Benthic-Pelagic Interactions: Nutrient and Oxygen Dynamics

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Introduction

In Chesapeake Bay production of organic matter tends to be dominated by phytoplankton; such production is autotrophic in that phytoplankton synthesize their own food from inorganic nutrients and sunlight. Though autotrophic activity occurs in the pelagic zone (throughout the water column), it is generally restricted to the euphotic, or upper, region of the water through which there is enough light penetration for photosynthesis to occur. Much of the consumption of organic matter, a heterotrophic process, is concentrated at or near the sediment surface (the benthos) where a great deal of biological and chemical activity occurs. The various mechanisms by which these pelagic and benthic zones are functionally

Oxygen Dynamics in the Chesapeake Bay

A Synthesis of Recent Research

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connected have been referred to as pathways of *benthic-pelagic coupling*. It is the dynamic nature of this coupling that influences the levels of dissolved oxygen in the Chesapeake Bay estuary.

Two major pathways which have received much attention in recent years include (1) delivery of particulate organic matter (POM) from the water column, where it is produced, to the benthos, where it is stored and consumed; and (2) decomposition of particulate organic matter in the benthos and the resulting regeneration and transport of nutrients from sediments back to the euphotic zone, where they are assimilated again by phytoplankton for primary production. In some cases, benthic-pelagic coupling also provides a means by which organic and inorganic materials may be transported horizontally (across salinity and depth gradients) while being used reciprocally in autotrophic and heterotrophic processes (Kemp and Boynton 1984; Malone et al. 1986).[1]

The cumulative effect of complex pathways of benthic-pelagic coupling on dissolved oxygen concentrations in Chesapeake Bay and other estuaries depend largely on physical hydrodynamic processes (Boicourt, this volume). For example, density and pressure gradients, turbulence and internal waves set up by wind, tides and riverflow all affect the nature of interactions between benthic and pelagic components of the ecosystem. It is this acute dependence of ecological processes on physical transport which distinguishes aquatic systems, and particularly estuaries, from other major ecosystems.

Figure 1 depicts the principal processes of benthic-pelagic coupling for estuarine ecosystems. Nutrients — in particular, nitrogen, phosphorus and silicon — enter the estuary each year primarily during spring runoff/riverflow and support the new growth of phytoplankton communities. These communities are dominated by diatoms in spring and flagellated forms in summer (Malone, this volume). Much of this phytoplankton production of organic matter is

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[1] On the one hand, the fate of many pollutants entering an estuary like Chesapeake Bay can be controlled by the nature of benthic-pelagic coupling mechanisms, while on the other, these benthic-pelagic interactions may themselves be altered by the introduction of various anthropogenic substances into coastal waters.

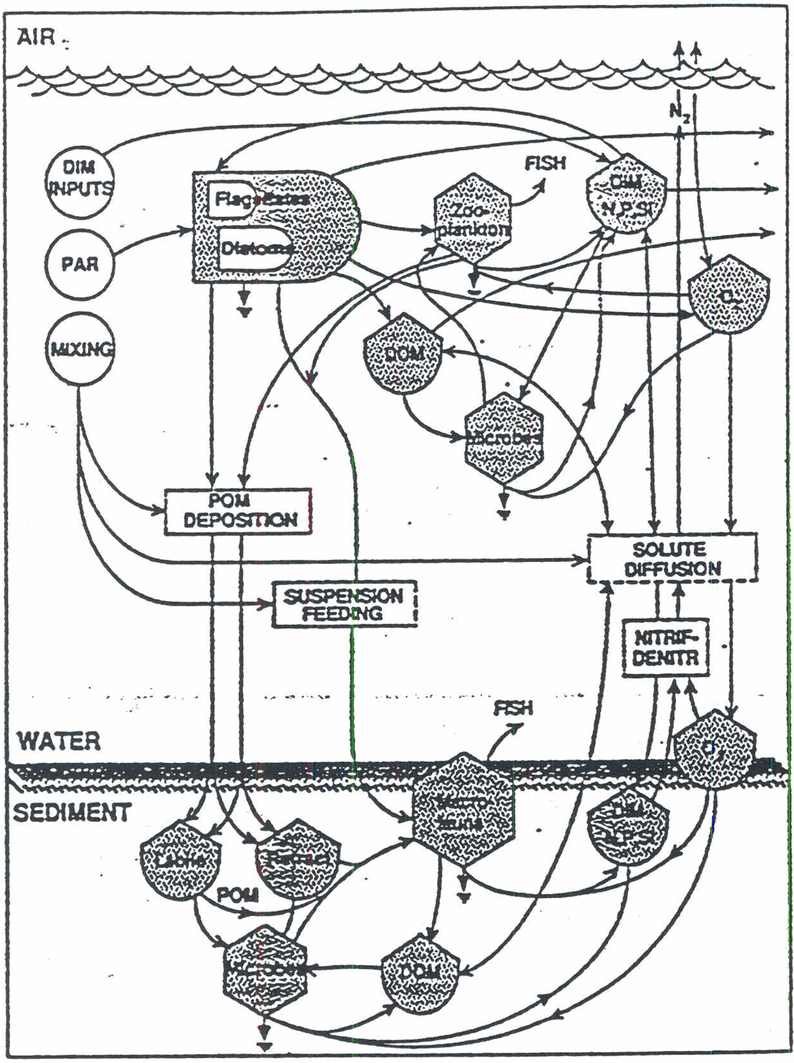

Figure 1. Conceptual diagram depicting three major ecosystem processes of benthic-pelagic coupling in an estuarine environment: (1) deposition of particulate organic matter (POM); (2) diffusion of solutes across the sediment-water interface; (3) benthic macrofaunal suspension feeding on POM in overlying waters. Other processes shown include (1) plankton trophic interactions which affect POM deposition; (2) recycling of dissolved inorganic matter (DIM: N,P,Si) via planktonic and benthic metabolic processes; (3) the planktonic microbial loop mediated by excretion of dissolved organic matter (DOM); and oxygen exchanges and effects on redox-sensitive processes such as nitrification-denitrification.

consumed in the water column by zooplankton grazing and by microbial processes which involve dissolved organic matter excretion, bacterial consumption and protozoan grazing (Jonas, this volume). A significant portion of this production may also sink through the water column and be deposited as particulate organic matter to the sediment surface; in general this organic matter will be in the form of intact diatom cells or zooplankton fecal pellets.

The transfer of planktonic particulate organic matter to the sediments can be facilitated substantially by the suspension-feeding and active pumping of benthic macrofauna, such as clams and oysters. These invertebrates metabolize organic matter and convert it to biomass, which is in turn consumed by fish through a variety of pelagic and benthic food chains.

Protozoa, bacteria and metazoan animals — as a consequence of their metabolic consumption of the organic matter produced by phytoplankton — excrete dissolved inorganic nutrients. These recycled nutrients are then available to support further growth of phytoplankton.

Nutrient recycling in the planktonic subsystem tends to be rapid, while cycling in the benthos is slower: there are significant time delays between the large quantities of particulate organic matter deposition, decomposition and vertical diffusion (recycling) of nutrients back to the overlying water. For example, certain labile or rapidly degraded organic compounds such as sugars, lipids and amino acids in the particulate organic matter deposited to the sediment surface are decomposed readily; others such as lignins and cellulose are more refractory, or resistant to decomposition. Differences in decomposition of these compounds result in a spectrum of recycling rates from the benthos. Nutrients contained in the benthic subsystem, in contrast to the water column, are less susceptible to physical transport from the estuary to the continental shelf. Thus, deposition of particulate organic matter to the bottom and the resulting benthic processes of nutrient recycling represent a mechanism of retaining nutrients which enter the estuary in winter and spring long enough to support continued phytoplankton production in summer and fall (Kemp and Boynton 1984).

In the upper portion of the water column, dissolved oxygen is generated through phytoplankton photosynthesis. Oxygen is also exchanged by diffusion across the air-water interface, and consumed in heterotrophic metabolism of bacteria, animals and plants. In the benthic subsystem and lower portion of the water column, oxygen is consumed either directly or indirectly by most heterotrophic processes; oxygen can only be replenished, however, by vertical exchange with the upper layer of the water column. Under conditions of vertical density stratification that occur in late spring and summer, a strong stratified boundary, or pycnocline, develops between dense, salty lower waters and lighter, fresh, oxygenated upper waters. Stratification impedes physical exchange between these layers (Boicourt, this volume), thus preventing oxygen from reaching the lower waters and leading to the condition of oxygen depletion, or hypoxia (Kemp and Boynton 1980). While oxygen decline as a result of stratification is a naturally occurring phenomenon in many estuaries, including portions of Chesapeake Bay, there is widespread evidence that the process is accentuated by increasing inputs of nutrients from anthropogenic sources (Officer et al. 1984).

The trend of increasing anthropogenic nutrient enrichment, or eutrophication, of coastal waters can significantly affect estuarine ecosystems by several mechanisms which directly involve benthic-pelagic coupling. Typically, on the one hand, nutrient enrichment fertilizes phytoplankton production and abundance to such an extent that the phytoplankton, or algal, blooms will blanket large surface areas of the Bay. These algae sink to bottom waters, where they are decomposed by heterotrophic processes which consume oxygen (Malone, this volume). On the other hand, if bottom water remains oxygenated, higher algal biomass and production will lead to larger rates of particulate organic matter deposition, which may result in increased production of such benthic macrofauna as oysters (Grassle et al. 1985). Otherwise, in regions susceptible to depletion of oxygen in bottom waters, nutrient enrichment and high production will lead to decreased macrofauna (Cederwall and Elmgren 1980).

Nutrient fertilization can cause changes in the species composition and trophic structure of plankton communities, which in turn affect the rates, timing and quality of particulate organic matter deposition to the benthos (Smetacek 1984). In fact, it appears that the proportion of primary production delivered to the benthos actually decreases with increasing production along a eutrophication gradient (Oviatt et al. 1986). Relative rates of nutrient recycling from sediments tend to increase with fertilization; this is especially true for ammonium recycling because nitrification and denitrification — the reduction of nitrate to nitrogen gas — will be inhibited by oxygen limitation under eutrophic conditions. It is likely, therefore, that eutrophication results both in shifts between plankton and benthic food chains and in recycling pathways.

To better understand the role sediments and overlying waters play in the development of hypoxia and anoxia in Chesapeake Bay, it is important to characterize spatial and temporal trends for major benthic-pelagic processes, the factors controlling these processes, and the effects of eutrophication on them.

During the last five years there have been several active research programs focusing on various aspects of benthic-pelagic coupling in upper Chesapeake Bay (above the Potomac River mouth). A long term monitoring program (supported by the Maryland Department of Environment) was established in 1984 to measure fluxes of oxygen and nutrients across the sediment-water interface at ten permanent sampling stations (Figure 2) in the mainstem Bay (4 stations) and in three major tributaries (Patuxent, Potomac and Choptank rivers — two stations each). Data on phytoplankton production and benthic macrofauna abundance are being collected at these stations as part of this monitoring effort. Vertical arrays of fixed sediment traps have also been established at one of these stations (M4) in the mainstem Bay. The cross-Bay Chop-Pax transect of five stations intersecting the sediment trap site was created subsequently as part of a study of factors regulating seasonal oxygen depletion in the Chesapeake Bay (see Introduction). In 1987 the geographic scope of these studies was expanded to include sediment-water exchanges in the lower Bay and provide data needed for calibrating water quality models (supported by the U.S. EPA). In

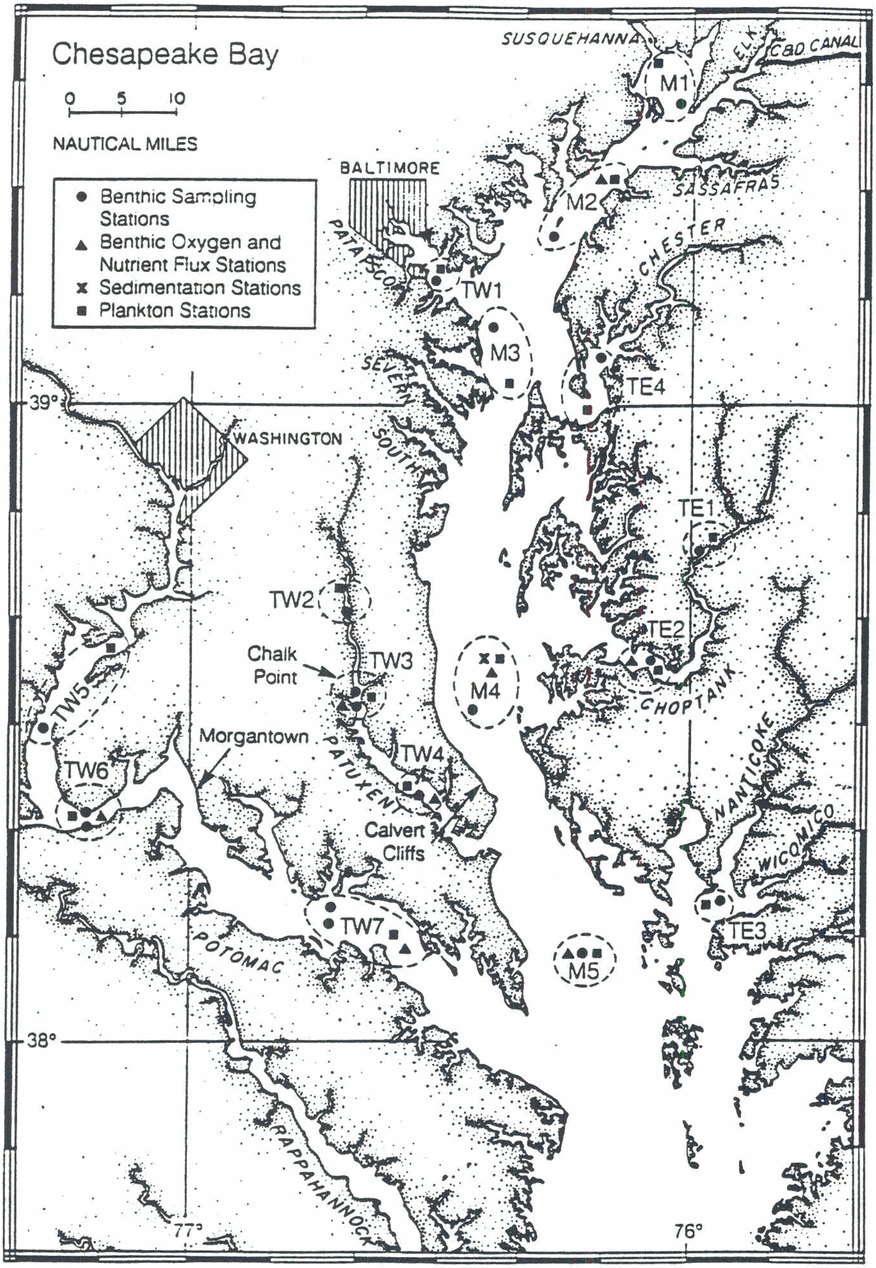

Figure 2. Map of Maryland portion of Chesapeake Bay showing the location of sampling stations where benthic-pelagic processes are being measured in the Maryland Chesapeake Bay Water Quality Monitoring Program.

addition, a large five-year research program was initiated in 1989 to investigate the fate and effects of nutrient inputs to estuaries as part of a new land-margin ecosystem research (LMER) initiative, supported by the National Science Foundation. Information generated from these diverse research and monitoring programs provides the primary basis for this chapter.

