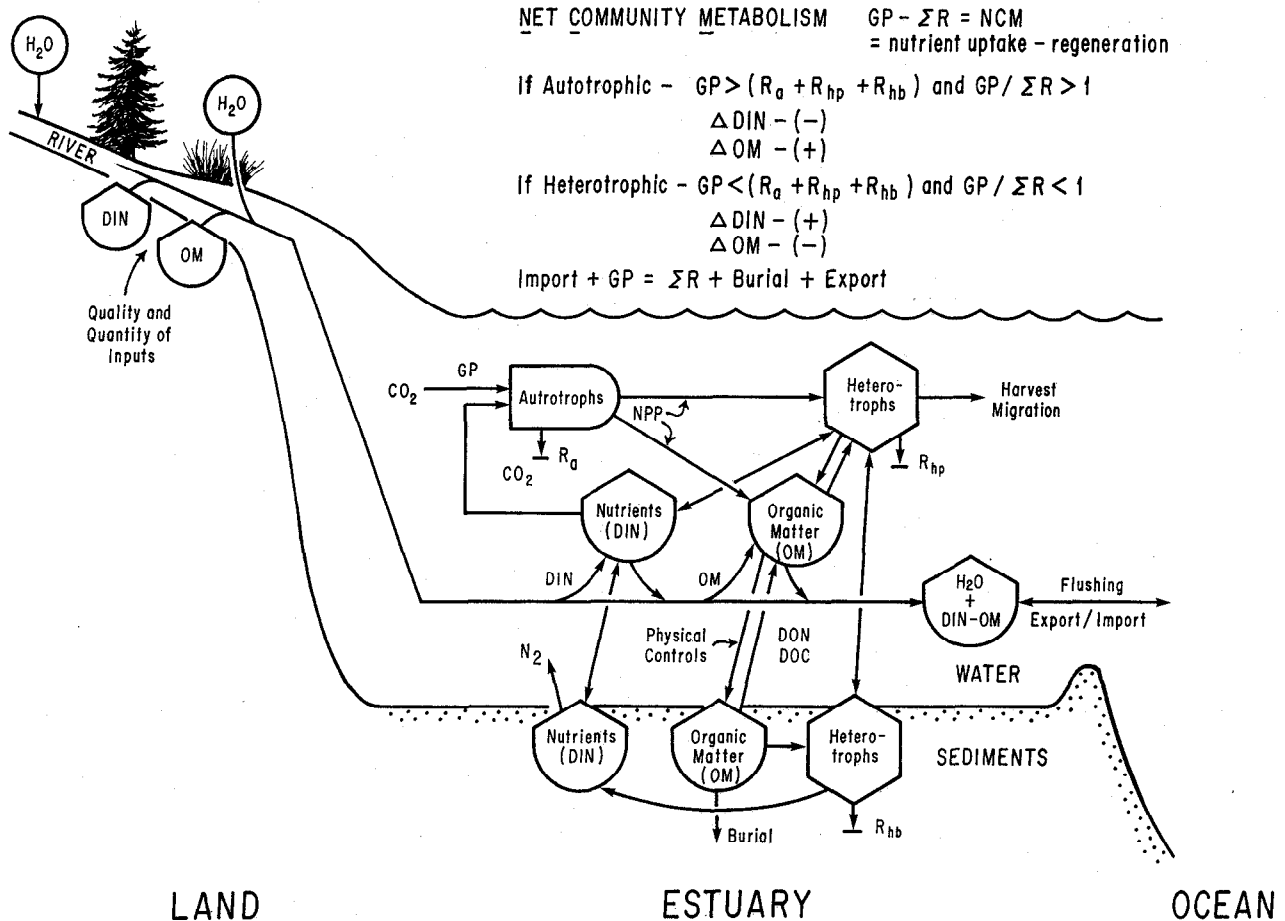


Fig. 6. A diagrammatic model of an estuarine ecosystem illustrating the processing and transport of allochthonous material from the land and sea. The basic equations describing the autotrophic-heterotrophic nature of an ecosystem are included.

ter, the concentration of suspended solids (which controls light levels and hence primary production in the estuary), water residence time in the estuary, the ratio of POC to TOC, the percentage of POC that settles out and is trapped in an estuary, and the percentage of DOC that flocculates and settles. The C:N ratio of allochthonous organic matter is important as it determines whether inorganic N is immobilized or remineralized by bacteria, which have a C:N of about 6. The time constant for allochthonous organic matter decomposition relative to the water turnover time indicates whether decomposition is a significant process in the estuary. Likewise the relative time constants for water turnover and autotrophic and heterotrophic production determines whether biomass increases in the estuary or is flushed out without increasing in mass. The process of allochthonous organic matter settling to the bottom in an estuary is important

because it effectively lengthens the residence time of the material in the system, allowing decomposition when it might otherwise be flushed from the system.

GENERALIZED SYSTEMS-LEVEL  
RESPONSES OF AN ESTUARINE  
ECOSYSTEM TO VARIATIONS IN THE  
TIMING, MAGNITUDE AND QUALITY OF  
ALLOCHTHONOUS INPUTS

Three factors thought to be the primary controls of the autotrophic-heterotrophic nature of an estuarine ecosystem are dissolved inorganic nitrogen: organic nitrogen (DIN:OM) loading ratio, the decomposability of allochthonous organic matter, and the residence time of estuarine water (Fig. 7). A system will be autotrophically balanced if two general conditions are met: one, residence time is long enough for all DIN inputs to be completely

## SYSTEM RESPONSE TO ALLOCHTHONOUS INPUTS

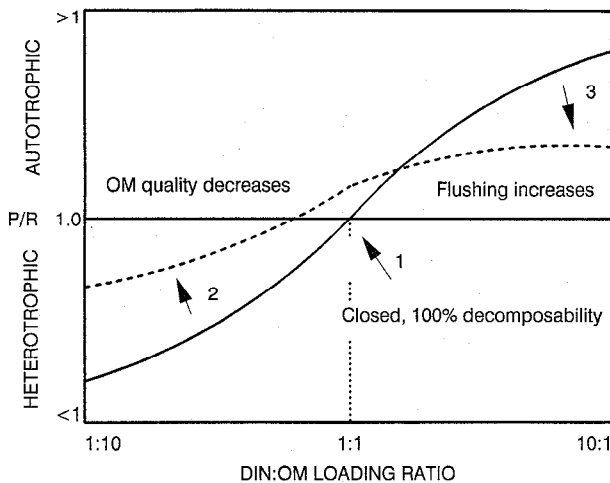


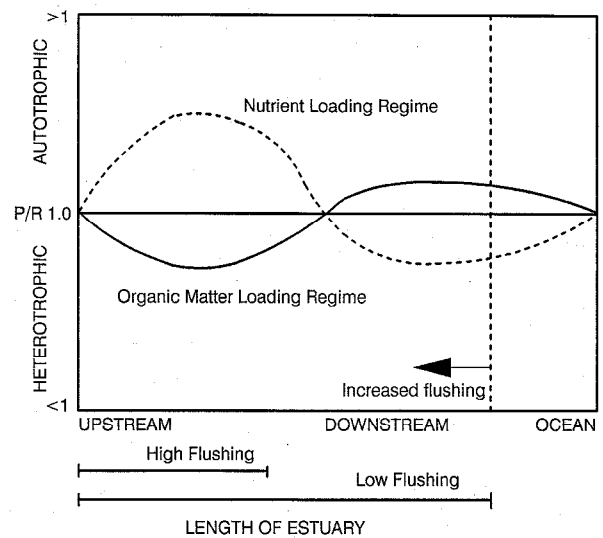
Fig. 7. Hypothetical curves relating the effects of the ratio of allochthonous inorganic to organic nitrogen inputs, allochthonous organic matter lability, and estuarine water residence time on the overall autotrophic-heterotrophic nature of an estuarine ecosystem. Arrow 1, on the solid line curve, indicates the P:R ratio for a closed system, receiving equal loading of inorganic and organic material. As either the quality (C:N) or degradability of the organic material decreases, the P:R versus loading relation will shift toward the dashed line as indicated by arrow 2. A similar shift will occur as flushing increases, as indicated by arrow 3. See text for further explanation.

recycled (e.g., DIN is taken up by autotrophs and all autotrophic biomass is grazed, incorporated into heterotrophic biomass, and remineralized); two, the assimilation rates of DIN and OM are equivalent and the DIN:OM loading ratio is 1. Figure 7 illustrates what we hypothesize to be the general responses of a system to variations in the three primary factors.

If the assimilation rates for DIN and OM are equal (but they of course never are) and the ratio of inputs are equal then a system will be balanced (arrow 1 in Fig. 7). As the loading ratio is moved in one direction or the other, the P:R ratio increases or decreases (along the trajectory described by the solid sigmoidal line in Fig. 7). For example, if DIN input is increased relative to OM input, then the system is shown to become autotrophic.

As the quality (sensu decomposability) of the organic matter decreases, then the potential for the system to be heterotrophic decreases (arrow 2 in Fig. 7). This occurs because as the decomposability decreases a smaller percentage of the organic matter can be decomposed prior to being exported from the system. Organic matter that settles to the bottom and is trapped within an estuary behaves differently. It essentially has an infinite amount of time to decompose once it settles to the bottom of the system.

## GENERAL RESPONSE TO NUTRIENT OR ORGANIC MATTER LOADING



## KEY PARAMETERS

Residence Time, Light, Organic Matter Quality

Fig. 8. Hypothetical curves relating the spatial pattern of metabolism in an estuary dominated by either allochthonous inorganic (dashed line) or organic material (solid curve) inputs. The effect of flushing can be visualized by moving the vertical dashed line to the left while holding the curves fixed in space. Thus the effect of high flushing would be to have only the initial autotrophic or heterotrophic portions within the estuary. The portions of the curves on the right of the new position of the dashed line would then be in the ocean.

Another important factor affecting the autotrophic-heterotrophic nature of the system is the water residence time. The effect of decreasing the residence time of water is similar to the effect of decreasing the decomposability of organic matter. The faster the inputs are flushed through a system, the less time for the materials to be processed in the system (the curve in Fig. 7 moves in the direction shown by arrow 3). It is hypothesized that variations in the water residence time will have a more pronounced effect on organic matter inputs than inorganic nutrient inputs. This is because the DIN uptake rate for bacteria and phytoplankton is so high that the DIN pool often turns over in hours (Maloney and Field 1991). In contrast, the decay constant for organic matter is more on the order of months to years (e.g., bulk DOM is often found to be metabolized at a rate of <math>< 10\%</math> per month [Sottile 1973]).

The spatial pattern of net community metabolism within an estuary is also controlled by the three primary factors—the ratio of DIN:OM inputs, the water residence time, and the decomposability of allochthonous organic matter (Fig. 8). In a system with sufficiently long water residence time

(low flushing), systems dominated by either nutrient or organic matter loading will follow trajectories of community metabolism as illustrated (slow flushing). For a DIN-dominated system, we expect upper portions of the estuary to be progressively autotrophic as distance down estuary increases (dashed line in Fig. 8), as gross production (GP) increases, and phytoplankton biomass accumulates. Further downstream, following nutrient depletion, GP decreases, and heterotrophic metabolism (R) increases. At some point downstream, R can exceed GP and the system becomes net heterotrophic. For the estuary as a whole to be metabolically balanced, the integral of P-R versus distance must equal 0 and P:R = 1. At this point the export of nutrients or organic matter will balance inputs.

Variations in the water flushing rate will strongly influence whether a system is autotrophic or heterotrophic, as the length of time materials are in the estuary determines the extent to which reactions can go to completion. Consider for example the DIN-dominated system just discussed. If the flushing rate is greatly increased, the length of the estuary is in effect shortened (high flushing line for the X-axis in Fig. 8) and only those reactions that have time to occur prior to being carried out of the estuary can occur. Thus a DIN-dominated system can become more autotrophic and an OM-dominated system can become more heterotrophic as the water flushing time decreases.

The spatial pattern of autotrophy-heterotrophy in the Chesapeake Bay illustrates some of these processes. Chesapeake Bay is thought to be a DIN-dominated system but because of the long water residence time, the bay as a whole is considered to be only slightly autotrophic (Kemp personal communication, 1993). Along the estuarine transect, the bay experiences heterotrophic and autotrophic regions reflecting the utilization of allochthonous and autochthonous organic and inorganic matter inputs. Overall, the bay imports inorganic nutrients, exports organic nutrients, and is thus slightly autotrophic. The water residence time for the bay is on the order of months. Patterns in the Merrimack River contrast with those in the Chesapeake Bay. The Merrimack River has a water residence time of 1-3 d. It is also a DIN-dominated system, but it is autotrophic not only in the estuary (probably light limited) but also out onto the continental shelf (presumably ample nutrients and light).

#### **A Simulation Model of Estuarine Ecosystem Metabolism**

##### SCENARIOS MODELED

On the basis of our conceptual model of what we believe to be the important factors controlling

the autotrophic-heterotrophic balance of an estuarine ecosystem and on the basis of the major shifts in allochthonous material inputs due to man's activities in watersheds, we chose four scenarios to investigate further with a simulation model. Each scenario is presented in comparison to a "Nominal Simulation;" the nominal simulation represents a system similar to the Parker River system in northern Massachusetts with the important distinction that the system as modeled does not include intertidal marshes along the length of the estuary. Thus our simplified system considers dynamics more representative of a drowned river system without lateral marshes.

##### SCENARIO I—VARIATIONS IN THE INPUT RATIO OF DIN AND OM

This simulation examines how the metabolic balance of an estuary is influenced by shifts in the ratio of inorganic nutrient versus organic matter inputs. This is accomplished by increasing the DIN input concentration and decreasing the organic matter concentration by factors of 3.

##### SCENARIO II—VARIATIONS IN WATER RESIDENCE TIME

This simulation examines the importance of turnover time of water in an estuary. Turnover time is modified by increasing the freshwater input rate by a factor of 10. Loading is held constant.

##### SCENARIO III—VARIATIONS IN LABILITY OF ALLOCHTHONOUS ORGANIC MATTER

Here we investigate the effect of decreasing the degradability of allochthonous organic matter inputs from watersheds. This is accomplished by decreasing the decay coefficient controlling the flux of recalcitrant carbon to labile carbon pools and decreasing the percentage of allochthonous organic matter inputs that are labile. Both factors are decreased an order of magnitude.

##### SCENARIO IV—VARIATIONS IN DOC:TOC RATIO OF ALLOCHTHONOUS ORGANIC MATTER

Meybeck (1982) reports very large variations in DOC:TOC ratios for major world rivers. The average value varies between 0.1 and 0.9. In lowland rivers, where erosion rates and POC levels are low, there is frequently 10 times more DOC than POC. In highly erosive systems influenced by man's activities, the relative importance of DOC decreases substantially. We simulate variations in input ratios by increasing the benthic settling coefficient an order of magnitude. Meade (1982) and Wollast (1983) report that 95% of particulate organic mat-