Deposition of Particulate Organic Matter

One of the benthic-pelagic interactions most difficult to quantify is the deposition rates of particulate organic matter, largely because of problems in interpreting data from sediment traps.[2] Particle deposition rates have been measured using cylindrical traps that are deployed in the mesohaline reach of Chesapeake Bay. Seasonal patterns for particle deposition rates are relatively distinct, with three periods of high sedimentation generally occurring in April, August and October (Figure 3). These data, which have not been corrected for resuspension effects, represent particulate organic carbon (POC) and total chlorophyll *a* (Chl) collection rates in traps fixed at 9 m, which is the nominal depth of the pycnocline. Rates for 1985–1986 show that the broad seasonal trends appear to vary little from year

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[2] In recent decades, there have been substantial developments in sediment trap methodologies which have improved our ability to measure particle deposition in lakes and oceans. Although the altered hydrodynamic flow fields induced by the traps themselves certainly affect particle dynamics around sediment traps (Gardner 1979a; Butman 1986; Butman et al. 1986), several design features can minimize these sampling biases. In accordance with recommendations of several trap analyses in flumes (Gardner 1979a,b; Bloesch and Burns 1980; Blomqvist and Hakanson 1981), sediment traps used in Chesapeake Bay (Boynton et al. 1988) have employed a cylindrical shape with a 10:1 ratio of height to diameter. In shallow, hydrodynamically active environments such as estuaries, resuspension (followed by sinking) of bottom sediments (Oviatt and Nixon 1975) tends to confound measurements of deposition of autochthonous, newly formed particles (e.g., algal cells and zooplankton fecal pellets). Sediment trap rates of POM settling can be corrected for contributions of resuspended material using a pro rata scheme which compares the % organic content of trapped material with those of bottom sediments and suspended material in the surface waters (Gasith 1975; Taguchi 1982). In addition, rates of total chlorophyll pigment

to year. Similar interannual consistency of seasonal patterns has also been reported for the Kiel Bight region of the southern Baltic Sea (Smetacek 1984). The spring and summer deposition events are closely associated with the annual maxima in euphotic zone chlorophyll *a* concentration and phytoplankton production, respectively. There is a small increase in chlorophyll *a* stocks during the summer period of higher deposition, but not so in the autumn. The seasonal trends are more pronounced for sedimentation of chlorophyll *a* than particulate organic carbon.

The carbon to chlorophyll ratio (C:Chl) of sedimented particulates varies seasonally in relation to the changing character of deposited material (Figure 3). The ratio is lower in the spring than in the summer, possibly indicating a shift in trapped material from intact algal cells to zooplankton fecal pellets, respectively (Steele and Baird 1972; Bodungen et al. 1981; Forsskahl et al. 1982; Smetacek 1984). Indeed, microscopic examination of these materials revealed that in 1986, 97% of the total mass trapped in April was associated with centric diatoms, while 76% in August was fecal pellets (K. Sellner, personal communication). The rapid deposition of diatoms from April to May is consistent with typical life-cycle sequences for diatoms (Smetacek 1985) and may result from incipient silicon limitation for their growth. The dominance of fecal pellets in the trapped

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deposition estimated with sediment traps are less susceptible to resuspension effects because of the relatively rapid rate of pigment decomposition in bottom sediments (e.g., Carpenter et al. 1986).

Another potential problem with interpreting sediment trap data is the decomposition of organic particles within the traps occurring during the deployment period (Honjo and Roman 1978; Ducklow et al. 1985). In attempting to rectify this problem, some investigators have added preservatives to the traps to retard bacterial activities (Knauer et al. 1984); however, others have observed that preservatives can further complicate interpretations by causing an accumulation of dead invertebrates which swim into the trap (Peterson and Dam 1990). Experiments have been conducted to test effectiveness of preservatives for sediment traps in Chesapeake Bay. Although Chl rates were unaffected by poisoning, particulate organic carbon was increased significantly, suggesting artificially induced mortality of "swimmers" (Boynton et al., unpublished). In general, the relatively short deployment intervals (4 to 7 days) used in the Bay sediment trap studies appear to be sufficient to minimize problems associated with degradation of particulate organic matter in traps (Boynton et al. 1988).

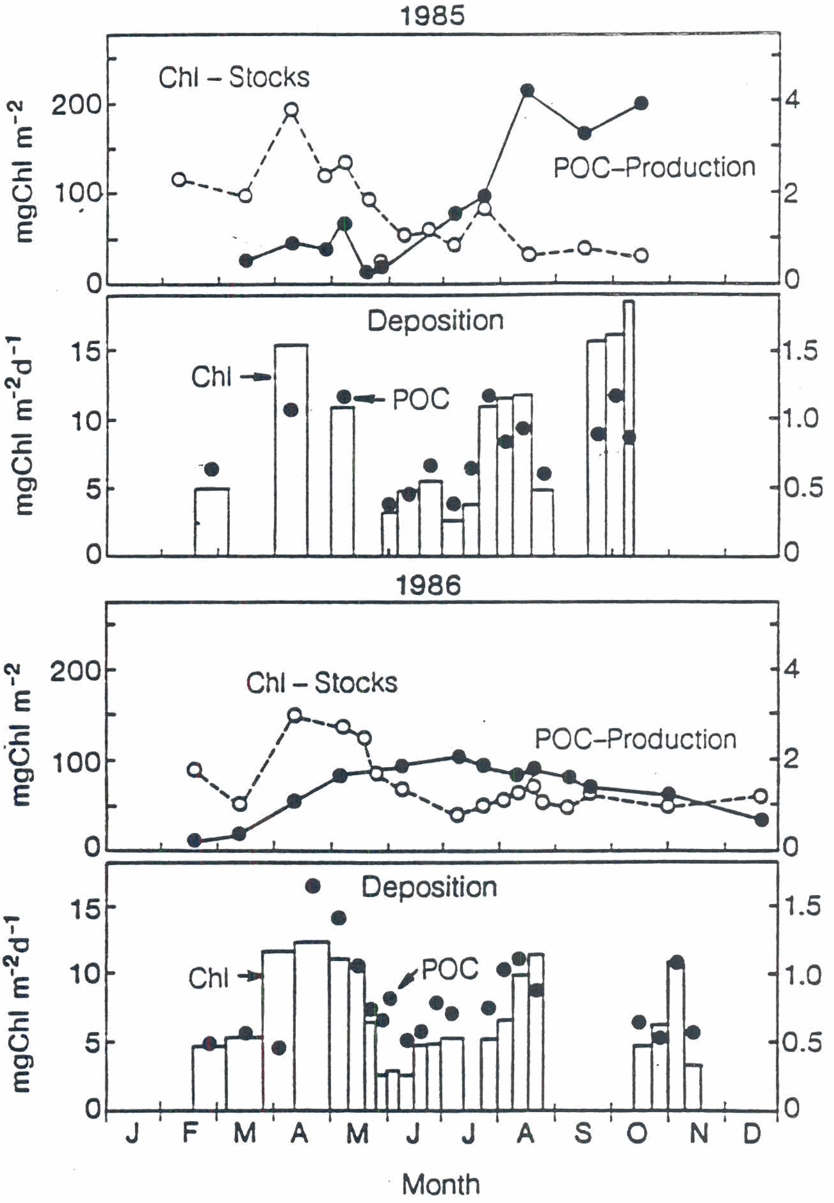

Figure 3. Annual patterns of chlorophyll a (Chl) stocks and deposition rates and particulate organic carbon (POC) production and deposition rates in 1985 and 1986 in the mesohaline region of Chesapeake Bay (Boynton et al. 1988).

material in summer is coincident with the timing of maximal zooplankton grazing (Malone, this volume).

In addition, the relative rate at which euphotic zone chlorophyll *a* biomass is depleted via sinking can be inferred from the slope of chlorophyll *a* deposition versus chlorophyll *a* stocks (Billen and Lancellot 1988). Using data in Figure 3 from both years, statistically significant relationships between chlorophyll *a* deposition and concentration are obtained for both spring ($r^2 = 0.88$) and summer ($r^2 = 0.70$), with the slope for the latter period being twice that of the former. Evidently, the phytoplankton community turns over via sinking at a rate of approximately once every 14 days in spring and once every 7 days in summer. In spring, the relatively ungrazed algal stocks which accumulate with great abundance are dominated by large diatoms, and even though sinking rates are high, the algal biomass turns over more slowly. In contrast, the smaller flagellated cells which predominate in summer are heavily grazed with less build-up of biomass, so that turnover of algal stocks is faster even though rates of particulate organic matter sinking are lower. From the perspective of the benthic community, the food quality of intact diatom cells deposited in the spring probably exceeds that of the fecal material sedimenting in summer (Marsh and Tenore 1990).

Although much of the particulate organic matter caught in sediment traps derives from the sinking of algal cells and fecal pellets that are produced in the overlying euphotic zone, indirect evidence suggests that a considerable fraction is from production occurring in the shallower regions flanking the main Bay channel. For example, significant correlations were observed between phytoplankton production in both the east and west flanks and sediment trap collections in the main channel; however, no relation was seen between deposition and production in the overlying water column (Malone et al. 1986). Sediment traps deployed 1 m above the sediment surface (20 m deep) in the channel collected 5-10 times more particulate organic matter than in the pycnocline and euphotic zone traps described above (Boynton et al. 1988), even though most of the resuspension of bottom sediments occurs at depths less than 10 m (Ward 1985). This observation further emphasizes the importance of lateral transport of resuspended particulate material from shallow waters flanking the Bay channel to the channel bottom.

This process of bottom resuspension and lateral transport to pycnocline traps could cause serious overestimates of deposition of newly produced (as opposed to resuspended) particulate organic matter from overlying water. However; such effects would be expected to be minimal for chlorophyll *a*, because these algal pigments degrade relatively rapidly on the sediment surface and are thus less available for resuspension. The seasonal patterns of chlorophyll *a* deposition estimated with traps and reported in Figure 3, therefore, are probably representative of actual conditions (see footnote 2). The effects of resuspension on estimates of new particulate organic carbon deposition can be corrected by the ratio of new:total carbon deposited estimated by pro rata of the percent of organic carbon in seston, bottom sediments and trapped particulates ($= [\%C_{seston} - \%C_{bottom}] [\%C_{trap} - \%C_{bottom}]^{-1}$).

Annual rates of new particulate organic carbon deposition were estimated for 1985 at the mesohaline Bay trap by applying the above corrections (factors ranged from 0.4-0.9 over the year), and these rates compared favorably (within 20%) to particulate organic carbon deposition calculated from annual chlorophyll *a* rates, multiplied by the C:Chl ratio for surface particulates (Boynton et al. 1988). In addition, annual rates for deposition of total dry mass, estimated from the particulate organic carbon rates divided by the %C of surface seston, minus the loss of mass associated with sediment respiration, were compared to long-term sediment burial rates obtained from ^{210}Pb analyses (Officer et al. 1984). Mean rates for 1985 sediment traps were 0.24 g dry wt $cm^{-2}y^{1}$ compared to ^{210}Pb rates which ranged from 0.1-0.3 g dry wt $cm^{-2}y^{-1}$. While these annual rates have been calculated for comparative purposes and must be considered crude estimates, they do lend credibility to the quantitative aspects of the Chesapeake Bay sediment trap data. Similar close correspondence between sediment trap and ^{210}Pb estimates of deposition have been reported in lacustrine environments (Bloesch and Evans 1982).

A preliminary calculation for the balance of organic carbon metabolism in the water column at the mesohaline site of the sediment traps provides yet another test of trap rates with regard to actual particulate organic carbon deposition. In this analysis, all rates are based on oxygen measurements converted to carbon, assuming photosynthetic and respiratory quotients of 1.2. Previous measurements (Kemp and Boynton 1980; 1981) at a nearby site (6 m depth) revealed significant correlations between plankton production and both the respiration of the plankton ($r^2 = 0.66$) and of the benthic communities ($r^2 = 0.35$). These measurements suggest that production and respiration are closely coupled, and the combined slopes of these relations indicate that 85-90% of the autochthonous production — primary production that occurs in the water column — is consumed in place.

On time scales of days to weeks, however, particulate organic carbon deposition is poorly correlated with primary production, and it is the variability of the respiration-production relationship which may be more important than production alone in determining deposition rates. Using 1986 measurements from the sediment trap station and subtracting the upper layer (0-8 m) and lower layer (8-20 m) water column respiration rates from this production, a "residual" term is left in the carbon budget (Figure 4) that corresponds to the particulate organic carbon available for deposition to the sediment surface. If this residual, calculated at 2-4 week intervals, is compared to sediment trap collection rates for the same time periods, a remarkably close correlation is obtained (slope=0.94, r^2=0.96), further supporting the quantitative robustness of the traps.

Comparisons with Other Systems

Measurements of various aspects of benthic-pelagic coupling throughout the world permit comparisons of results with Chesapeake Bay. For example, strong correlations are evident in a variety of systems between planktonic primary production (adjusted for depth of the upper mixed layer) and annual sedimentation of organic matter (Figure 5a) (Suess 1980; Hargrave 1984). Annual data from studies in Chesapeake Bay fit the general pattern and are at the top end of data from shallow systems. In a similar fashion the percentage of annual primary production that is sedimented appears to be a function of depth (Suess 1980), ranging from as much as 80% in shallow systems to less than 1% in the deep ocean. In systems less than 50 m in depth (Figure 5), proportionally less organic material sediments from the water column per unit of production than in deeper systems; this is an indication of a shift to more thorough utilization of organic material in the water column. Again, data from Chesapeake Bay fit this pattern: between 20-80% of annual production is sedimented.

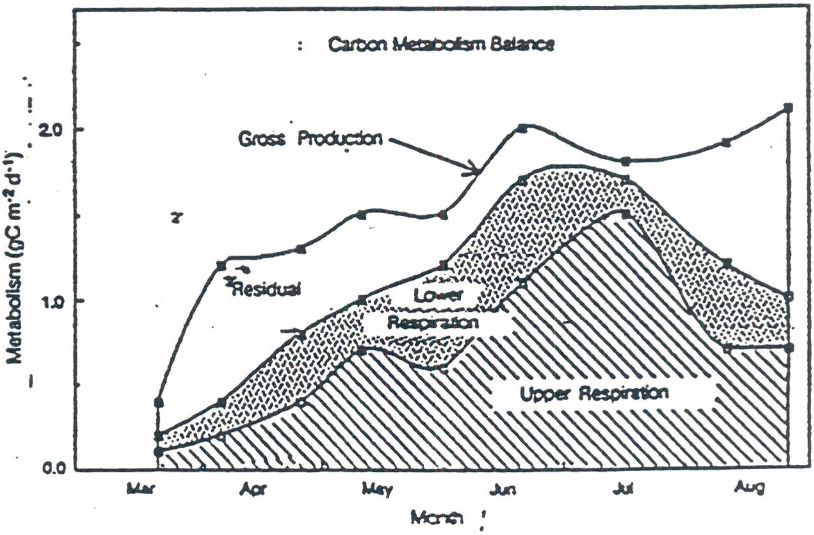

Figure 4. Calculated seasonal balance of organic carbon gross production, plankton respiration in the upper layer, and plankton respiration in the lower layer. The residual is taken as production minus upper and lower layer respiration rates (Kemp et al. unpublished).

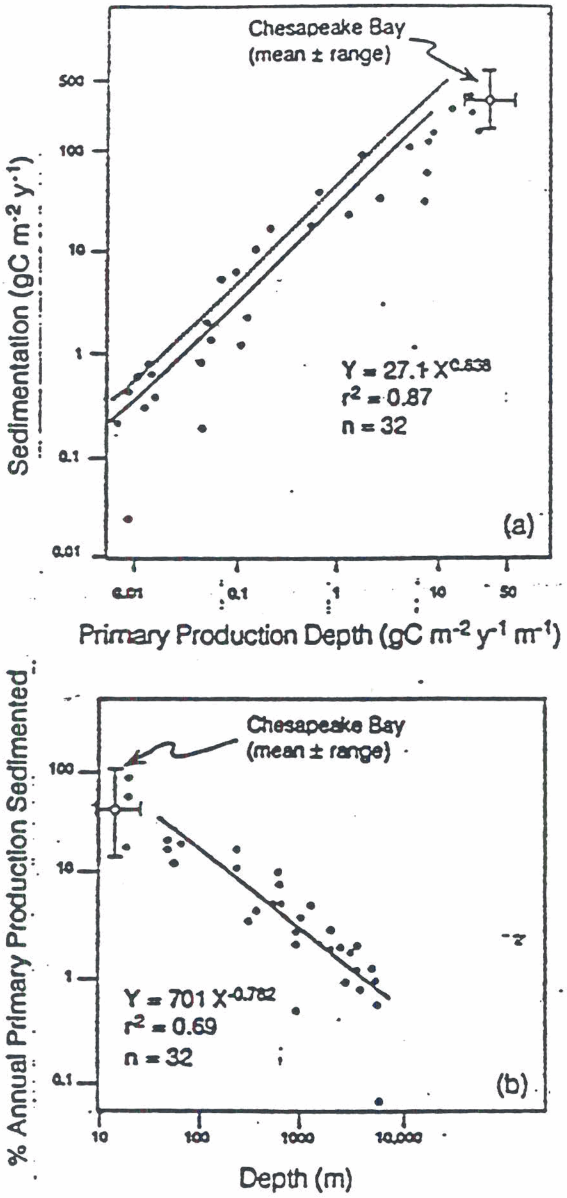

Figure 5. Summary of benthic-pelagic coupling processes from the literature (Hargrave 1984) with values for annual means and ranges from Chesapeake Bay (Boynton et al. 1988; Holland 1988; Sellner et al. 1988) presented for comparisons: (a) sedimentation versus production per mixed layer depth; (b) % production sedimented versus water column depth.