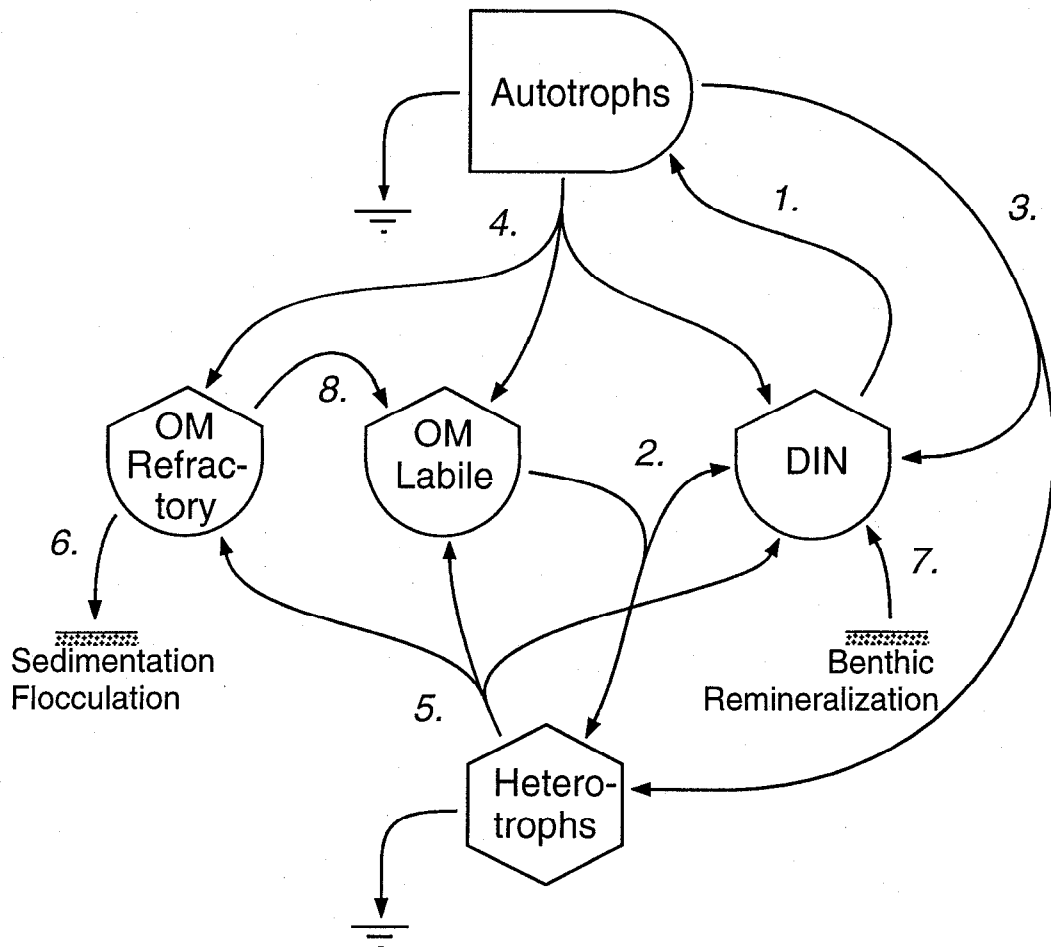


Fig. 9. Conceptual model of foodweb used in simulation. Numbers correspond to: 1. Autotrophic net production; 2. Uptake of labile organic matter (OM) and immobilization (or remineralization) of dissolved inorganic nitrogen (DIN); 3. Grazing of autotrophs by heterotrophs; 4. Mortality of autotrophs; 5. Mortality of heterotrophs; 6. Flocculation or sedimentation of refractory OM to the benthos; 7. Benthic remineralization of refractory OM less denitrification; 8. Abiotic decomposition of refractory OM into labile OM.

ter inputs to estuaries settle out. Hence this simulation specifically represents the situation where POC increases in importance relative to DOC.

#### SIMULATION DESCRIPTION

The estuarine ecosystem is represented by a five-compartment model consisting of autotrophs (A), heterotrophs (H), dissolved inorganic nitrogen (DIN), labile organic matter ( $OM_L$ ), and refractory organic matter ( $OM_R$ ) (Fig. 9). Carbon and nitrogen are coupled by assuming a constant C:N ratio for autotrophs and heterotrophs ( $CN_L$ ) that differs from that of OM ( $CN_D$ ). Autotrophs are assumed to be only N limited. Heterotrophs graze autotrophs as well as utilize  $OM_L$ . Refractory OM decays to  $OM_L$  as well as settles out to the benthos where it is remineralized and partially denitrified. Although the model presented below is only intended to examine generalities, data from Plum

Island Sound were used to set many of the model's parameters so that a convenient reference point could be established. This estuary is well mixed and tidally dominated (Wright et al. 1987).

A steady-state, one-dimensional advection-dispersion model,

$$\frac{d^2 \mathbf{C}(x)}{dx^2} = \left( \frac{R}{\alpha(x)D(x)} - \frac{1}{\alpha(x)} \frac{d\alpha(x)}{dx} - \frac{1}{D(x)} \frac{dD(x)}{dx} \right) \frac{d\mathbf{C}(x)}{dx} - \frac{\mathbf{r}(x)}{D(x)} \quad (1)$$

is used to represent the hydrodynamics of the estuary (Vörösmarty and Ioder 1994), where  $\mathbf{C}(x)$  is the concentration of the five biotic variables (in  $\text{mg C m}^{-3}$ , except DIN, which is in  $\text{mg N m}^{-3}$ ) and salt ( $\text{‰}$ ),  $R$  is the river discharge rate ( $\text{m}^3 \text{d}^{-1}$ ), and  $\mathbf{r}(x)$  is the production rate for each state vari-

able along the estuary. The functions for area  $\alpha(x)$  and dispersion  $D(x)$ ,

$$\alpha(x) = \alpha_1 x^2 + \alpha_0 \quad (2)$$

$$D(x) = \frac{bD_m}{b + x_m - x} \quad (3)$$

are based on experimental data from Plum Island Sound. Boundary conditions are imposed at the head of the estuary and offshore in the coastal zone ( $x_L$  and  $x_R$ , respectively). A fixed flow of material into the estuary forces the left boundary condition (at  $x_L$ ), and the right boundary condition (at  $x_R$ ) specifies the concentration of the state variables in the coastal zone, as given by

$$\left[ -\alpha(x)D(x) \frac{dC(x)}{dx} + RC(x) \right]_{x=x_L} = RC_L \quad (4)$$

$$C(x)|_{x=x_R} = C_R \quad (5)$$

where  $C_L$  and  $C_R$  are the concentrations of the state variables in the riverine input and coastal zone, respectively. The elements of  $r(x)$  in Eq. 1 are governed by the model as described below.

#### Autotrophs

The production rate of the autotrophs is governed by their specific growth rate less their mortality rate and the rate at which they are grazed by the heterotrophs, as given by

$$r_A(x) = (\mu_A - k_{DA})A(x) - \frac{\mu_{HA}H(x)}{Y_{HA}} \quad (6)$$

Growth rate of the autotrophs is assumed to be  $N$  limited only, so a simple Monod growth equation is used

$$\mu_A = \frac{V_A N(x)}{k_{NA} + N(x)} \quad (7)$$

#### Heterotrophs

Heterotrophs are supported by the direct grazing of the autotrophs as well as by the utilization of labile organic matter via the microbial loop (Azam et al. 1983),

$$r_H(x) = (\mu_{HA} + \mu_{HA} - k_{DH})H(x) \quad (8)$$

Growth supported by grazing is governed by a simple Monod-type equation:

$$\mu_{HA} = \frac{V_{HA}A(x)}{k_{AH} + A(x)} \quad (9)$$

The specific growth rate of the heterotrophs on OM is more complex, since growth can either be carbon or nitrogen limited depending on the C:N ratio of the heterotrophs ( $CN_L$ ), the C:N ratio of

the OM ( $CN_D$ ), and the yield of heterotrophs on OM ( $Y_{HC}$ ) (Caron and Goldman 1988; Anderson 1992). To capture these possibilities, we use a Monod growth expression with dual substrate limitation; however, dependency on DIN is adjusted by nitrogen available in the OM, as given by

$$\mu_{HC} = \frac{V_{HC}OM_L(x)}{k_{CH} + OM_L(x)} \times \left[ \left( \frac{N(x)}{k_{NH} + N(x)} (1 - \phi) + \phi \right) \right] \quad (10)$$

where

$$\phi = \begin{cases} \frac{CN_L}{CN_D Y_{HC}} & \text{for } \frac{CN_L}{CN_D Y_{HC}} < 1 \\ 1 & \text{for } \frac{CN_L}{CN_D Y_{HC}} \geq 1. \end{cases} \quad (11)$$

From these equations it is apparent that inorganic nitrogen will be immobilized only if  $\phi$  is less than one. For our lumped model, this criterion does not occur for typical values of the parameters, since heterotrophic growth on OM represents the entire microbial loop and higher trophic levels (from bacteria to macrozooplankton and fish) so that the yield ( $Y_{HC}$ ) is expectedly low. Consequently, the microbial loop will act to remineralize  $N$  as opposed to immobilizing it. Although the immobilization of  $N$  by bacteria introduces a time lag in an actual ecosystem, the high turnover rates typically associated with the microbial community (Hagström et al. 1988; Maloney et al. 1991) would imply that this time lag should be short compared to the growth rate of the higher trophic levels, so that immediate  $N$  remineralization, as occurs in this model, may not be far removed from reality.

#### Dissolved Inorganic Nitrogen

The balance around dissolved inorganic nitrogen (DIN) is given by

$$r_N(x) = \frac{\beta k_S OM_R(x)}{CN_D} - \frac{\mu_A A(x)}{CN_L} + \left( \frac{1}{Y_{HA}} - 1 \right) \frac{\mu_{HA} A(x)}{CN_L} + \left( \frac{1}{CN_L} - \frac{1}{CN_D} \right) k_{DA} A(x) + \left( \frac{1}{CN_D Y_{HC}} - \frac{1}{CN_L} \right) \mu_{HC} H(x) + \left( \frac{1}{CN_L} - \frac{1}{CN_D} \right) k_{DH} H(x) \quad (12)$$



TABLE 2. Parameter values used in the simulation for nominal case.