Benthic Metabolism and Nutrient Cycling

Exchanges of solutes across the sediment-water interface have been measured routinely in numerous coastal marine environments (Harrison 1980; Nixon 1981; Nixon and Pilson 1983; Klump and Martens 1983). Typically, these rates are estimated from changes in solute concentrations in water enclosed under chambers placed on the sediment surface or in water overlying intact sediment cores incubated in temperature-controlled laboratories. In principle, total metabolism of the benthic community can be estimated as uptake of oxygen or as efflux of dissolved inorganic carbon (TCO_2). Burial and temporary storage of the end-products of anaerobic respiration (primarily sulfide) can confound interpretations of oxygen flux as community metabolism. Although only a small fraction (5 to 15%) of the sulfide formed in sulfate reduction is buried permanently, it is thought that significant quantities are temporarily stored as iron-sulfides (Jørgensen 1983). This storage implies that, while instantaneous rates of oxygen exchange and community metabolism may not correspond to one another, integrated annual rates may be comparable. Indeed, recent analyses indicate that annual rates of sediment oxygen consumption (SOC), sulfate reduction and dissolved inorganic carbon efflux compare favorably for the mesohaline region of Chesapeake Bay (E. Roden, personal communication).

Sediment Water Fluxes[3]

Seasonal sequences for sediment-water fluxes of dissolved oxygen (O_2), ammonium (NH_4^+), nitrate (NO_3^-), silicon dioxide (SiO_2) and phosphate (PO_4^{3-}) are available for ten stations in the upper and middle Bay and for three major tributaries since 1985 (Boynton et al. 1988). Mean patterns for the upper and middle main Bay stations are summarized in Figure 6; they illustrate representative

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[3] The following discussion focuses on information available since 1987 with regard to seasonal and spatial patterns of solute fluxes across the sediment surface in upper Chesapeake Bay and its tributaries. Garber (1988) thoroughly reviewed data until 1986.

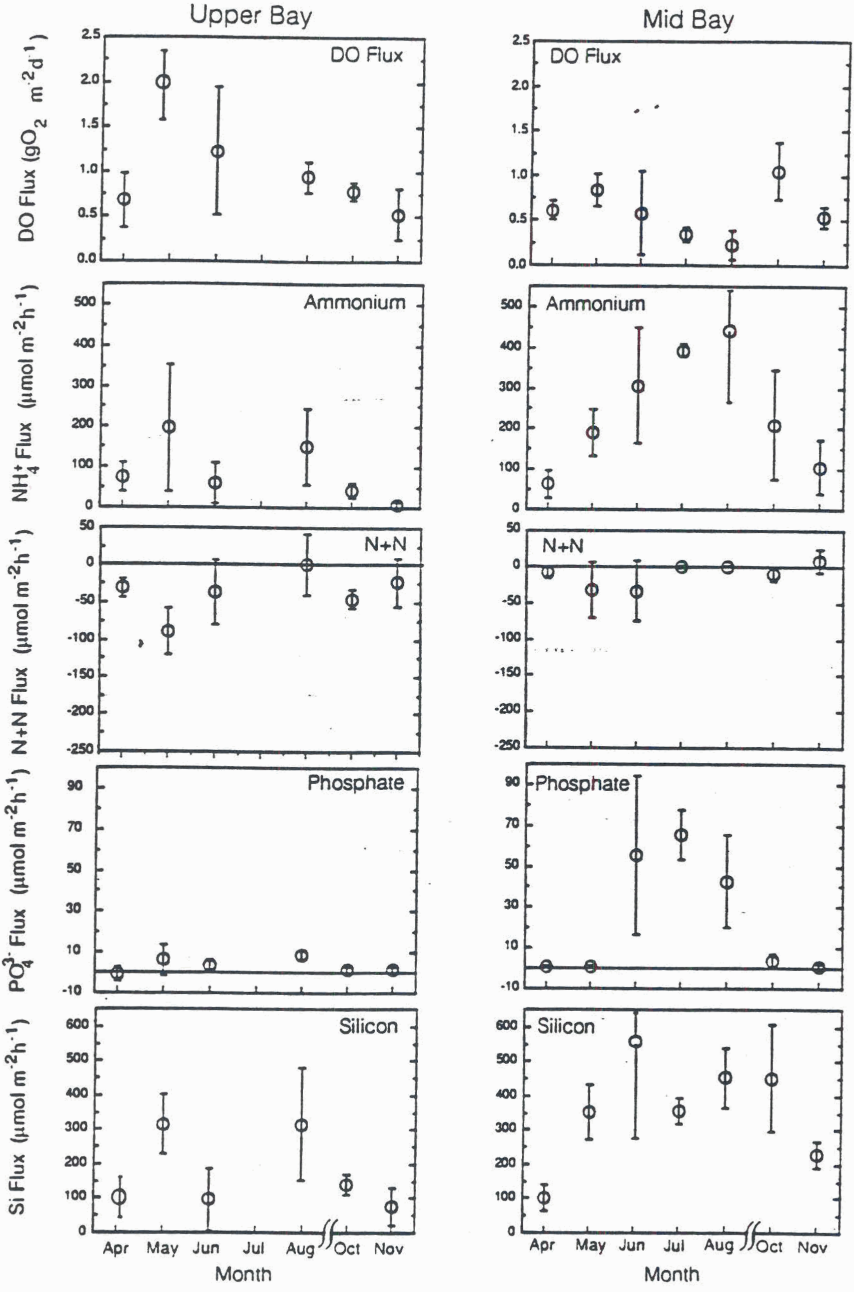

Figure 6. Composite of annual cycles (mean ± S.E.) for sediment-water exchanges of oxygen, ammonium, nitrate plus nitrite (N+N), silicate and phosphate for 1984-1988 at two stations (Sta. M2 and M4, Figure 2) in the main stem of Chesapeake Bay (Boynton et al. 1988).

trends in the estuary. Seasonal maxima for dissolved oxygen flux occurred in May for the upper Bay site and in October for the mesohaline Bay, with slightly higher mean annual rates in the upper Bay. The low rates in August for the mid Bay were related to the dissolved oxygen depletion which often prevails at this time. Under anoxia there was, obviously, no dissolved oxygen flux at the sediment surface, but the sulfide diffusing from sediments to anoxic overlying water consumed dissolved oxygen at the pycnocline.

Rates of ammonium efflux from sediments for both stations tended to be highest in August, but annual mean values were 2 to 3 times higher at the mid-Bay site. This seasonal pattern closely follows that for water temperature. In contrast, fluxes of nitrate (plus nitrite, NO$_2^-$) were generally directed into the sediments. However, the seasonal patterns differed considerably between the upper- and mid-Bay sites: at the upper-Bay site, seasonal mean fluxes ranged from about −80 to −10 µmol m^{-2}h^{-1} with no apparent relationship to nitrate concentrations in overlying waters. At the mid-Bay site, maximum fluxes were about half those observed at the upper Bay but were clearly related to the pattern of nitrate in overlying waters with highest fluxes being recorded in the spring and then declining through the summer period as the nitrate associated with the spring freshet was depleted. While the general pattern of nitrate flux at both stations was from water to sediments, there are times of the year when nitrate released from these sediments is indicative of nitrification activity in excess of denitrification.

At the upper-Bay site nitrate release has been frequently observed during summer and fall when nitrate concentrations in overlying waters are reduced although the magnitude of these fluxes is not sufficient to change the 1984 to 1988 average from negative to positive. Positive nitrate fluxes at the mid-Bay site are more sporadic and seemingly occur whenever the sediments are in contact with oxygenated waters and NO$_3^-$ concentrations in overlying waters are relatively low (Boynton and Kemp 1985). These trends in sediment-water fluxes of dissolved inorganic nitrogen are similar to those reported previously for Bay sites (Boynton et al. 1980; Callender and Hammond 1982; Boynton and Kemp 1985).[4]

Fluxes of silicon exhibited a bimodal pattern at the upper Bay site, ranging from about 300 µmol $m^{-2}h^{-1}$ in the early spring and summer to around 100 µmol $m^{-2}h^{-1}$ in the late spring and fall. In contrast to this complex pattern, fluxes of silicon at the mid-Bay site exhibited a strong unimodal pattern with highest fluxes observed following the completion of the spring diatom bloom but prior to the annual temperature maxima. Fluxes of silicon at the mid-Bay site are also among the highest observed throughout the Bay system with some measurements in excess of 1000 µmol $m^{-2}h^{-1}$. Sediment releases of silicon at locations 40 km up and downstream of the mid-Bay site were significantly smaller, suggesting that the mid Bay region may be a focal point of diatom deposition fueling the substantial releases observed.

Net exchanges of phosphate were distinctively different between sites (Figure 6). At the low salinity upper Bay site phosphate fluxes were always relatively low (< 15 µmol $m^{-2}h^{-1}$) and occasionally were directed into sediments. Average annual values were about 4 µmol m^{-2} h^{-1}. Fluxes of this magnitude have little influence on ambient concentrations of phosphate in overlying waters. Fluxes of phosphate at the mid-Bay site were very large during the summer period, averaging about 50 µmol $m^{-2}h^{-1}$ and ranging as high as 120 µmol $m^{-2}h^{-1}$. At this site fluxes were low whenever bottom water oxygen concentrations were above 1 to 2 mg L^{-1}. It is apparent that redox conditions of sediments exerted a strong influence on these phosphate fluxes.

With the exception of oxygen fluxes, sediment-water exchanges at the mid-Bay site were considerably larger than those at the upper-Bay location and were, without exception, characterized by strong

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[4] Similar seasonal patterns of ammonium fluxes, with peak rates in mid summer, have been described for a wide variety of coastal environments. However, in contrast to the patterns in the Bay, nitrate sediment-water exchanges exhibited a predominance of effluxes from sediments throughout the year for most other sites (Davies 1975; Nixon 1981; Fisher et al. 1982; Hopkinson and Wetzel 1982; Flint 1985; Hopkinson 1987).

unimodal seasonal patterns with peak rates in the summer. The magnitudes and seasonal patterns of oxygen, silicon and phosphate fluxes are within the ranges of those reported previously for a diversity of coastal marine environments (Nixon 1981; Fisher et al. 1982; Hammond et al. 1985; Hopkinson 1987).

In addition to the distinctive seasonal patterns of sediment-water fluxes, strong spatial variability was also evident. Figure 7 characterizes fluxes of oxygen, nitrate, phosphate, ammonium and silicate at 10 stations along the Bay's longitudinal axis for April and August. August fluxes of phosphate and ammonium, for example, were low in the Bay's upper and lower region, but reached maxima in the mid region. These high summer fluxes (Figure 3) were probably supported in part by the large amounts of organic matter reaching the sediment surface from direct deposition of locally produced organic matter and by horizontal transport of organic matter produced along the flanks of the Bay.

The largest fluxes occurred in the summer (August) when dissolved oxygen concentrations are typically low (< 1 mg L^{-1}). Some variability is evident in the spatial patterns of nitrate fluxes, but nitrate fluxes were highest in the upper Bay and decreased seaward. However, this pattern shifted dramatically between seasons with fluxes directed into sediments during April — presumably because of high nitrate concentrations in overlying waters — and out of the sediments to overlying waters in summer as a result of nitrification exceeding denitrification. Except in the upper Bay, nitrate fluxes were small in comparison to ammonium fluxes.

Strong seasonal differences in the magnitude and spatial pattern of fluxes for other nutrients were also observed. For example, ammonium and phosphate fluxes were quite small in April throughout the Bay, but were large and exhibited mid-Bay maxima in August. Sediment oxygen consumption, or oxygen fluxes, were rather uniform through the Bay in April (approximately –0.7 gO_2 $m^{-2}d^{-1}$), but tended to be higher at the freshwater and ocean ends and depressed in the central Bay regions during summer. Fluxes of silicon exhibited similar patterns in spring and summer, differing mainly in magnitude with summer fluxes being 2 to 5 times larger.

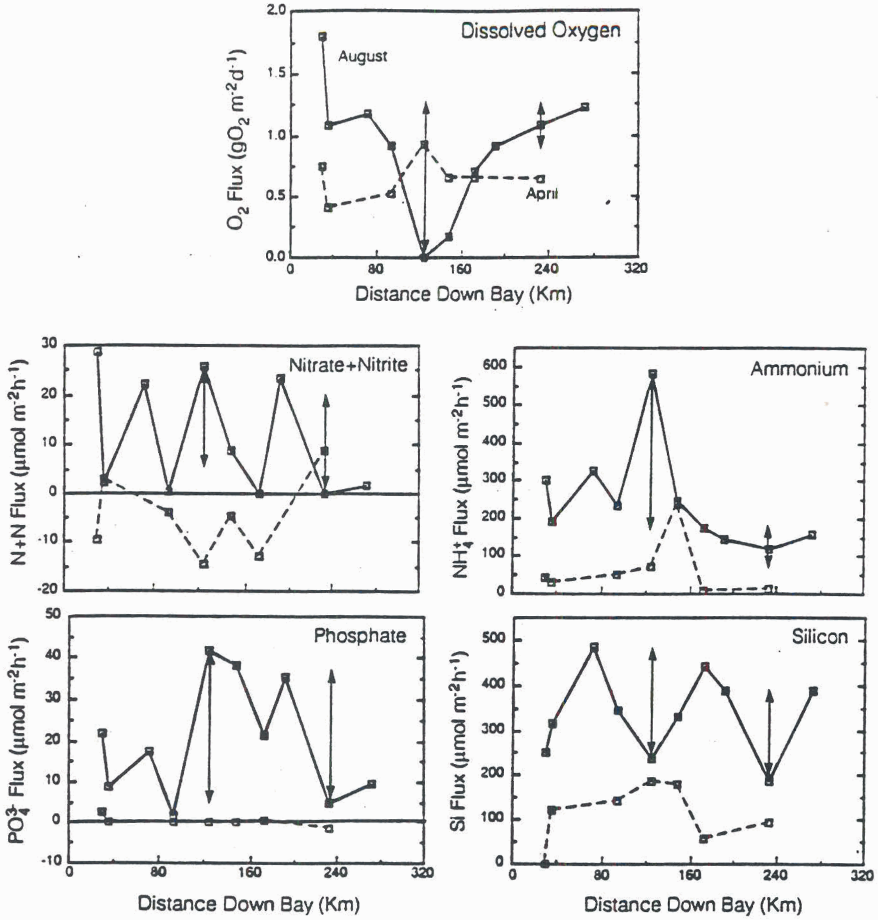

Figure 7. Sediment-water exchanges of oxygen, nitrate plus nitrite (N + N), ammonium, phosphate and silicon for April and August 1988 at stations along the Chesapeake Bay mainstem, from the Susquehanna Flats to Cape Charles. Vertical arrows indicate range of rates for three stations in a cross-Bay transect measured in August in mid- and lower-Bay areas (Boynton et al. unpublished).

During August 1988, two additional lateral stations were sampled in the mid and lower Bay to provide an indication of cross-bay variation in the magnitude of fluxes. As indicated in Figure 7, fluxes of some nutrient species differed considerably between shallower flank and deep stations. Some of these differences can be explained by higher oxygen concentrations in overlying waters and surficial sediments at the lateral stations. Lateral station differences at the lower Bay transect were not as pronounced nor were the differences in depth and redox conditions of overlying waters and sediments.

Environmental Factors

A number of environmental factors are potentially important in regulating sediment-water fluxes in estuarine systems — among them temperature and redox conditions. In the mid-Bay region oxygen and ammonium fluxes follow the seasonal temperature cycle. Previous studies in the Patuxent River also found strong correlations between some nutrient fluxes and temperature (Boynton et al. 1980). When all data from all stations in the Bay since 1985 were combined, a strong relation was evident between oxygen concentration in overlying waters and phosphate fluxes. In this case, when oxygen concentrations in overlying waters were greater than about 1.5 mg L^{-1}, phosphate fluxes were small (being directed either into or out of sediments); only when oxygen concentrations were below 1.5 mg L^{-1} were phosphate fluxes large, reaching 87 μmol m^{-2} h^{-1}. Rates of sediment oxygen consumption were also correlated (though weakly) with oxygen concentrations in the overlying water (Boynton et al. 1988). The fact that there were also low phosphate fluxes observed under low oxygen conditions indicates that other environmental variables (e.g., quality and quantity of organic matter reaching the sediment surface, macrofaunal composition and abundance) are also involved in regulating phosphate fluxes.

One measure of the overall strength of benthic-pelagic coupling can be found in correlations between water column and sediment processes. For selected sites in the Bay where contemporaneous rates were available, annual estimates of sediment oxygen consumption, or oxygen fluxes, are plotted as a function of primary production in the water column (Figure 8). In this case, annual rates of primary production have been divided by the depth of the mixed layer to account for the potential losses of organic material to water column respiration (Hargrave 1973). As indicated in Figure 8a, there is a significant positive relationship between these processes, which explains about 50% of the observed variability. However, such simple relationships do not appear to exist for other sediment fluxes such as ammonium (Figure 8b). As was the case for phosphate fluxes, it appears that oxygen conditions in deep waters and surficial sediments strongly modify what might otherwise be a clear relationship indicative of direct benthic-pelagic coupling. At some sites with oxic overlying water, rates of ammonium releases may have been lower than anticipated from production in overlying waters, because of nitrogen losses associated with coupled nitrification-denitrification. On the other hand, relatively high ammonium releases under a range of organic matter loading regimes could result if the nitrification pathway was inhibited by low oxygen conditions (Kemp et al. 1990).

While deposition of autochthonous phytoplankton particulate organic matter to the sediments appears to influence annual rates of benthic metabolism (e.g., Figure 8), nutrient regeneration from benthic processes might, in turn, exert reciprocal influence on plankton production in overlying waters. Previous studies in Chesapeake Bay and its tributary estuaries have shown that rates of ammonium and phosphate release from sediments to overlying waters are quantitatively sufficient to support 20-80% of the demands for phytoplankton growth (Callender and Hammond 1982; Kemp and Boynton 1984; Boynton and Kemp 1985). In general, benthic recycling of both nitrogen and phosphorus represents larger fractions of respective plankton nutrient requirements in summer than in spring.

A conceptual model proposed by Kemp and Boynton (1984) suggests that plankton production is supported primarily by inputs of new nutrients from land in spring and benthic recycling in summer. They further postulate that the sequential processes — dis-

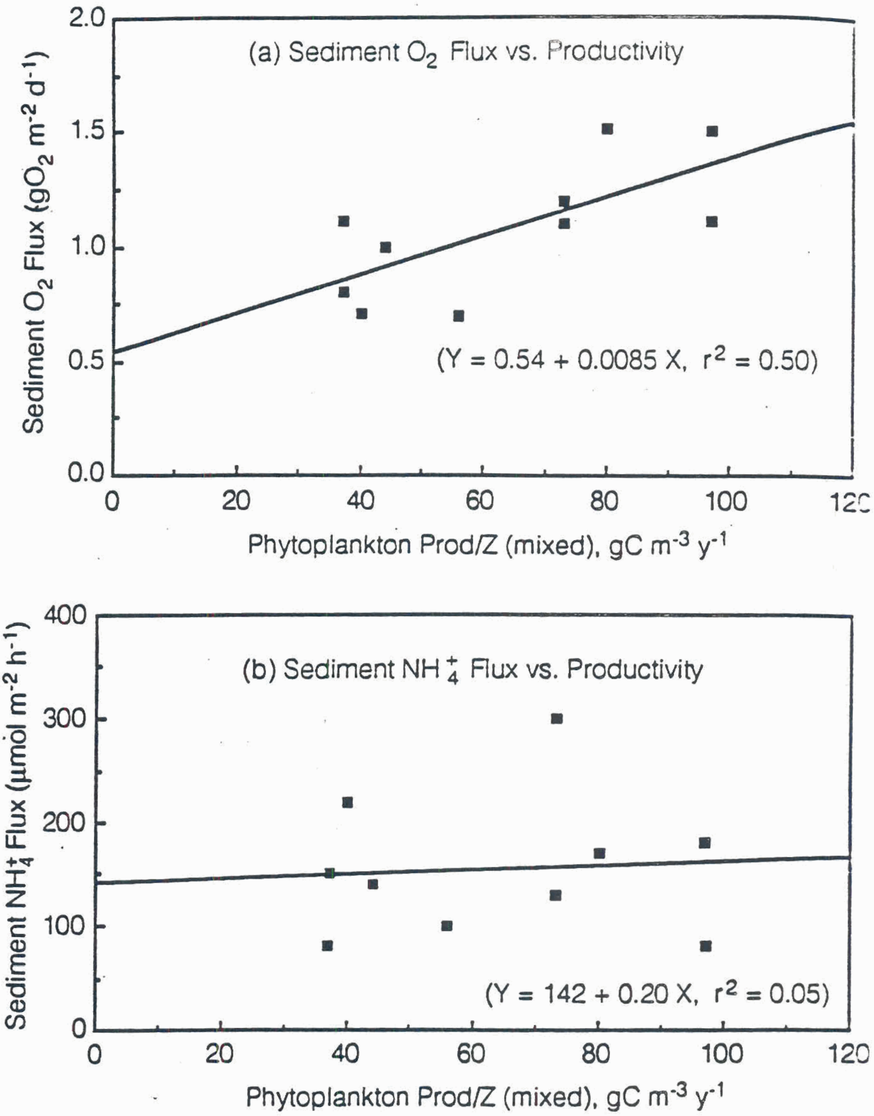

Figure 8. Correlations between annual mean phytoplankton production divided by the mean depth of the upper mixed water column layer versus (a) annual mean rates of sediment oxygen consumption (SOC) and (b) annual mean sediment-water exchanges of ammonium. Each point represents a different station in the main stem or tributaries of the Bay (data taken from Boynton et al. 1988 and Sellner et al. 1988).

solved nutrient uptake by phytoplankton, particulate organic matter deposition to sediments, benthic decomposition of particulate organic matter, and nutrient recycling to overlying water — present a means for retaining the winter-spring peak of nutrient inputs such that they can be used by phytoplankton in the summer peak of primary production.

A simple numerical simulation model of the major ecological processes involved in organic production and nutrient recycling was used to test this reasoning (Kemp and Randall 1988). Figure 9 summarizes simulation results for phytoplankton abundance (mgC L^{-1}) in the Bay's mesohaline region under two hypothetical scenarios, compared to the nominal base conditions (1986) for which the model was calibrated. In Figure 9a, nutrient inputs from the land were set to zero, resulting in virtual loss of the spring bloom, which is evidently supported primarily by "new nutrients" from external sources. In Figure 9b, vertical exchanges of nutrients from deep to euphotic waters were restricted in the model; this had the effect of greatly reducing summer phytoplankton production, which evidently depends on benthic recycling processes. Thus, the distinct seasonality of this benthic-pelagic coupling appears to play a strong role in regulating the magnitude and timing of summer production (Malone, this volume).

Comparisons with Other Systems

Data are also available to compare plankton production and/or deposition with benthic metabolic processes and fluxes among a number of coastal ecosystems. Nixon (1981) found direct evidence of coupling between sediments and overlying waters by comparing benthic remineralization of carbon — actually, sediment oxygen consumption — with organic matter supply for a selection of shallow estuarine and coastal systems (Figure 10a). Data from Chesapeake Bay generally fall within the range observed for other systems, where a large fraction, approximately 50%, of organic inputs to the system (primary production plus import of allochthonous material) are metabolized in sediments.

The sites compared in Figure 10a are all relatively shallow

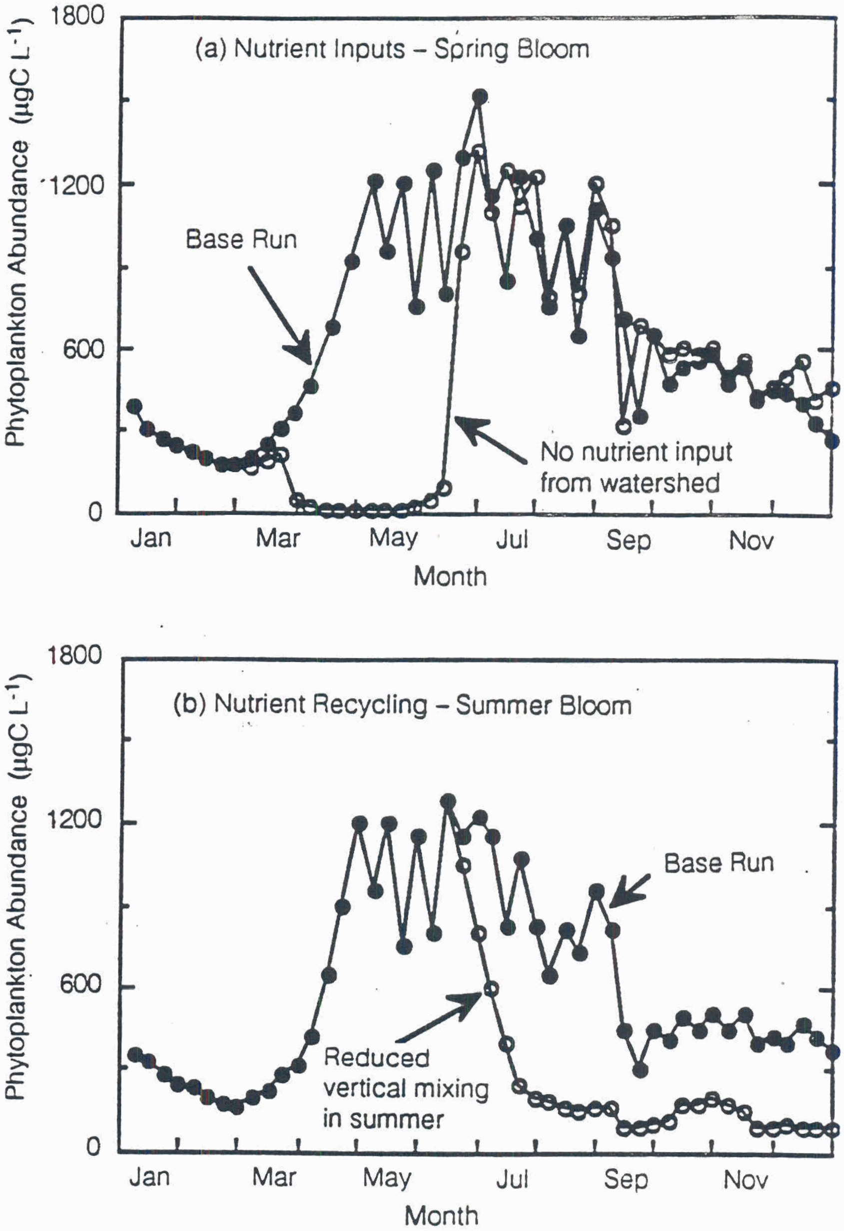

Figure 9. Results from-ecosystem simulation studies for the mesohaline region of Chesapeake Bay comparing nominal base-run conditions (1985) with (a) conditions with no new nutrient inputs from the watershed and (b) conditions with greatly reduced vertical mixing between bottom and upper layers of the water column (Kemp and Randall 1988).

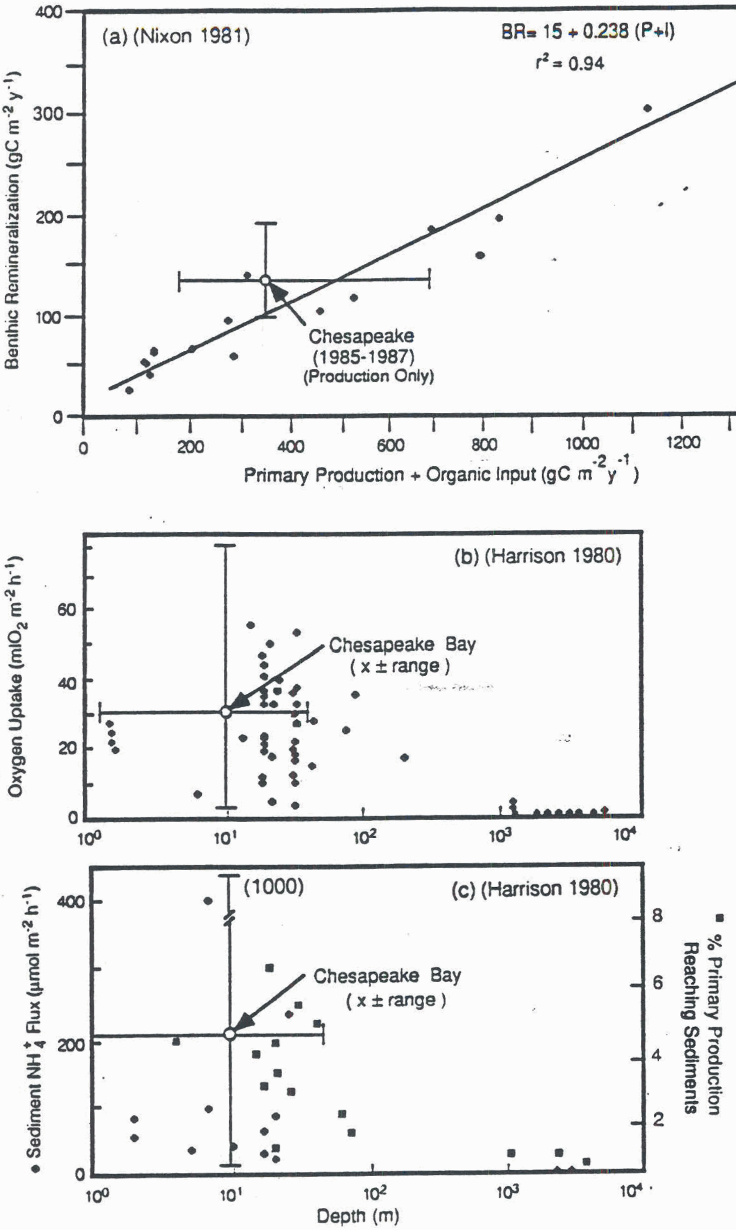

Figure 10. Summary of benthic-pelagic coupling processes from the literature (Nixon 1981; Harrison 1980) with values for annual means and ranges from Chesapeake Bay (Boynton et al. 1988; Holland 1988; Sellner et al. 1988) presented for comparisons: (a) benthic remineralization versus primary production plus organic inputs; (b) benthic oxygen uptake versus depth; and (c) ammonium regeneration versus depth.

(< 50 m), such that depth differences had little effect on the relation. Across a wider depth gradient, however, Harrison (1980) illustrated that sediment oxygen consumption rates decrease with water depth, presumably indicating a decrease in the fraction of organic production reaching sediments. There is considerable scatter in these data (Figure 10b) with the exception of deep ocean sites where sediment oxygen consumption rates were very low, as might be expected. Over the limited depth range of the Chesapeake Bay sites, sediment oxygen consumption values varied from close to zero to 80 $\mathrm{mlO_2\ m^{-2}h^{-1}}$, exceeding the range of values observed from a variety of other systems. The highest rates for Bay stations correspond to regions of high particulate organic matter deposition. The low sediment oxygen consumption rates may, however, be related to low oxygen at some deep water stations in summer.

Harrison (1980) also compared sediment ammonium fluxes across a large depth range (Figure 10). Again, low fluxes were observed from sites located in waters in excess of 1000 m. In shallower systems ammonium fluxes were rather uniform with most being less than 100 $\mu\mathrm{mol\ m^{-2}h^{-1}}$. Average fluxes from Chesapeake Bay exceed all but two observations from other systems and maximum values (approximately 1000 $\mu\mathrm{mol\ m^{-2}h^{-1}}$) are among the highest yet recorded. While substantial ammonium fluxes have been found in many areas of the Bay's mainstem and tributaries (Boynton et al. 1988), highest fluxes have consistently been associated with areas exposed to low redox conditions. In these areas it appears that most of the particulate organic nitrogen deposited on the sediment surface is decomposed to form ammonium, which is recycled back to the water column rather than being temporarily sequestered in macrofaunal biomass or lost to nitrogen gas via coupled nitrification-denitrification.