Parameter	Value	Description
$R$	86,400	River discharge ( $\text{m}^3 \text{d}^{-1}$ )
$\alpha_I$	$3.4 \times 10^{-6}$	Area parameter, Eq. 2 (unitless)
$\alpha_0$	17	Area parameter, Eq. 2 ( $\text{m}^2$ )
$D_m$	$1.36 \times 10^6$	Dispersion at estuary mouth ( $\text{m}^2 \text{d}^{-1}$ )
$b$	5,000	Dispersion parameter, Eq. 3 (m)
$x_m$	23,330	Length of estuary (m)
$V_A$	2.0	Maximum growth rate, autotrophs ( $\text{d}^{-1}$ )
$\epsilon$	0.9	Fraction of gross production that is net production
$V_{HA}$	1.0	Maximum grazing rate of heterotrophs on autotrophs ( $\text{d}^{-1}$ )
$V_{HC}$	0.5	Maximum growth rate of heterotrophs on labile OM ( $\text{d}^{-1}$ )
$k_{NA}$	30	Half saturation constant, autotrophs on DIN ( $\text{mg N m}^{-3}$ )
$k_{AH}$	400	Half saturation constant, heterotrophs on autotrophs ( $\text{mg C m}^{-3}$ )
$k_{CH}$	120	Half saturation constant, heterotrophs on labile OM ( $\text{mg C m}^{-3}$ )
$k_{NH}$	15	Half saturation constant, heterotrophs on DIN ( $\text{mg N m}^{-3}$ )
$Y_{HA}$	0.1	Yield of heterotrophs from autotrophs ( $\text{mg C mg}^{-1} \text{C}$ )
$Y_{HC}$	0.01	Yield of heterotrophs from labile OM ( $\text{mg C mg}^{-1} \text{C}$ )
$k_{DA}$	0.1	Mortality rate of autotrophs ( $\text{d}^{-1}$ )
$k_{DH}$	0.1	Mortality rate of heterotrophs ( $\text{d}^{-1}$ )
$f_{AL}$	0.8	Fraction of autotrophic biomass that is labile
$f_{HL}$	0.8	Fraction of heterotrophic biomass that is labile
$CN_L$	6	C:N ratio of living biomass (autotrophs and heterotrophs)
$CN_D$	15	C:N ratio of dead biomass (labile and refractory OM)
$k_S$	0.001	Settling or flocculation rate ( $\text{d}^{-1}$ )
$k_{DOM}$	0.0001	Abiotic degradation rate of refractory OM ( $\text{d}^{-1}$ )
$\beta$	0.6	Fraction of settled OM that is remineralized

The first term in this expression represents benthic N remineralization from the refractory OM that settles or flocculates to the benthos. This assumes that a  $(1 - \beta)$  fraction of the N input is denitrified by the benthos. The next three terms account for N consumption by the autotrophs, remineralization of N by heterotrophs grazing the autotrophs, and N released following the death of the autotrophs. N release is required to maintain a constant C:N ratio of dead OM. The final two terms account for N remineralization (or immobilization) by heterotrophic utilization of  $OM_L$  and death of the heterotrophs.

#### Labile Organic Matter

The production rate of labile OM is given by

$$\mathbf{r}_{OML}(x) = f_{AL}k_{DA}A(x) + f_{HL}k_{DH}H(x) - \frac{\mu_{HC}}{Y_{HC}}H(x) + k_{DOM}OM_R(x). \quad (13)$$

The first two terms account for the fraction of autotrophic and heterotrophic mortality that contributes to the labile OM pool, and the third term accounts for the uptake of  $OM_L$  by the heterotrophs. The last term is an abiotic, first-order decay of refractory OM into the labile pool.

#### Refractory Organic Matter

The balance around the refractory OM pool is similar to that for the labile pool,

$$\mathbf{r}_{OMR}(x) = (1 - f_{AL})k_{DA}A(x) + (1 - f_{HL})k_{DH}H(x) - (k_{DOM} + k_S)OM_R(x) \quad (14)$$

except that a flocculation-sedimentation term is included, and there is no biotic consumption of  $OM_R$ . The parameter  $k_{DOM}$  represents the quality or degradability of the refractory OM, while  $k_S$  captures, in a simple manner, the relative ratios of particulate to dissolved OM. High particulate OM loadings are expected to settle faster.

#### Model Parameters

Parameter values used in the nominal simulation are given in Table 2, and are based on values typically used in many food web modeling studies (Evans and Parslow 1985; Childers and McKellar 1987; Fasham et al. 1990; Taylor and Joint 1990; Maloney and Field 1991; Maloney et al. 1991). Input from experimental observations from Plum Island Sound (Wright et al. 1987) were also used to tune the model. Values for the boundary conditions are given in Table 3. A Fortran collocation routine (COLNEW) (Ascher et al. 1981; Bader and Ascher 1987) was used to solve the boundary-value problem (Eq. 1).

#### Simulation Results

##### NOMINAL SIMULATION

Results of the Nominal Simulation are presented as a transect along a hypothetical estuary in Fig. 10. In the upper reaches of the estuary the model

TABLE 3. Values used for boundary conditions. The left boundary corresponds to the pool concentrations in river discharge, while the right boundary corresponds to pool concentrations offshore.

Variable	Left Boundary $C_{L, x_L = 0 \text{ m}}$	Right Boundary $C_{R, x_R = 28,250 \text{ m}}$
Autotrophs ( $\text{mg C m}^{-3}$ )	20.	100.
Heterotrophs ( $\text{mg C m}^{-3}$ )	1.	30.
DIN ( $\text{mg N m}^{-3}$ )	120.	15.
Labile OM ( $\text{mg C m}^{-3}$ )	500.	12.
Refractory OM ( $\text{mg C m}^{-3}$ )	5,000.	1,200.
Salt (‰)	0.	31.

indicates the development of an algal bloom and a concomitant decrease in inorganic nitrogen concentration (Fig. 10a). Immediately downstream of the bloom, there is a marked increase in heterotrophic biomass, and in conjunction with increased heterotrophic activity, a regenerative increase in inorganic nutrients. DIN concentration increases in the region 5 km and 10 km downstream (Fig. 10a). The spatial pattern of organic matter concentration is shown in Fig. 10c. Once the growth rate of

heterotrophs balances their removal rate due to downstream mixing, there is a marked reduction in the concentration of labile organic matter reflecting heterotrophic uptake. The larger refractory organic matter pool, however, shows little downstream dynamics; it mixes almost conservatively with low organic matter seawater. The spatial patterns of autotrophy and heterotrophy are seen in Figs. 10b and 10d. Net autotrophy is confined to the upper 5 km. Net heterotrophy is greatest just below the region where algal biomass peaks. The system never returns to net autotrophy, remaining heterotrophic throughout the remainder of the estuary. Net system heterotrophy is confirmed by the spatial patterns of organic carbon and DIN (Fig. 10d); there is a net increase in DIN (exports > imports) and a net reduction in organic carbon (TOC output < TOC import).

This model was not rigidly parameterized to any specific estuarine system. Our simulation goals in this study were not to mimic a specific complex, real system but rather to qualitatively investigate