Sediment Nitrogen Cycling

Substantial evidence exists that nitrogen is the most important nutrient limiting growth and biomass accumulation of phytoplankton in Chesapeake Bay and other coastal waters (Boynton et al. 1982; D'Elia et al. 1986; Malone et al. 1988; Malone, this volume). Although phosphorus may also be an important limiting nutrient for algal growth in spring in oligohaline, or fresher water, sites and in general on geological time scales (Smith et al. 1987), nitrogen limitation tends to dominate on seasonal and annual scales in most estuaries. A number of explanations have been postulated for this pattern of nitrogen limitation in coastal marine systems. One such explanation is that high rates of loss of fixed nitrogen via denitrification in these estuarine environments results in nitrogen deficiency (Nixon 1981). Previous studies in Chesapeake Bay tributaries suggested that denitrification was indeed an important process in their nitrogen budgets (Boynton et al. 1980; Jenkins and Kemp 1984; Twilley and Kemp 1986). Furthermore, a recent review of denitrification processes (Seitzinger 1988) indicated that some 50% of the nitrogen inputs from surrounding watersheds was removed through denitrification as nitrogen gas (N_2). Nitrogen gas is virtually unavailable to phytoplankton for uptake in estuaries (Day et al. 1988).

Numerous studies of estuaries worldwide have demonstrated the importance of recycled inorganic nitrogen compounds from sediments to overlying water as a source of nitrogen to support phytoplankton growth (Billen 1978; Blackburn and Henriksen 1983; Klump and Martens 1983; Nixon and Pilson 1983; Kemp and Boynton 1984; Christensen et al. 1987). For this reason, research activities have focused on the relative importance of sediment nitrogen cycling in the main stem of Chesapeake Bay.

Seasonal cycles (March through November) of nitrogen fluxes and transformation processes have been described for 10 m and 20 m (depth) stations in the Bay's mesohaline region (Figure 2, near station M4). Figure 11 summarizes rates for the 10 m station: ammonium and nitrate fluxes across the sediment-water interface were similar to those shown in Figure 6 for the mid-Bay station (20 m depth), where effluxes of ammonium from sediments follow the seasonal temperature cycle, peaking in August; nitrate fluxes are small except for the substantial uptake by sediments in spring. In contrast, nitrification and denitrification rates were highest in spring and fall, and they were virtually zero in summer.[5]

Denitrification measurements probably underestimated actual rates by about 30-60% because deficiencies in the methodology under high sulfide, low nitrate conditions at these sites (Christensen et al. 1989). The two processes were nonetheless highly correlated over the seasons, suggesting that denitrification was probably limited by nitrate produced in nitrification. Seasonal patterns of nitrification were, in turn, controlled by depth of oxygen penetration into the sediments (Kemp et al. 1990). Evidently, sediments at these sites were characterized by such high oxygen demand in summer that the oxygenated nitrification zone in surficial sediments was negligible (Henriksen and Kemp 1988); this was so even at the shallow station when relatively high oxygen concentrations were present in the overlying water.

Simple budgets of nitrogen fluxes and transformations were developed for this 10 m station in the mesohaline Bay in April, August and November (Figure 12). In April and November, inputs of particulate organic nitrogen to the sediment surface far exceeded outputs of ammonium and nitrogen gas (through denitrification) to overlying water; this imbalance was further exaggerated by the uptake of nitrate in April. In August, inputs to and outputs from the sediments were reasonably well balanced. For the 20 m station, similar nitrogen budgets indicate that efflux of solutes (primarly ammonium) generally exceeded inputs, especially in summer. The excess organic nitrogen inputs at the shallow site, compared to the deficiency estimated for the deeper site, represents further indirect evidence for bedload transport of particulate organic matter from shallow to deep areas of the Bay. These budgets also emphasize the relatively reduced role of nitrification and denitrification (calculated by budgeting the nitrate pools) compared to ammonium regeneration to overlying water, where the former constitutes only 10-20% of the latter (Kemp et al. 1990).

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[5] These nitrogen transformation processes were measured by inhibitor techniques (N Serve [Henriksen et al. 1981] and acetylene [Sørensen 1978], respectively).

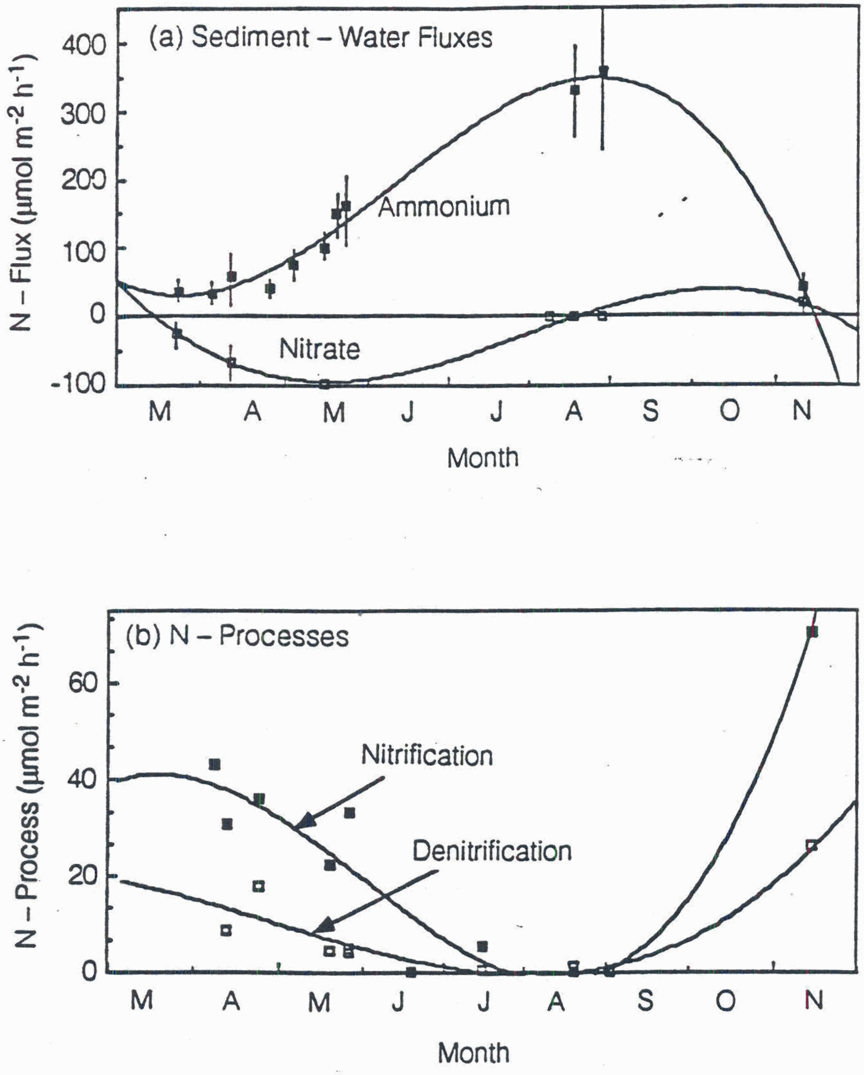

Figure 11. Annual cycles (March to November) of (a) net sediment-water exchanges of ammonium and nitrate plus nitrite and (b) sediment nitrification and denitrification rates for a shallow (10 m) station in the mesohaline region of Chesapeake Bay (Kemp et al. 1990).

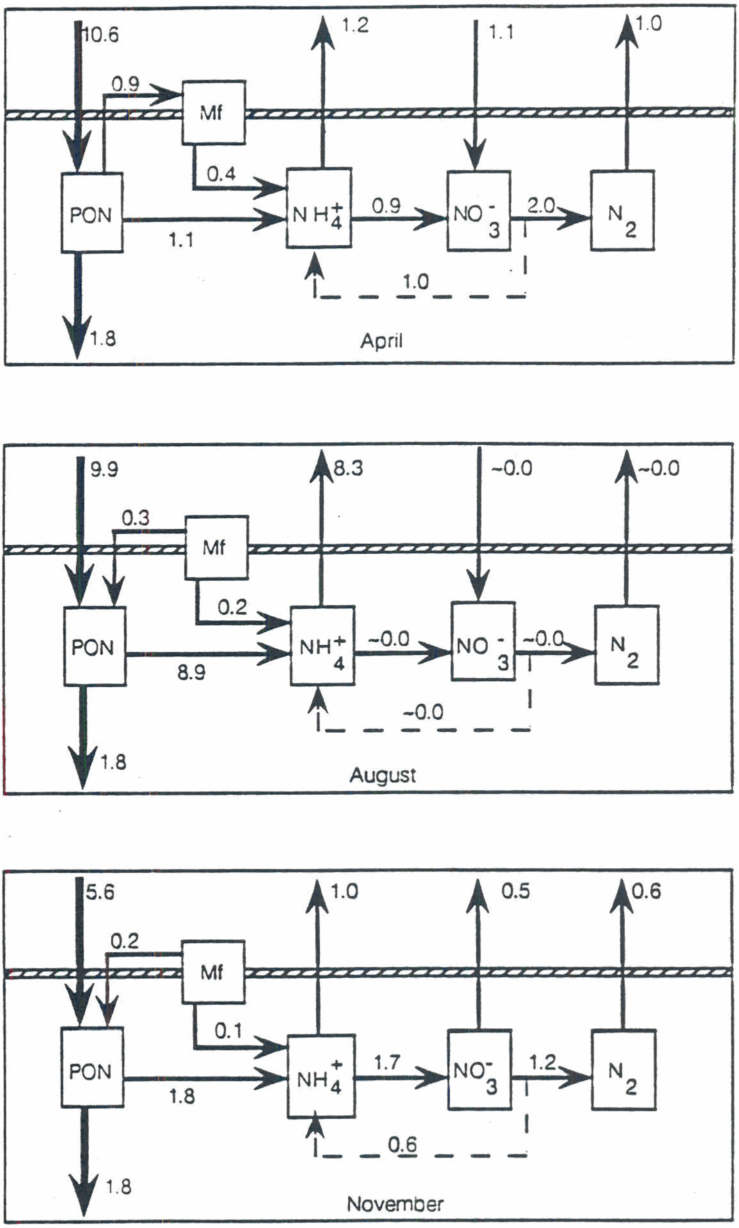

Figure 12. Budgets of nitrogen transformation processes and net exchanges across the sediment-water interface for three periods at a shallow (10 m) station in the mesohaline region of Chesapeake Bay (Kemp et al 1989). Rates are in units of mmoles N $m^{-2}d^{-1}$. Nitrogen pools considered include: particulate organic N (PON); ammonium, nitrate, dinitrogen gas and macrofauna biomass (Mf).

Recent measurements of nitrification and denitrification, as well as nitrate and ammonium fluxes, at stations all along the main salinity gradient of the Bay (Kemp unpublished), indicate somewhat different seasonal patterns for upper- and lower-Bay stations. Rates in the upper Bay were relatively high throughout the year, while nitrification (and associated denitrification) rates at the more saline stations appeared to be limited by low ammonium concentrations in late spring and summer. Preliminary time-space integrated estimates of denitrification for the whole main stem Bay suggest that nitrogen losses (i.e., nitrogen gas through denitrification) account for only 25 to 30% of the nitrogen inputs from the watershed. This is in contrast to the general pattern reported by Seitzinger (1988), where denitrification appeared to account for 50% (or more) loss of all nitrogen inputs to various estuaries. It appears that this relatively reduced importance of denitrification in the main Bay results from the decreased availability of dissolved oxygen in summer to support nitrification. When hypoxic conditions become chronic, normal nitrogen processing in sediments is suppressed and ammonium release predominates. This has the effect of reinforcing the hypoxic conditions by further supporting the cycle of algal production in overlying waters, followed by particulate organic matter deposition and consumption as well as oxygen depletion from bottom waters.

We can summarize pelagic-benthic nitrogen cycling at the 20 m mesohaline station site by comparing rates of nitrogen incorporation in phytoplankton growth to rates of organic nitrogen deposition to the sediments to rates of ammonium return from sediment processes back to the overlying water (Table 1). Mean data are provided for the period April to November from 1985 to 1987. Peak rates of organic nitrogen production occurred in mid summer, while deposition averaged over 1 to 2 month periods was relatively constant. As reported for other coastal sites, seasonality of ammonium regeneration from sediments corresponded closely to that for production (Kelly and Nixon 1984; Wassmann 1984). Deposition ranged from about 30 to 80% of production, and regeneration accounted for 40 to 210% of deposition. The overall averages of the four monthly mean rates suggest that 40% of the organic nitro-

Table 1. Summary of major benthic-pelagic exchanges of nitrogen over an annua cycle in the mesohaline region of Chesapeake Bay: production and depositon o particulate organic nitrogen (PON) and benthic regeneration of ammonium.

Months	Plankton PON Production[a]	Net PON Deposition[b]		Benthic NH_4^+ Regeneration[c]	
	(mg N $m^{-2}d^{-1}$)	(mg N $m^{-2}d^{-1}$)	%Prod	(mg N $m^{-2}d^{-1}$)	% Dep
Apr-May	189	89	47	38	43
Jun	238	81	34	118	146
Aug	334	86	26	182	212
Oct-Nov	143	110	77	73	66
Totals	904	366	40	411	112

[a] Data adapted from Sellner et al. 1988.
[b] Data adapted from Boynton et al. 1988.
[c] Does not include nitrogen loss via denitrification.

gen production is deposited. Regeneration averaged more than 110% of the deposition, possibly indicating additional sources of organic nitrogen inputs to sediments such as lateral transport of resuspended material along the bottom.

Interactions Between Phytoplankton and Benthic Macrofauna

Benthic invertebrate macrofauna are important components in coastal marine ecosystems such as Chesapeake Bay. These organisms constitute key food sources for many commercial finfish, including striped bass, spot, flounder, white perch and as valuable fisheries in themselves, in particular, blue crabs, oysters and soft clams. The soft bottom habitats of the Bay are dominated by polychaete worms and various bivalves (clams, for example) with crustacean amphipods also quantitatively important in some regions at different times of the year. Although other suspension-feeding macrofauna which attach to hard substrates — for instance, oysters, hydroids and barnacles — may have been dominant forms of benthic biomass in previous times, they now appear to be of secondary importance because of the generally impoverished oyster beds (Gerritsen et al. 1988).

Seasonal trends of macrofauna biomass and numerical abundances have been described for the upper and middle Bay's muddy and sandy sediment habitats (Holland 1988). While numerical abundances are similar for all areas, peak biomass values are an order of magnitude higher in the upper Bay because of the dense populations of molluscs (Holland et al. 1977). Similar patterns have been described for several major tributaries of the Bay which have also been studied extensively (Holland 1988). The importance of polychaetes increases down the Bay especially in muddy sediments. In fact, macrofaunal communities are dominated by large polychaetes in the polyhaline regions of the estuary (R. Diaz and L. Schaffner personal communication).

Seasonal maxima in macrofaunal abundance occur in June for most areas of the upper and middle Bay, followed by a precipitous decline in abundance and biomass with the onset of low oxygen conditions in summer, especially at the deeper muddy habitats. Various explanations have been postulated for the July decline. Anoxia, *per se*, is probably responsible at the deep (greater than 9 m) stations, while intensified predation in the shallower regions above the pycnocline (Holland et al. 1980) may account for the summer macrofaunal declines there (Kemp and Boynton 1981). With the crash of the spring diatom bloom in May (Malone, this volume), the marked decline in particulate organic matter deposition (Figure 3) may also result in food limitations for the benthos in some areas of the Bay (Marsh and Tenore 1990). The higher carbon to nitrogen (C:N) and carbon to chlorophyll *a* (C:Chl) ratios of particulate organic matter deposited in summer indicate a lower nutritional content of food available to support benthic macrofauna after June (Christensen and Kanneworff 1985; Gardner et al. 1989).

Feeding guilds of benthic macrofauna grade sharply from predominantly "head up" feeders, for example, the clam *Macoma balthica* and the polychaetes *Nereis succinea* in the upper and middle Bay to predominantly "head down" feeders, for example, the polychaete *Macroclymene zonalis* in the lower Bay; predatory forms are more important in sandy sediments of the middle and lower Bay (Holland 1988). This transition in predominance of head-up to head-down macrofaunal feeding types roughly parallels the decreasing organic content and increasing redox conditions of sediments from the upper-middle to lower Bay. Presumably, low redox conditions and relatively high rates of particulate organic matter deposition in the northern regions of the Bay favor infaunal species which respire in the overlying water and feed at the sediment-water interface. In contrast, the lower inputs of particulate organic matter to sediments of the lower Bay select for animals capable of reworking the organic pools in the relatively oxidized sediments (Jumars and Fauchald 1977).

To the extent that food availability limits growth of benthic animals, expectations are that on broad time and space scales biomass and secondary production of macrofauna would be directly proportional to deposition rates of particulate organic matter from overlying waters to sediments (Rowe 1971; 1985; Parsons et al. 1979; Josefson et al. 1987; Grebmeier et al. 1988). In Chesapeake Bay, contemporaneous seasonal data for particulate deposition (i.e., sediment traps) and benthic biomass are available for only one mesohaline site (Figure 2, Sta M4); however, on seasonal time scales no significant correlation between particulate organic matter deposition and benthic biomass could be found for this station. The absence of a relationship here is largely a consequence of the seasonal loss of benthic macrofauna associated with oxygen depletion from bottom waters (Holland et al. 1977; Kemp and Boynton 1981). Therefore, it would be more likely to find a relationship between plankton deposition and benthic biomass by comparing seasonal or annual mean values among different stations with similar seasonal patterns of dissolved oxygen.

Since there is only one sediment trap site in Chesapeake Bay, it is impossible to make spatial comparisons of relations between macrofaunal abundance and particulate organic matter deposition. Contemporaneous measurements are available, however, for phytoplankton production and abundance as chlorophyll *a* (Sellner personal communication) and biomass of benthic macrofauna (Holland personal communication) at several stations in the mainstem and tributaries of the Bay. Statistically significant correlations were observed between annual mean biomass of polychaetes (g ash free dry weight m^{-2}) and euphotic zone chlorophyll *a* (mg m^{-2}) in spring among these Bay sites when the benthic data were partitioned to separate stations experiencing summer hypoxia or anoxia in bottom waters (Figure 13). The slope of the relation for the hypoxic stations is, however, an order of magnitude less than that for the oxic stations, indicating the stress effects of seasonal oxygen depletion on the metazoan benthic community (Kemp and Boynton 1981). No significant correlation was observed between values for benthic macrofauna and phytoplankton abundance in summer. The absence of such relations emphasizes the importance of the spring deposition events in supporting these benthic populations (Parsons et al. 1979; Townsend and Cammen 1988).

In the above analysis, the other main group of organisms composing the majority of benthic biomass in Chesapeake Bay — bivalves — was purposely omitted from the macrofauna because these animals, which are primarily suspension feeders, are not just passive recipients of particulate organic matter deposition. In fact, their active grazing can directly reduce plankton abundance and production (Officer et al. 1982; Cloern 1982). When the biomass of suspension-feeding bivalves is compared with plankton abundance and production, the patterns are quite different than those for polychaetes (Figure 14). Note that the independent variable (x-axis) has been reversed between Figures 13 and 14 to emphasize a shift in the dominant direction of causality. An inverse relationship between spring biomass of bivalves and annual mean values of euphotic-zone chlorophyll *a* and phytoplankton production was obtained for the monitoring stations which do not experience seasonal anoxia. This pattern suggests that phytoplankton are unaffected by bivalve abun-

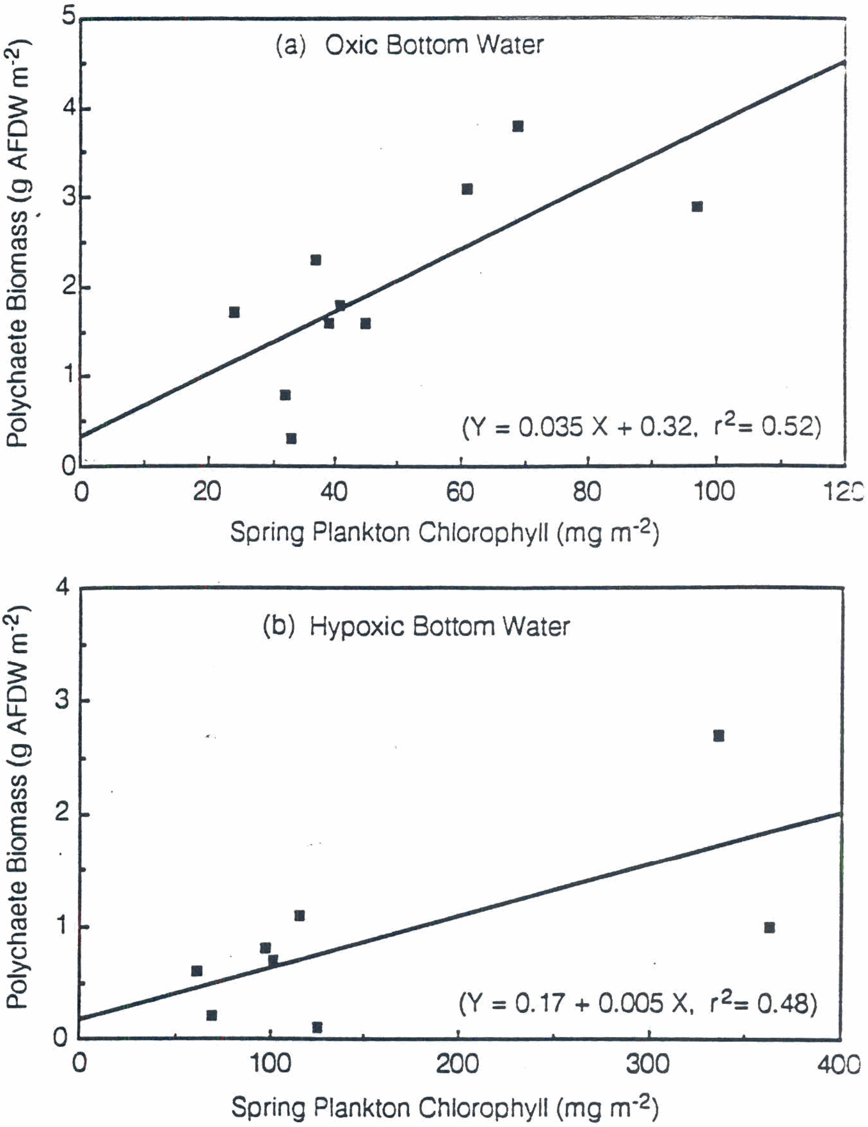

Figure 13. Correlations between annual mean macrofaunal biomass (excluding clams) versus (a) spring peak phytoplankton production and (b) spring peak phytoplankton chlorophyll a. *Each point represents a different station in the main stem or tributaries of the Bay (data taken from Sellner 1988 and Holland 1988).*

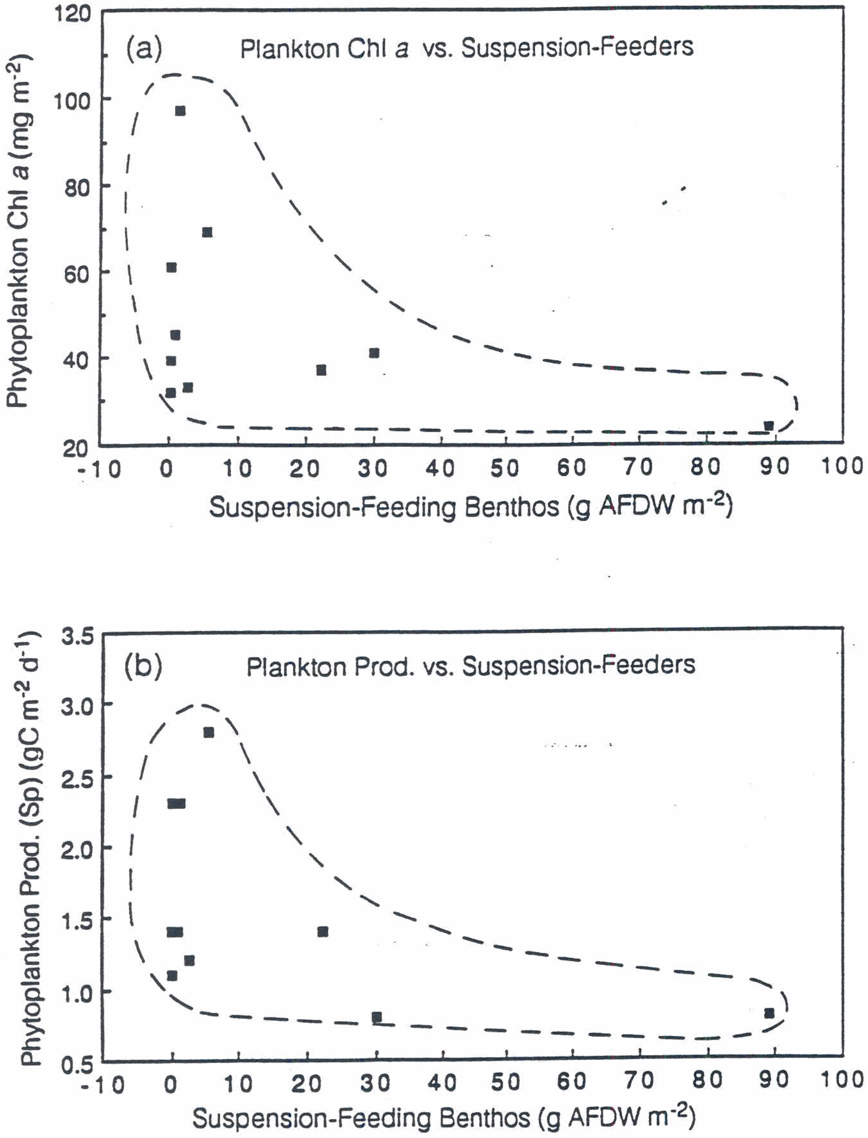

Figure 14. Relations between annual mean biomass of suspension-feeding macrofauna versus (a) spring peak phytoplankton chlorophyll a *and (b) spring peak phytoplnkton production. Each point represents a different station in the main stem or tributaries of the Bay (data taken from Sellner 1988 and Holland 1988).*

dance for most stations in the middle to lower regions of the Bay and its tributaries, whereas phytoplankton are markedly reduced at the upper estuarine stations (mainstem Bay, Patuxent and Potomac rivers) which support abundant clam populations. Light limitation on algal growth may also contribute to low phytoplankton abundance in low salinity Bay regions.

Previous analyses of the impact of the asiatic clam, *Corbicula fluminea*, on phytoplankton in the upper Potomac River estuary by Cohen et al. (1984) have reported similar inverse relations between plankton and clam abundances. These investigators have also demonstrated experimentally the ability of the animals to dramatically graze plankton from the water column. While the invasion of this exotic species into the upper Potomac may represent an unusual event, recent calculations (Gerritsen 1988; Gerritsen et al. 1988) suggest that clam populations in the fresh water regions of other tributaries as well as the mainstem Bay are sufficient to significantly reduce phytoplankton abundance.

Prior to the latter part of the nineteenth century, the largest population of suspension-feeding animals in Chesapeake Bay was probably the American oyster, *Crassostrea virginica.* Intensive harvesting of oysters since the turn of the century and more recently, disease has resulted in dramatic (100-fold) declines in their abundance throughout the Bay (Kennedy and Breisch 1981). Newell (1988) has, therefore, postulated that the significant decrease in grazing by oyster populations across the Bay is responsible for much of the increase in phytoplankton biomass since the 1930s which has otherwise been attributed to eutrophication of this estuary (Boynton et al. 1982; Officer et al. 1984). Because clam abundances are so large in the upper Bay regions, it is difficult to ascertain whether the total activity of suspension-feeding benthic macrofauna has decreased with the decline of oysters (Gerritson et al. 1988). It is clear, however, that spatial distributions of suspension-feeders have changed significantly. An important consideration is the effect of reef-forming animals like oysters on the increasing transport of plankton to the bottom by reducing the height of the benthic boundary layer (Frechette et al. 1989). On the other hand, increased recycling of nutrients and consumption of oxygen associated with the metabolism of suspension feeding benthic animals themselves and with their fecal and pseudofecal matter (see Jordan 1985) could serve to stimulate phytoplankton growth and oxygen depletion during summer (Doering et al. 1987). Thus, it remains an open question as to the ultimate effect of shifts in abundance of suspension-feeding benthic macrofauna on the "greening" of the Bay with increased phytoplankton and/or the depletion of oxygen from its bottom waters.

Comparisons of Macrofaunal Interactions with Other Systems

Parsons et al. (1979) have reported a clear relationship between spring biomass of phytoplankton and peak macrofaunal abundance across a wide range of coastal marine environments (Figure 15). Presumably, this kind of correlation would be even stronger if rates (i.e., particulate organic matter deposition and macrofaunal

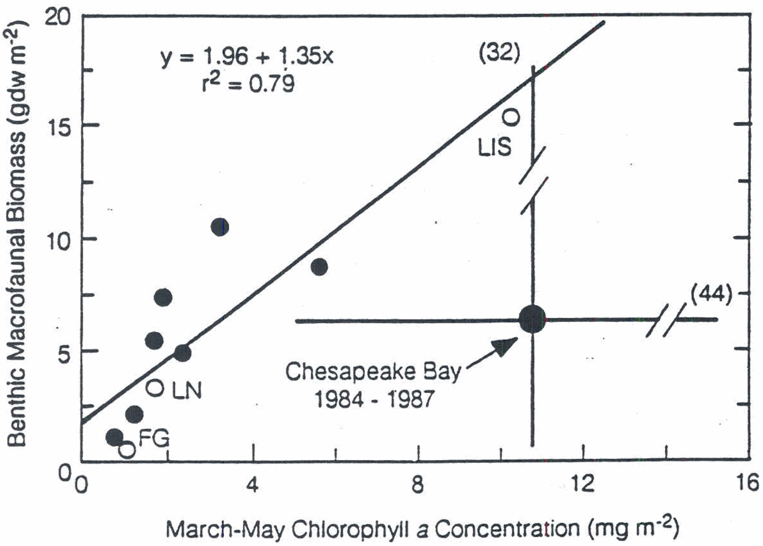

Figure 15. Summary of benthic macrofaunal biomass versus spring chlorophyll a for various marine sites reported in the literature (Parsons et al. 1979), with values for annual means and ranges from Chesapeake Bay (Holland 1988; Sellner et al. 1988) presented for comparisons.

production) were compared rather than stocks, though such data are rarely available for annual cycles at a given site. No significant relation from these data was obtained when summer phytoplankton biomass were considered instead of spring values (B. Hargrave personal communication). Other investigators have emphasized the importance of the spring diatom bloom as the primary source of food to sustain growth and recruitment of benthic macrofauna in temperate marine regions (Graf et al. 1982; 1983; Hargrave and Phillips 1986). The importance of the spring bloom in providing large quantities of high quality food for the benthos lies in the fact that much of this spring bloom is deposited as intact, ungrazed diatoms (Smetacek 1984). In fact, Townsend and Cammen (1988) have postulated that the relative magnitude of benthic invertebrate production and associated success of juvenile demersal fish recruitment for a given year in the Gulf of Maine depends on the timing of the spring bloom, where maximum deposition and recruitment success occur for early blooms which precede the period of intense zooplankton grazing. Indeed, sinking particulate organic matter has maximum nutritional value for growth of benthic animals when dominated by intact diatoms (Christensen and Kanneworf 1985; Gardner et al. 1989).

In nutrient-rich stratified coastal systems such as Chesapeake Bay, the seasonal depletion of oxygen from bottom waters in late spring to early summer complicates this relation between phytoplankton and benthic macrofauna (e.g., Figure 13). The mean and range of spring values for phytoplankton chlorophyll *a* and macrofauna biomass at all Chesapeake Bay stations (see Figure 2) are also plotted on Figure 15. Given the relatively high chlorophyll *a* levels in the Bay, mean macrofauna biomass is much less than expected from the relation. This deficiency in the abundance of Chesapeake Bay macrofauna, compared with the high phytoplankton production, again emphasizes the negative effects of eutrophication and associated oxygen depletion from the Bay's bottom waters.

Nixon (1988) recently pointed out the relatively low rate of fisheries yield per unit primary production for fresh water ecosystems compared to coastal marine regions. Previous studies have established strong correlative relations between nutrient loading and phytoplankton production (Schindler 1981) and between benthic macrofaunal abundance and fisheries yields for various lakes. Nixon (1988) attributed this pattern of higher relative fish yields per unit primary production in marine ecosystems to the seasonal anoxia in bottom waters of most temperate lakes compared to the oxic bottom waters of most tidally mixed estuaries. However, in estuaries such as Chesapeake Bay which undergo seasonal anoxia, this reasoning implies that demersal fisheries may also be significantly depressed, due to the impact of anoxia on benthic-pelagic coupling.