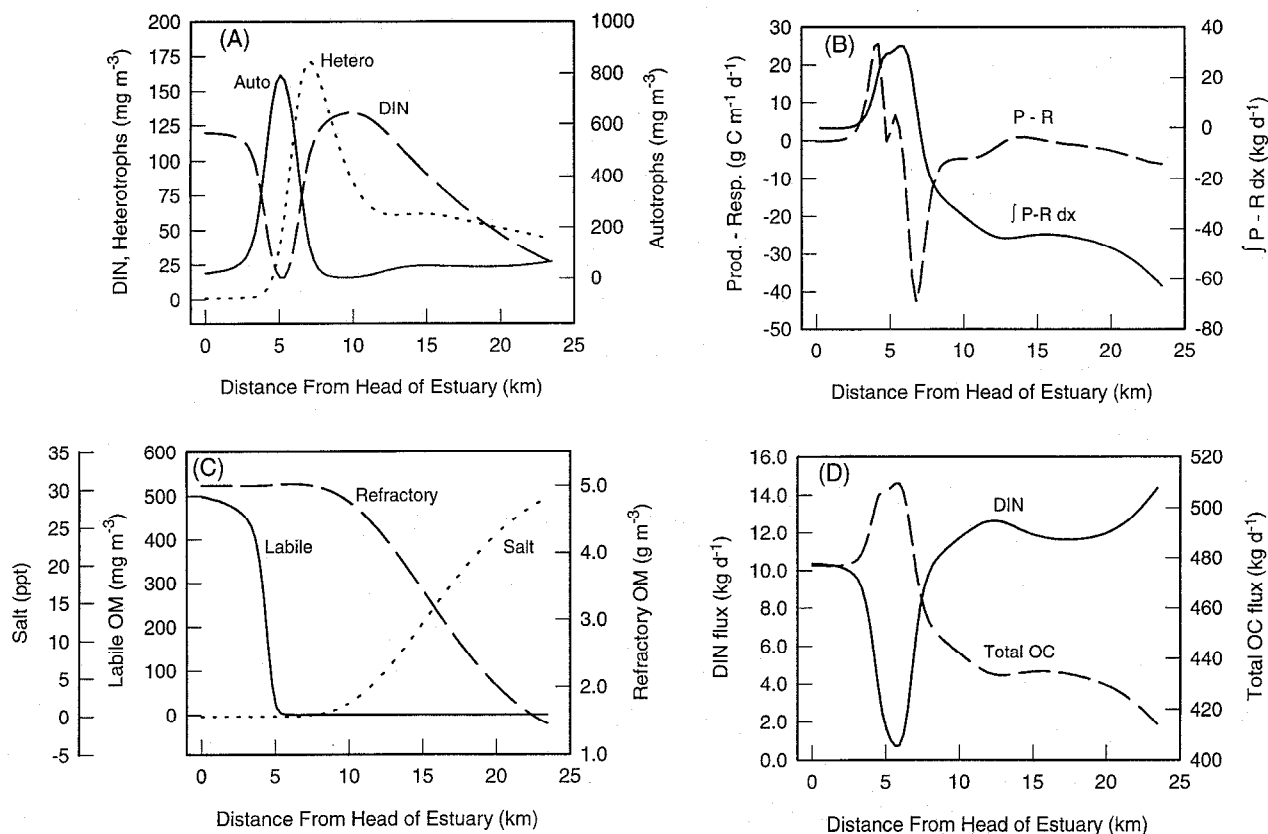


Fig. 10. Results of simulation run for nominal case (Tables 2 and 3). Concentrations of (A) dissolved inorganic nitrogen (DIN), heterotrophs, autotrophs, and (C) refractory and labile organic matter (OM) and salt as a function of distance along the estuary terminating at the mouth of the estuary ( $x_m$ ). (B) Gross production, P, minus total respiration, R, (heterotrophic plus autotrophic) along the estuary, as well as the integrated value of (P-R)  $d\sigma$  from  $\sigma = x_L$  to  $x$ . (D) Flow of total organic carbon ( $A + H + OM_L + OM_R$ ) and DIN through an estuarine cross section at  $x$ .

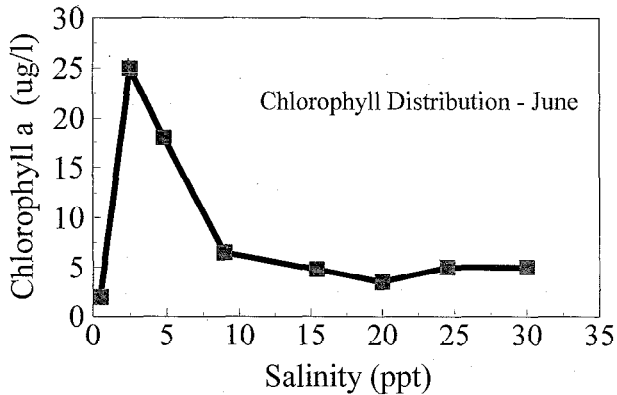


Fig. 11. Spatial distribution of chlorophyll *a* in the Parker River-Plum Island Sound estuary of northeastern Massachusetts during summer. From Wright et al. (1987) and Fry et al. (1992).

general responses of a generic estuarine system to variations in quantity and quality of organic matter and nutrient inputs. We chose as our generic system a tidally driven estuary with a river input. Where possible we chose values for parameters appropriate for the Parker River-Plum Island Sound estuary in northeastern Massachusetts. Such parameters include estuarine physical dimensions (length, width, depth, etc.), riverine inputs of water, nutrients and organic matter, advection-dispersion characteristics, oceanic concentrations of organic matter and nutrients, and phytoplankton and bacterial growth rates.

Comparisons of simulation results with field data indicate that our model captures the essence of the Parker River system. The simulated spatial pattern of phytoplankton biomass closely resembles the pattern of chlorophyll distribution in the estuary during summer (Fig. 11). During summer when river flow is low, the occurrence of a phytoplank-

ton bloom in the upper estuary is a regular phenomenon. Chlorophyll concentrations are elevated 20–120  $\mu\text{g}/\text{l}^{-1}$  in this region (Wright et al. 1987; Fry et al. 1992). The model-predicted pattern of autotrophy and heterotrophy also closely resembles that in the estuary as indicated by the pattern of oxygen saturation (Balsis et al. 1995). In the region of the chlorophyll peak, dissolved oxygen (DO) is supersaturated. Immediately downstream, in the region of the estuarine turbidity maximum, DO is well below saturation but then approaches saturation as the ocean is approached. The simulated pattern of allochthonous organic matter utilization is also similar to that observed in the field. Fry et al. (1992) showed a marked depletion in the  $\delta^{13}\text{C}$  signature of dissolved inorganic carbon in the upper reaches of the estuary in summer, reflecting the remineralization of isotopically light terrestrial DOC. In about the same region of the estuary, our model shows rapid utilization of the labile fraction of terrestrial DOC.

#### SCENARIO I—VARYING THE DIN:DON LOADING RATIO

This scenario compares the metabolic response of systems that are organic matter loading-dominated (Nominal Simulation—120:333, DIN:DON) to DIN loading-dominated (scenario I—370:118, DIN:DON). Switching to DIN loading has two primary effects: one, primary and secondary production and biomass increase substantially; and two, the system becomes slightly net autotrophic (Fig. 12). While there is no spatial difference in the enhanced production, algal biomass increases from about 800  $\text{mg m}^{-3}$  to 2,000  $\text{mg m}^{-3}$ . The switch in loading ratios stimulates both autotrophy and heterotrophy in the region of the bloom, indicating

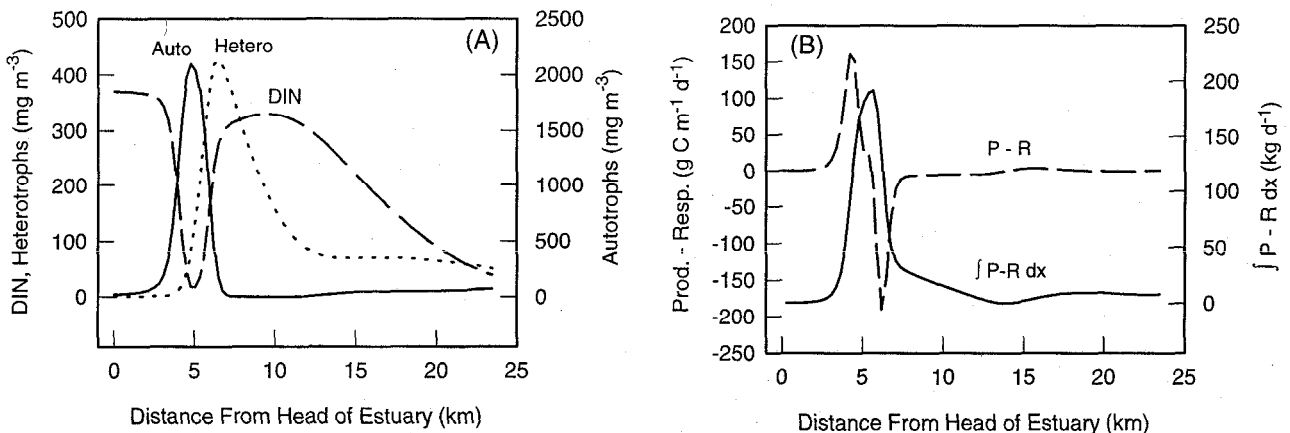


Fig. 12. Simulation results for scenario I: Change in the ratio of DIN to organic matter inputs (input transposed from nominal case). New boundary conditions:  $C_L(\text{DIN}) = 370 \text{ mg N m}^{-3}$ ,  $C_L(\text{OM}_L) = 178$ ,  $C_L(\text{OM}_R) = 1,606 \text{ mg C m}^{-3}$ ; all other parameters and boundary conditions as in nominal case. See text and caption of Fig. 10 for details.