Role of Benthic and Pelagic Processes in Oxygen Depletion

During spring in the mesohaline region of the Chesapeake Bay main stem, vertical stratification of the water column combines with springtime warming and the deposition and consumption of the diatom bloom to produce a rapid decline in oxygen concentration in the bottom waters (Taft et al. 1980; Malone, this volume). Similar patterns of seasonal anoxia have been reported for numerous coastal marine systems (Richards 1965; May 1973; Jørgensen 1980; Falkowski et al. 1980; Caumette et al. 1983). Vertical density stratification, which reduces the exchange of oxygen between the upper and lower layers of the water column, plays a key role in this phenomenon (Turner et al. 1987). Therefore, meteorological and hydrological processes strongly influence the magnitude of anoxic events in Chesapeake Bay (Seliger et al. 1985; Seliger and Boggs 1988; Boicourt, this volume). However, it is the production, deposition and consumption of organic matter which fuels this process each year (Malone et al. 1986). In principle, the elevated inputs of nutrients in eutrophic coastal ecosystems could increase the spatial and temporal dimensions of bottom water anoxia by increasing algal production (Boynton et al. 1982; Malone et al. 1988). Recent evidence suggests that this may be the case for Chesapeake Bay (Officer et al. 1984), and ecosystem simulation modeling studies corroborate the rationale for this relationship (Kemp and Randall 1988).

The mean and range of time delays between organic production in the upper layers and subsequent consumption (and associated oxygen depletion) in the lower water column and benthos are poorly understood. How much organic production is carried over between seasons and years to support subsequent consumption processes? This question is important from a management standpoint because of a need to know how rapidly oxygen concentrations and related ecological processes will respond to controls on eutrophication. Understanding how total oxygen consumption is divided between planktonic and benthic processes would provide some insights on this question because there tends to be a more rapid coupling between production and planktonic respiration than between production and benthic respiration (Oviatt et al. 1986). A portion of the benthic metabolism of coastal marine systems involves complex sequences of microbial and geochemical processes which may require considerable time to complete (Berner 1980). In addition, the relative contributions of biological processes (production, respiration) and physical processes (stratification, transport) to oxygen depletion is of concern to managers because most control measures for eutrophication (e.g., reduced nutrient inputs) involve only the biological factors.

Both planktonic and benthic respiration processes in the Bay increase rapidly with vernal warming in spring. The rate of increase between March and June is more rapid for planktonic respiration, peaking in early July compared to an early August maximum for benthic oxygen consumption (Kemp unpublished data). Pre-incubation filtration experiments indicated that most of the plankton respiration in bottom waters was associated with bacteria and protozoa (< 3 µm) (Jonas, this volume). Similar microbial dominance of planktonic respiration has been reported for other coastal systems (Williams 1981; Hopkinson et al. 1989). The high August rates associated with the benthos actually occur in the water column at the pycnocline (oxycline) via oxidation of sulfides produced in sulfate reduction and diffusing from sediments to overlying water (e.g., Indrebo et al. 1979; Dyrssen 1986). These rates of sulfide efflux from sediments do not occur until several days after oxygen has been depleted from bottom waters. Considering the mean depth of the bottom layer in this region of the Bay, the relative magnitudes of benthic and planktonic rates can be compared over the spring summer period (Figure 16a). Although benthic rates exceeded planktonic rates in early April and late August in 1986, for most of this period planktonic respiration was 1.5 to 2 times greater.

The magnitude of physical transport processes in the seasonal budget of oxygen is more difficult to ascertain (Boicourt, this volume). However, rates can be inferred from careful analysis of budgets of oxygen inputs to and outputs from the upper and lower layers of an average square meter of water column in the mesohaline region (e.g., Kemp and Boynton 1980). For the present analysis of 1986 data, it was assumed that net longitudinal exchanges of oxygen were negligible in the upper layer (Kemp, unpublished data). This assumption is supported by the absence of any consistent longitudinal gradient of oxygen content (as % saturation) of the surface waters. Vertical exchange between layers was then calculated as the difference between observed rates of change in oxygen and those calculated as the sum of all measured rates. Horizontal oxygen transport was, however, allowed in the budget for the bottom layer (Kuo and Neilson 1987), and net rates were calculated as above, by difference. Table 2 summarizes details of these calculations for April, May and August. By way of an independent check, the fact that calculated rates of vertical and horizontal oxygen transport were significantly correlated ($r^2 > 0.60$) to their respective oxygen concentration gradients lends credibility to this indirect approach.

For purposes of comparing biological and physical processes, monthly means for the algebraic sum of oxygen fluxes associated with physical transport were plotted against mean total respiration rates for the bottom layer from March to October in 1986. It can be seen that respiration exceeds oxygen replenishment by physical transport for most of the spring and early summer, but especially in

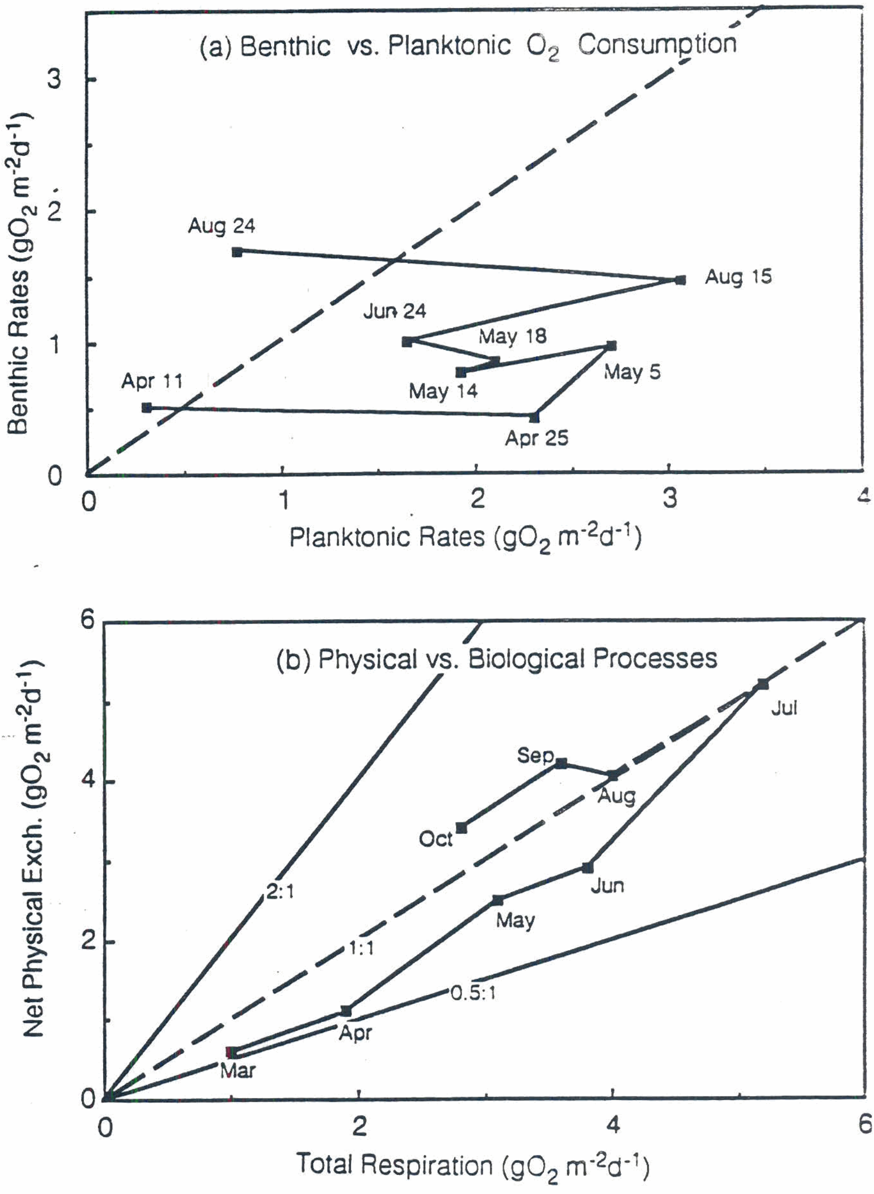

Figure 16. Seasonal sequence of (a) benthic versus planktonic oxygen consumption rates (April-August 1986) and (b) oxygen consumption by biological processes versus net oxygen exchange via physical processes (March-October 1986). Taken from Kemp et al. (unpublished).

Table 2. Summary balance of oxygen fluxes ($gO_2\ m^{-2}d^{-1}$) for upper and lower layers of water column in the mesohaline reach of Chesapeake Bay during Spring and Summer.

Water Column Layer Oxygen Fluxes	April	May	August
Upper Layer:			
Production[a]	+5.4	+6.8	+9.4
Plankton Respiration[b]	-3.0	-4.3	-5.3
Air-Water Exchange[c]	-1.2	-1.2	-1.2
Temporal Change	0	-0.1	-0.3
X-Pycnocline Exchange[d]	-1.2	-1.4	-3.2
Lower Layer:			
X-Pycnocline Exchange[d]	+1.2	+1.2	+3.2
Plankton Respiration	-1.3	-2.2	-1.9
Benthic Respiration[e]	-0.5	-0.9	-1.6
Temporal Change	-0.8	-0.6	0
Net Horizontal Exchange[f]	-0.1	+1.1	+0.8

[a] Gross O_2 production estimated from net daytime (apparent) production plus half of the dark respiration (assuming day and night respiration rates are equal and 12 h daylight).

[b] Dark respiration of whole water; assumes upper layer height of 8 m and mean depth of lower layer equal to 6 m, except in August when lower layer is anoxic and pycnocline thickness of 3 m is used.

[c] Assumes air-water exchange coefficient equal to 1.0 $gO_2\ m^{-2}h^{-1}$ at 100% saturation deficit (Kemp and Boynton 1980); diel mean % O_2 saturation taken at 105%.

[d] Net O_2 exchange across pycnocline estimated as residual term in upper layer O_2 balance.

[e] Benthic O_2 consumption estimated as mean of rates measured at 10 m and 20 m depth; rates at 20 m include sulfide efflux in August.

[f] Net longitudinal O_2 exchange estimated as residual term in lower layer O_2 balance.

April (Figure 16b). During most of the year, the balance between physical and biological processes does not stray far from the 1:1 line, which is intersected in July and continually exceeded until October.

These data illustrate the fact that biological and physical processes of oxygen transformation and transport are poised in near balance throughout the period from spring to autumn. This is not surprising because of the interdependence of the two kinds of processes. Physical transport depends on concentration gradients which are created only by biological processes. On the other hand, at low concentrations of oxygen, biological processes follow first-order kinetics and are directly proportional to the rate of physical transport of oxygen. This balance is analogous to that in the diffusion-reaction model which characterizes many biogeochemical processes.

In summary, we find that planktonic respiration is quantitatively more important than benthic processes for most of the spring period of declining bottom water oxygen. Benthic respiration is, however, more significant at the beginning and end of the anoxia period. Biological consumption of oxygen in the bottom layer is reasonably balanced with physical replenishment processes throughout the period between March and October, such that small changes in either could have marked effects on the magnitude and timing of seasonal anoxia. Numerical ecosystem modeling studies of this system have illustrated the importance of this balance between biological and physical processes: in the absence of vertical wind mixing in summer, anoxia persisted until November, while removal of external nutrient inputs resulted in virtual elimination of anoxia within one year (Kemp and Randall 1988).

Effects of Eutrophication on Benthic-Pelagic Coupling

Limnologists have long recognized that for many lakes, the process of continual nutrient enrichment is part of a natural sequence in the long-term history of these aquatic ecosystems (Hutchinson 1974). It is well documented that the anthropogenic acceleration of this process — that is, nutrient enrichment in river flow and airborne deposition — tends to produce a range of dramatic changes in the structure and function of lake ecosystems, including depletion of bottom water oxygen, losses of submersed vascular plants and alterations in food chains and associated fisheries (e.g., Edmondson 1969; Lehman 1988). In contrast, for coastal marine ecosystems evidence has been scant that eutrophication is a natural biogeochemical process, though there is growing recognition that the widespread pattern of rapidly increasing anthropogenic nutrient inputs to coastal marine waters is resulting in pronounced alterations of organism abundances and ecological interactions (Nixon et al. 1986).

Indirect evidence exists that in Chesapeake Bay responses of ecological processes to changes in nutrient loading from the surrounding watershed may be relatively more pronounced than for many other estuaries. In fact, significant positive relationships between rates of phytoplankton production and nitrogen inputs (Boynton et al. 1982) were observed both for Chesapeake Bay and its tributaries and for a variety of other estuaries combined together (Figure 17a). We have postulated that the higher production per unit nutrient inputs in the Bay may indicate greater retention and recycling of these inputs (Kemp and Boynton 1984). Since most of the other estuaries in Figure 17a are vertically well mixed, it can be inferred that the efficient trapping of particles in the Bay's two-layer gravitational circulation may be an important factor (Boicourt, this volume). Evidently, this nutrient retention occurs at interannual time scales (Boynton et al. 1982). For instance, a significant correlation between river flow, the primary source of nutrients to the Bay, and phytoplankton was observed only when a two-year running mean flow was used, implying a residual effect of one year's nutrient inputs on the next year's production (Figure 17b) (Sellner personal communication). Because this same physical mechanism of vertical stratification which evidently leads to enhanced nutrient retention, also contributes to reduced reoxidation of bottom waters, estuaries such as the Chesapeake may be more susceptible to increased anoxia in response to eutrophication.

While we have already described several observed or postulated changes in Chesapeake Bay's benthic-pelagic interactions which

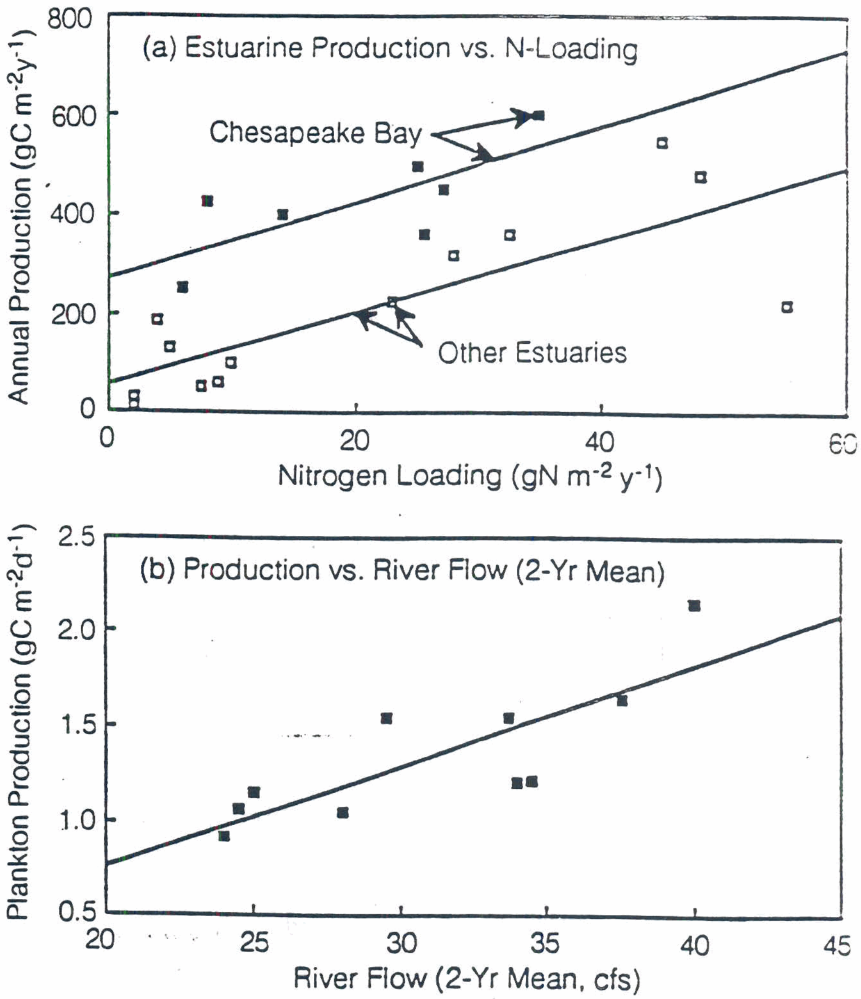

Figure 17. Phytoplankton production versus nutrient loading from river flow: (a) annual production versus nitrogen loading rates for Chesapeake Bay and other estuaries (Boynton et al. 1982); (b) annual mean daily production versus two-year running mean of river flow for the mesohaline region of Chesapeake Bay (Sellner unpublished data).

might be attributable to eutrophication, here we summarize these relationships between coastal eutrophication and benthic-pelagic couplings in an integrated framework. Our discussion focuses on the following major mechanisms by which nutrient enrichment might alter key processes of benthic-pelagic coupling: (1) effects on plankton trophic dynamics and resulting particulate organic matter deposition; (2) effects on benthic macrofaunal abundance and demersal fisheries; (3) effects on rates and temporal scales of benthic regeneration processes. The causal connections and pathways by which these mechanisms occur can be illustrated by referring back to the conceptual scheme presented in Figure 1.