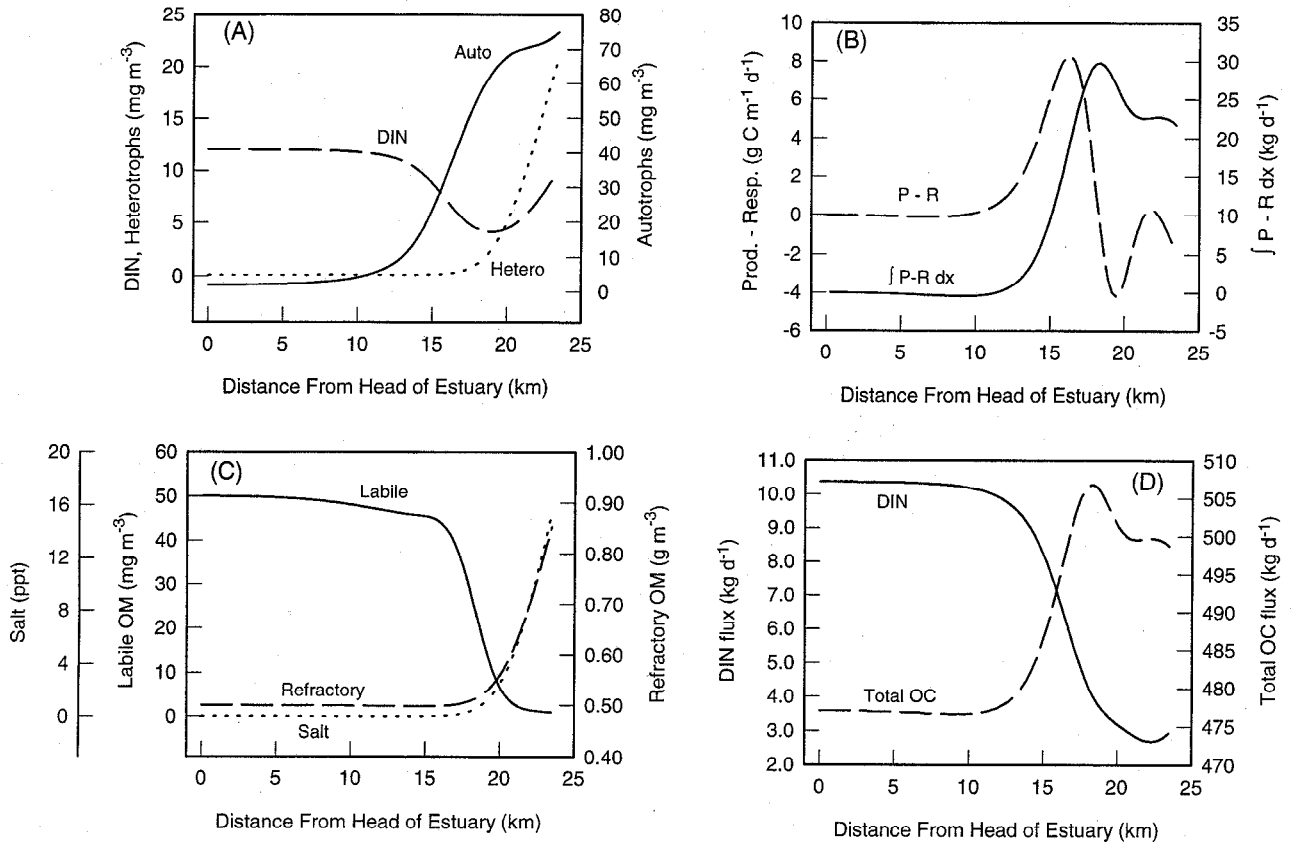


Fig. 13. Simulation results for scenario II: A 10-fold increase in river discharge with the same carbon and nitrogen loading:  $R = 8.64 \times 10^5 \text{ m}^3 \text{ d}^{-1}$ ; left boundary conditions,  $C_L(A) = 2.0$ ,  $C_L(H) = 0.1$ ,  $C_L(\text{DIN}) = 12.0$ ,  $C_L(\text{OM}_L) = 50$ ,  $C_L(\text{OM}_R) = 500$ ,  $C_L(\text{Salt}) = 0 \text{ mg m}^{-3}$ ; all other parameters as in nominal case. See text and caption of Fig. 10 for details.

very tight coupling between productive and consumptive processes. The decrease in overall level of system heterotrophy is more a response to the decrease in DOM than to an increase in DIN. Apparently algal production is consumed and remineralized so rapidly that there is little net difference between production and decomposition, hence little biomass accumulation, hence little chance for net autotrophy.

#### SCENARIO II—INCREASED RATE OF FLUSHING

In this scenario water inputs increase an order of magnitude, thus greatly increasing the rate of flushing. The two main effects of increasing water throughput are to push the algal bloom toward the mouth of the estuary, and to drive the system markedly toward net autotrophy (Fig. 13). The level of algal biomass production is less than in the nominal case, primarily because biomass is flushed out almost as fast as it is produced. Heterotrophs with their longer turnover times are essentially pushed out of the estuary and unable to keep up with the autotrophs. Thus considerable algal production is

ungrazed and exported. The net consumption of DIN in the estuary and net export of organic matter, also indicates that the system is net autotrophic.

#### SCENARIO III—DECREASED LABILITY OF ALLOCHTHONOUS ORGANIC MATTER

Here we are investigating the heterotrophic importance of variations in the degradability of allochthonous organic matter. The effect of lowering the degradability of organic matter was seen mainly in the magnitude of autotrophy and heterotrophy in the regions where autotrophs and heterotrophs reach their maximum biomass (Fig. 14). Relative to the Nominal Scenario, peak algal and heterotrophic biomasses are reduced 20–25%, presumably because less N was remineralized from allochthonous organic matter. The upstream region of autotrophy was enhanced about 50%, reflecting the dominance of autotrophy over heterotrophy, following the reduction in lability of allochthonous organic matter inputs to the head of the estuary. The magnitude of heterotrophy in mid bay was

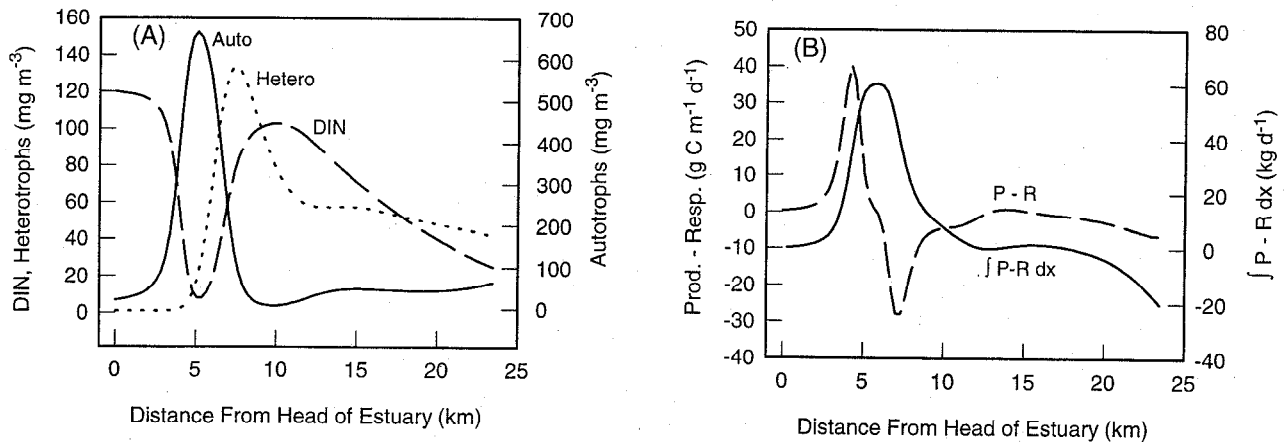


Fig. 14. Simulation results for scenario III: Change in degradability of allochthonous organic matter:  $k_{DOM} = 0.00001 \text{ d}^{-1}$ ;  $C_L(OM_L) = 5 \text{ mg C m}^{-3}$ ; all other parameters and boundary conditions as in nominal case. See text and caption of Fig. 10 for details.

also reduced substantially, again reflecting the decreased degradability of allochthonous OM. Overall, the estuary became substantially less net heterotrophic with total production balancing total consumption.

#### SCENARIO IV—INCREASING THE POC TO DOC RATIO OF ALLOCHTHONOUS ORGANIC MATTER

As we do not explicitly separate dissolved from particulate carbon in this model, the effect of DOC:POC variations is simulated by altering the settling coefficient (as a great deal of POC settles out upon entering estuaries [Meade 1982]). The dynamics of the upstream algal bloom and heterotrophic consumption of the bloom are virtually unchanged from the Nominal Scenario (Fig. 15). The major difference is seen in the level of heterotrophy in the lower half of the estuary. Here, heterotrophy dominates the system due to the en-

hanced benthic metabolism associated with increased C sedimentation. Net heterotrophy of the system was increased from 20 kg C d<sup>-1</sup> to about 200 kg C d<sup>-1</sup> under this scenario.

#### SUMMARY OF SIMULATION EXPERIMENTS

The relative insensitivity of the model to large variations in the DIN:DON loading ratio was not as expected. Large increases or decreases in DIN loading did translate into substantial algal responses, but the overall autotrophic-heterotrophic balance was not greatly affected. In contrast, even small additions of organic matter tended to exert significant influence over the level of net heterotrophy. The explanation for this behavior is that autotrophic production and heterotrophic consumption of that algal-produced material are very tightly linked, spatially and temporally. Generally, whatever level of autotrophy is produced, the het-

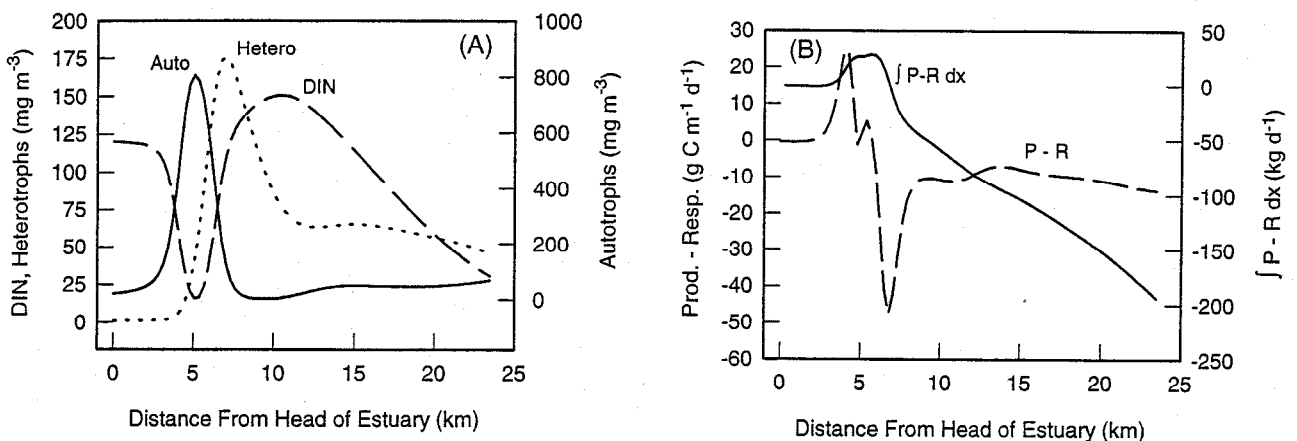


Fig. 15. Simulation results for scenario IV: Change in the ratio of DOC to POC inputs:  $k_s = 0.005 \text{ d}^{-1}$ ; all other parameters and boundary conditions as in nominal case. See text and caption of Fig. 10 for details.

erotrophs quickly crop that production, grow, and recycle the inorganic nutrients. Thus there is little net ecosystem production. Allochthonous organic matter inputs, however, have a high C:N ratio and considerable carbon is respired prior to much N being regenerated and made available to autotrophs. Thus respiration exceeds primary production. These results do not diminish the severity of the problem of nutrient-enhanced cultural eutrophication. The model suggests that large algal blooms are followed closely with enormous heterotrophic activity. What the model suggests is that algal blooms can be matched by heterotrophic activity such that the system stays balanced autotrophically-heterotrophically.

The response of the system to large shifts in flushing time was also not as predicted beforehand. It was initially thought that because of the short turnover time of nutrients relative to allochthonous organic matter turnover and water flushing, that a nutrient-dominated system would be relatively insensitive to changes in flushing. Because of the slow turnover of organic matter, however, it was thought that the metabolic response of a system dominated by organic matter loading would be sensitive to changes in flushing. The model suggests differently. Because of the close coupling between autotrophic and heterotrophic activity, an increase in water flushing was ineffective in driving the system toward net autotrophy, except for extreme events where the heterotrophic bloom was pushed offshore, such as in scenario II. Sufficient mechanisms exist within the estuary to trap a certain percentage of allochthonous organic matter inputs. Thus even with higher flushing rates, organic matter respiration is sufficient to drive the system toward net heterotrophy.

The importance of mechanisms that trap allochthonous organic matter was not appreciated prior to modeling. Modeling suggested that flocculation and particle settling within estuaries has the effect of increasing almost indefinitely the residence time of organic matter within an estuary. Thus compounds with even very long turnover times can be processed while retained in the estuary.

In light of these new "understandings" developed during this modeling study, we are redirecting some of our research efforts in the Plum Island Sound estuary. In particular we are interested in examining the suggested close coupling between algal and heterotrophic activity and the mechanisms that retain allochthonous organic matter in estuaries.

### Conclusions

Man's activities in watersheds regulate the composition of materials exported to streams and riv-

ers: their magnitudes, timing of discharge, and quality.

Rivers integrate basinwide activities. Materials entering rivers are subject to utilization, modification, and storage. Discharge of materials from rivers may differ substantially from the materials entering the river.

Man has altered the world's rivers by controlling their floods, constructing large reservoirs, removing floodplains and riparian forests, and channelizing their flow. These activities modify the nature of materials exported to the coastal zone.

The metabolism of estuaries is strongly influenced by the inputs of water, organic matter, and inorganic nutrients from rivers. Patterns of autotrophy and heterotrophy are regulated by the residence time of estuarine water, by the magnitude of inorganic nutrients and organic matter, by the relative ratio of inorganic nutrients to organic matter, by the quality of organic matter, and by the ratio of POC to DOC.

Our modeling work suggests that the autotrophic-heterotrophic balance of estuaries is more sensitive to increases in organic matter loading than to increases in inorganic nutrient loading.

### ACKNOWLEDGMENTS

This work was partially supported by grants from the National Science Foundation (OCE-9214461), the Sweetwater Trust, the Lakian Foundation, and the Department of Energy's Ocean Margins Program (DE-FG02-92ER61438). Many thanks are extended to Hap Garritt and Sue Donovan for help in literature surveys, and figure and manuscript preparation.

### LITERATURE CITED

- ANDERSON, T. R. 1992. Modelling the influence of food C:N ratio, and respiration on growth and nitrogen excretion in the marine zooplankton and bacteria. *Journal of Plankton Research* 14:1645-1671.
- ASCHER, U., J. CHRISTIANSEN, AND R. D. RUSSELL. 1981. Collocation software for boundary-value ODEs. *Association for Computing Machinery, Transactions on Mathematical Software* 7:209-222.
- ATTIWEILL, P. 1991. The disturbance of forested watersheds, p. 193-213. In H. Mooney, E. Medina, D. Schindler, E.-D. Schulze, and B. Walker (eds.), SCOPE 45: Ecosystem Experiments. John Wiley and Sons, New York.
- AZAM, F., T. FENCHEL, J. G. FIELD, J. S. GRAY, L. A. MEYER-REIL, AND F. THINGSTAD. 1983. The ecological role of water-column microbes in the sea. *Marine Ecology Progress Series* 10:257-263.
- BADER, G. AND U. ASCHER. 1987. A new basis implementation for a mixed order boundary value ODE solver. *Society for Industrial and Applied Mathematics Journal on Scientific and Statistical Computing* 8:483-500.
- BALSIS, B. R., D. ALDERMAN, I. BUFFAM, R. GARRITT, C. HOPKINSON, AND J. VALLINO. 1995. Total system metabolism at the Palm Island estuarine system. *Biological Bulletin* In Press.
- BORMANN, F. H. AND G. LIKENS. 1981. Pattern and Process in a Forested Ecosystem. Springer-Verlag, New York.
- BRINSON, M., M. BRADSHAW, AND E. KANE. 1984. Nutrient assimilative capacity of an alluvial floodplain swamp. *Journal of Applied Ecology* 21:1041-1057.
- BRINSON, M., B. SWIFT, R. PLANTICO, AND J. BARCLAY. 1981. Ri-

- parian ecosystems: Their ecology and status. United States Fish and Wildlife Service, Biological Service Program, FWS/OBS-81/17, Washington, D.C..
- BURELLI, M. 1992. Nile delta sinking. *Alternatives* 18:1-9.
- CARON, D. A. AND J. C. GOLDMAN. 1988. Dynamics of protistan carbon and nutrient cycling. *Journal of Protozoology* 35:247-249.
- CHILDERS, D. L. AND H. N. MCKELLAR, JR. 1987. A simulation of saltmarsh water column dynamics. *Ecological Modelling* 36: 211-238.
- COOK, E. 1976. *Man, Energy and Society*. W. H. Freeman and Co. San Francisco.
- CONNER, W. AND J. DAY. 1976. Productivity and composition of a bald cypress-water tupelo site and a bottomland hardwood site in a Louisiana swamp. *American Journal of Botany* 63:1354-1365.
- DAY, J., T. BUTLER, AND W. CONNER. 1977. Productivity and nutrient export studies in a cypress swamp and lake system in Louisiana, p. 255-269. In M. Wiley (ed.), *Estuarine Processes*, Vol. 2. Academic Press, New York.
- DIXON, R., S. BROWN, R. HOUGHTON, A. SOLOMON, M. TREXLER, AND J. WISNIEWSKI. 1994. Carbon pools and flux of global forest ecosystems. *Science* 263:185-190.
- DUNNE, T. AND L. LEOPOLD. 1978. *Water in Environmental Planning*. W. H. Freeman and Co. New York.
- ELDER, J. 1985. Nitrogen and phosphorus speciation and flux in a large Florida river-wetland system. *Water Resources Research* 2:443-453.
- EVANS, G. T. AND J. S. PARSLAW. 1985. A model of annual plankton cycles. *Biological Oceanography* 3:327-347.
- FASHAM, M. J. R., H. W. DUCKLOW, AND S. M. MCKELVIE. 1990. A nitrogen-based model of plankton dynamics in the ocean mixed layer. *Journal of Marine Research* 48:591-639.
- FRY, B., M. HULLAR, B. PETERSON, S. SAUPE, AND R. WRIGHT. 1992. DOC production in a salt marsh estuary. *Archiv Fuer Hydrobiologie* 37:1-8.
- HAGSTRÖM, A., F. AZAM, A. ANDERSON, J. WIKNER, AND F. RAS-SOULZADEGAN. 1988. Microbial loop in an oligotrophic pelagic marine ecosystem: Possible roles of cyanobacteria and nanoflagellates in the organic fluxes. *Marine Ecology Progress Series* 49:171-178.
- HOPKINSON, C. S. AND J. W. DAY. 1980a. Modeling hydrology and eutrophication in a Louisiana swamp forest ecosystem. *Environmental Management* 4:325-336.
- HOPKINSON, C. S. AND J. W. DAY. 1980b. Modeling the relationship between development and storm water and nutrient runoff. *Environmental Management* 4:315-324.
- HOWARTH, R., J. FRUCL, AND D. SHERMAN. 1991. Inputs of sediment and carbon to an estuarine ecosystem: Influence of land use. *Ecological Applications* 1:27-39.
- ITTEKKOT, V. 1988. Global trends in the nature of organic matter in river suspensions. *Nature* 332:436-438.
- ITTEKKOT, V. AND R. LAANE. 1991. Fate of riverine particulate organic matter, p. 233-242. In E. Degens, S. Kempe, and J. Richey (eds.), *Scope 42: Biogeochemistry of Major World Rivers*. John Wiley and Sons, New York.
- KEMPE, S. 1984. Sinks of the anthropogenically enhanced carbon cycle in surface fresh waters. *Journal of Geophysical Research* 89 D3:4657-4676.
- KEMPE, S., M. PETTINE, AND G. CAUWET. 1991. Biogeochemistry of European rivers, p. 169-211. In E. Degens, S. Kempe, and J. Richey (eds.), *Scope 42: Biogeochemistry of Major World Rivers*. John Wiley and Sons, New York.
- LIKENS, G. AND F. BORMANN. 1975. Nutrient-hydrologic interactions, p. 1-63. In A. Hasler (ed.), *Coupling of Land and Water Systems*. Springer-Verlag, New York.
- MALONEY, C. AND J. FIELD. 1991. The size-based dynamics of plankton food webs. I. A simulation model of carbon and nitrogen flows. *Journal of Plankton Research* 13:1003-1038.
- MALONEY, C. L., J. G. FIELD, AND M. I. LUCAS. 1991. The size-based dynamics of plankton food webs. II. Simulations of three contrasting southern Benguela food webs. *Journal of Plankton Research* 13:1039-1092.
- MEADE, R. 1982. Sources, sinks and storage of river sediment in the Atlantic drainage of the United States. *Journal of Geology* 90:235-252.
- MEYBECK, M. 1982. Carbon, nitrogen and phosphorus transport by world rivers. *American Journal of Science* 282:401-450.
- MILLIMAN, J., Q. YUN-SHAN, B. MEI-E, AND Y. SAITO. 1987. Man's influence on the erosion and transport of sediment by Asian rivers: The Yellow River (Huanghee) example. *Journal of Geology* 95:751-762.
- MITSCHE, W., C. DORGE, AND J. WIEMHOFF. 1979. Ecosystem dynamics and a phosphorus budget of an alluvial cypress swamp in southern Illinois. *Ecology* 60:1116-1124.
- NAIMAN, R. 1986. Ecosystem alteration of boreal forest streams by beaver. *Ecology* 67:1254-1269.
- OMERNIK, J. 1976. The influence of land use on stream nutrient levels. United States Environmental Protection Agency 600/3-76-014.
- PETR, T. 1986. The Volta River system, p. 163-199. In B. Davies and K. Walker (eds.), *The Ecology of River Systems*. W. Junk Publishers, Dordrecht, The Netherlands.
- RICHEY, J., A. DEVOL, J. HEDGES, B. FORSBER, R. VICTORIA, L. MARTINELLI, AND N. RIBEIRO. 1990. Distribution and flux of carbon in the Amazon River. *Limnology and Oceanography* 35: 352-371.
- SCHLESINGER, W. AND J. MELACK. 1981. Transport of organic carbon in the world's rivers. *Tellus* 33:172-187.
- SEDELL, J. AND J. FROGGETT. 1984. Importance of streamside forests to large rivers: The isolation of the Williamette River, Oregon, USA, from its floodplain. *Internationale Vereinigung für theoretische und angewandte Limnologie, Verhandlungen* 22:1828-1834.
- SHALASH, S. 1982. Effects of sedimentation on the storage capacity of the High Aswan Dam reservoir. *Hydrobiologia* 92:623-639.
- SHARAF-EL-DIN, S. 1977. Effect of the Aswan High Dam on the Nile flood and on the estuarine and coastal circulation pattern along the Mediterranean Egyptian coast. *Limnology and Oceanography* 22:194-207.
- SLAYMAKER, O. 1982. Land use effects on sediment yield and quality. *Hydrobiologia* 91:93-109.
- SOTILLE, W. 1973. Studies of microbial production and utilization of dissolved organic carbon in a Georgia salt marsh estuarine ecosystem. Ph.D. Dissertation, University of Georgia, Athens, Georgia.
- STANLEY, D. 1988. Subsidence in the northeastern Nile delta: Rapid rates, possible causes and consequences. *Science* 240: 497-500.
- STANLEY, D. AND A. WARNE. 1992. Nile delta: Recent geological evolution and human impact. *Science* 260:628-634.
- TAMM, C. 1991. What ecological lessons can we learn from deforestation processes in the past?, p. 45-58. In H. A. Mooney, E. Medina, D. Schindler, E. Schulze, and B. Walker (eds.), *Scope 45: Ecosystem Experiments*. John Wiley and Sons, New York.
- TAYLOR, A. H. AND I. JOINT. 1990. A steady-state analysis of the 'microbial loop' in stratified systems. *Marine Ecology Progress Series* 59:1-17.
- UNITED STATES SOIL CONSERVATION SERVICE. 1972. *Hydrology, Section 4. National Engineering Handbook*. Washington, D.C.
- VAN BENNEKOM, A. AND W. SALOMONS. 1981. Pathways of nutrients and organic matter from land to ocean through rivers, p. 33-51. In J. Martin, J. Burton, and D. Eisma (eds.), *River Inputs to the Ocean System*. UNESCO-UNEP, SCOR Workshop, United Nations, New York.
- VOLLENWEIDER, R. 1968. Scientific basis of eutrophication of

- lakes and flowing waters with emphasis on P and N as causative factors. DAS/CSI/Rept 68. Paris.
- VÖRÖSMARTY, C. J. AND T. C. LODER, III. 1994. Spring-neap tidal contrasts and nutrient dynamics in marsh-dominated estuaries: The spectrum effect. *Estuaries* 17:537-551.
- WADIA, W. 1982. Effect of regulation of the Nile River on the bioproductivity of southeastern Mediterranean Sea. *Journal of Ichthyology* 22:164-167.
- WHARTON, C., W. KITCHENS, E. PENDLETON, AND T. SIPE. 1982. The ecology of bottomland hardwood swamps of the southeast: A community profile, United States Fish and Wildlife Service Biological Services Program, FWS/OBS-81/37.
- WISCHMEIER, W. AND D. SMITH. 1978. Predicting rainfall erosion losses—A guide to conservation planning. Agricultural Handbook 537. United States Department of Agriculture, Washington, D.C.
- WOLLAST, R. 1983. Interactions in estuaries and coastal waters, p. 385-410. In B. Bolin and R. Cook (eds.), *The Major Biogeochemical Cycles and Their Interactions*. SCOPE 21. John Wiley and Sons, New York.
- WOLMAN, M. 1967. A cycle of sedimentation and erosion in urban river channels. *Geografiska Annaler* 49A:385-395.
- WRIGHT, R., R. COFFIN, AND M. LÉBO. 1987. Dynamics of planktonic bacteria and heterotrophic microflagellates in the Parker estuary, northern Massachusetts. *Continental Shelf Science* 7:1383-1397.
- YARBRO, L. 1983. The influence of hydrologic variations on phosphorous cycling and retention in a swamp stream ecosystem, p. 223-245. In T. Fontaine and S. Bartell (eds.), *Dynamics of Lotic Ecosystems*. Ann Arbor Science, Ann Arbor, Michigan.

*Received for consideration, February 15, 1994*

*Accepted for publication, May 7, 1995*