Planktonic Food-Chains and Particulate Organic Matter Deposition

Particulate organic matter can sink from the upper water column toward the sediment surface in a number of forms: as intact algal cells; as zooplankton fecal pellets; as carcasses of dead animals; and as miscellaneous plant debris. The deposition of particulate organic matter from overlying water to sediments can occur via passive sinking or through the active pumping by benthic suspension feeders. As suggested in Figure 1, the two primary pathways of passive sinking, as algal cells or zooplankton feces, are regulated by the magnitude of primary production and by trophic interactions in the plankton community.

Hargrave (1973) reported benthic community metabolism was significantly correlated with the ratio of primary production to mixed layer depth; this correlation was characterized by a power function (exponent = 0.39) for a variety of coastal sites. The fact that the exponent of this relation is less than unity implies that as primary production over the mixed layer increases (as might be the case with eutrophication), the relative importance of benthic metabolism in consuming that production decreases. Here, it is assumed that benthic metabolism is directly proportional to particulate organic matter deposition, with no change in the fraction buried. This same pattern of decreasing proportion of total oxygen consumption by benthic — compared with planktonic — processes was seen along an experimental nutrient enrichment gradient in the MERL mesocosms (Oviatt et al. 1986).[6] In addition, a similar relation was also evident over an annual cycle in the Georgia Bight, where benthic respiration was proportionately less important relative to planktonic respiration during periods of peak production (Hopkinson 1987).

Several investigators have suggested that the specific nature of plankton trophic interactions can greatly affect the quantity and quality of particulate organic matter deposition to the benthos in coastal ecosystems (Smetacek 1984). For example, Hargrave (1973) postulated that such a pattern (described in previous paragraph) might be attributable to the fact that zooplankton communities were more efficient in consuming the relatively dense assemblages of phytoplankton characterizing eutrophic waters. Alternatively, any increase in the importance of bacterial and protozoan respiratory consumption of organic matter would result in a relative reduction in particulate organic matter deposition (Williams 1981), while increased grazing by certain gelatinous zooplankton might lead to increases in deposition (Andersen and Nival 1988).

Benthic Macrofauna and Demersal Fisheries

Although eutrophication of coastal waters may result in an increase in the relative proportion of phytoplankton production consumed by planktonic as opposed to benthic processes, the absolute rates of particulate organic matter deposition will increase with eutrophication. In systems with vertically well mixed water columns, this increase in organic food available to the benthos would support greater growth of macroinvertebrates and demersal fish (e.g., Figure 13a). Indeed, higher abundance of benthic macrofauna (especially polychaetes) was observed in response to fertilization in the well-mixed overlying water columns of the MERL mesocsosms (Grassle

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[6] The Marine Ecosystem Research Laboratory (MERL) is a facility located at the University of Rhode Island designed around fourteen cylindrical mesocosms (5.5 m in depth and 1.8 m in diameter). These mesocosms are set up and maintained as experimental ecosystems, and are used to conduct studies on the behavior of natural systems and their response to perturbations.

1985). However, in estuarine regions with vertically stratified water columns, increased phytoplankton production associated with eutrophication can lead to oxygen depletion, resulting in a decrease of benthic animals. In the Baltic Sea, for instance, increased algal production and deposition between the 1930s and the 1970s, presumed to be associated with eutrophication, resulted in different changes in benthic macrofaunal abundance within different depth regimes. The shallow regions not subject to hypoxia experienced macrofaunal increases, while in the deeper parts of the Baltic macrofauna decreased during this time (Cederwall and Elmgren 1980). Likewise, because much of Chesapeake Bay is vertically stratified, it is reasonable to assume that benthic macrofaunal production is inhibited in some regions and that the continuing trends of increasing eutrophication will lead to further losses of production for benthic invertebrates and associated demersal fisheries.

Rates and Temporal Scales of Benthic Nutrient Recycling

Each year nutrient inputs to temperate estuaries such as Chesapeake Bay directly support organic production in the spring and indirectly support, through benthic recycling processes, continued high production in the summer. It is the benthic recycling processes which provide nutrients for most of the estuary's production in the warmer seasons (Kemp and Boynton 1984). For nitrogen, high rates of benthic recycling lead to large, rapidly exchanging sediment pools of ammonium in summer. If oxygen is available, a substantial portion of this ammonium will be oxidized to nitrate, which is in turn reduced to nitrogen gas (N_2) by nitrifying and denitrifying bacteria, respectively. Thus, high rates of nitrification-denitrification will occur in summer but only *under conditions of oxygenated bottom waters.* For many coastal ecosystems with well-mixed water columns, approximately half of the nitrogen entering from the watershed is transformed as nitrogen gas via nitrification-denitrification processes (Seitzinger 1988). For stratified eutrophic estuaries such as portions of the upper Chesapeake Bay, which experience severe hypoxia in bottom waters, this coupled nitrification-denitrification process is inhibited because of the lack of oxygen in bottom waters (Kemp et al. 1990). As a consequence, less than 30% of the nitrogen inputs to the mainstem Bay are removed as nitrogen gas. Therefore, while increased rates of nitrogen loading to the Chesapeake Bay have contributed to expanding eutrophication effects, associated hypoxic conditions appear to be resulting in an inhibition of nitrification and denitrification, which has the positive feedback effect of further stimulating the eutrophication process by increasing the retention and recycling of ammonium to support more phytoplankton production in summer.

Recent evidence suggests that interannual variations in benthic metabolic processes are proportional to changes in nutrient inputs to the Bay. Long-term records for these important ecological processes are not available to compare, for example, rates prior to European settlement with twentieth century rates. However, because river flow, which is the primary source of nutrients to the Bay, varies markedly from year to year, correlations between river flow and ecological processes during modern times can be used to infer relations over longer time-scales. For example, for the six years of data for which summer rates of benthic phosphorus recycling were available in the lower Patuxent River estuary, there was a significant relation to river flow in the preceding spring (Figure 18). Similarly, a continual decrease in rates of sediment oxygen consumption observed throughout the Bay main stem between 1985 and 1988 (Figure 19a) might be interpreted as a response to changes in plankton production. In fact, river inputs of nutrients in 1984 were among the highest on record, while the following four years were characterized by severe drought conditions with relatively little nutrient delivery to the Bay. One interpretation of this pattern is that a residual nutrient pool from inputs in 1984 contributed to recycling of nutrients in 1985 (Figure 17) to support relatively high plankton production (Malone et al. 1988) and benthic community metabolism (Figure 19b, c) in 1985. Consistent with this interpretation is the fact that despite the extremely low riverflow in 1985, bottom water anoxia in the mesohaline Bay was more severe in that year than in subsequent years (1986-1988), again suggesting a residual effect from 1984.

This concept that processes of benthic-pelagic coupling can be affected in one year by nutrient inputs from previous years has significant implications for strategies to manage nutrient waste inputs to the Bay. It is important to understand the extent to which manifestations from past eutrophication will continue to be experienced in the future even after reductions in nutrient inputs. Direct experiments have shown that particulate organic matter inputs to sediments will continue to produce high rates of benthic metabolism and nutrient recycling for several months but are generally dissipated to pre-treatment background levels in less than a year (Kelly and Nixon 1984; Rudnick and Oviatt 1986). These direct relationships between nutrient inputs in a given year and benthic recycling processes within that year or the next (Figures 18 and 19) suggest that most of the effects of nutrient loading are not retained for more than a year or two. It is still unclear, however, what is the extent to which small amounts of organic matter — retained in

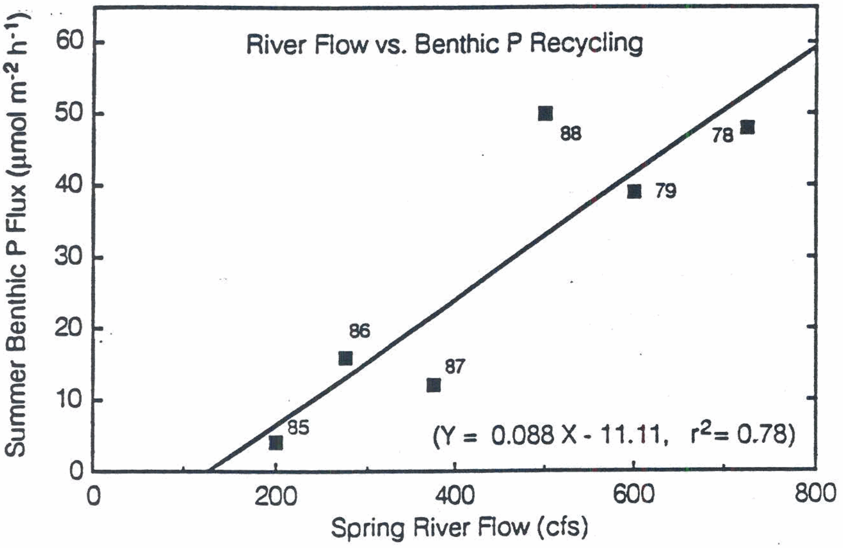

Figure 18. Relationship between fluxes of dissolved inorganic phosphorus across the sediment-water interface at a station in the lower estuary and average spring (March-May) river flow of the Patuxent River; numbers next to points indicate years (Boynton et al. unpublished data).

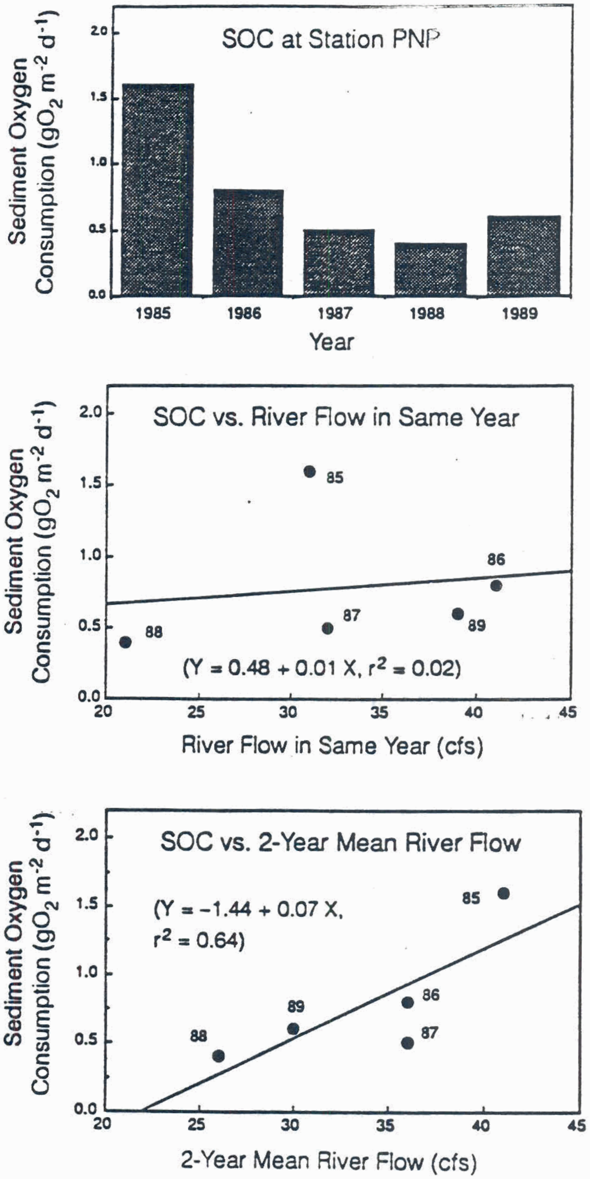

Figure 19. (a) Annual mean rates of sediment oxygen consumption (SOC) at a station in the Chesapeake Bay main stem near the mouth of the Potomac River for 1985-1988; (b) correlation between SOC and river flow for each year; (c) correlation between SOC and two-year running mean of river flow in given year and that in previous year.

sediments over decades and decomposing at slow rates — can contribute to the long term benthic process of oxygen consumption and nutrient recycling. With increasing eutrophication, the proportion of particulate organic matter deposition which is buried may well increase.

Research Needs and Management Implications

During the last decade a great deal has been learned concerning benthic-pelagic coupling in coastal and estuarine systems including Chesapeake Bay. As is generally the case, the results now available pose additional specific questions that should be addressed to further our understanding and ability to predict aspects of estuarine ecosystem dynamics.

Research Needs

At this time there is considerable uncertainty with regard to relations between plankton trophic dynamics and deposition rates of particulate organic matter. For example, our current understanding is that the spring bloom in the central regions of the Bay largely sinks as intact cells with little exposure to grazing in the water column. In contrast, summer phytoplankton stocks appear heavily grazed and large percentages of organic production are metabolized in the water column. The reasons for and implications of this seasonal shift are not clear. Secondly, it is uncertain how much of the deposited organic material is incorporated into benthic macrofaunal biomass or how important benthic food webs are to fisheries production. There is evidence which suggests that some benthic macrofaunal communities are food limited (Marsh and Tenore 1990) even in this relatively food-rich system and that predation is an important factor regulating benthic communities (Holland et al. 1980). Many potential interactions between benthic nutrient cycling and the eutrophication process remain unclear although there are tantalizing hints to the effect that strong positive and negative feedback mechanisms (i.e., destabilizing and stabilizing, respectively) dominate along the eutrophication gradient.

Explaining such phenomena will require a diversity of techniques. Experience in recent years has clearly indicated the value of generating long-term data sets collected at appropriate time scales. Such data sets are invaluable in developing understanding of linkages between system components and external factors believed to force the system. Due to climatic variability natural experiments are often contained within such data sets. In terms of developing clear linkages between benthic and pelagic system components and between external forcings such as nutrient loading and benthic components, it now appears that favoring more measurements at a limited number of locations provides more useful information than a strategy that emphasizes spatial at the expense of temporal coverage.

Secondly, utilization of improved technologies such as remote sensing and in-situ moorings designed to record selected environmental conditions would vastly improve our ability to determine the proper spatial and temporal scales, respectively, for study. It is possible to infer some cause-effect linkages from in-situ field studies and this has been the approach most frequently taken in studies in the Bay. Ecosystem simulation modeling, done in conjunction with such field studies, has proven to be a useful tool for integrating our understanding of community dynamics. Furthermore, there has been considerable success in using a variety of mesocosms as tools for conducting experimental ecosystem studies and this approach is capable of efficiently yielding many more insights on mechanisms controlling ecosystem processes. Finally, sufficient data are now available in both the published and gray literature to support intensive and reasonably detailed comparative studies of benthic-pelagic couplings among widely varying coastal ecosystems.

Management Implications

The natural two-layer circulation of Chesapeake Bay waters creates conditions which favor the retention of nutrients in particulate forms, allowing this plant foodstuff to be efficiently used and reused before being buried, lost to gaseous forms or exported to the sea. The resulting high production of phytoplankton is a major factor contributing to anoxia during the warmer months each year.

This two-layer water flow in the Bay also separates upper and lower layers of the water column, effectively reducing the ability of oxygen to be transported from the atmosphere to the bottom waters and leading to depletion of oxygen (i.e., anoxia). Thus, this two-layer circulation, which is common in many other estuaries around the world, but particularly effective in Chesapeake Bay, makes the Bay very susceptible to the effects of nutrient enrichment on bottom water anoxia.

The processes by which particulate organic foods are deposited from the water column to the sediments are regulated by the nature of the planktonic food-chains, which are, in turn, controlled by the extent of nutrient enrichment in Chesapeake Bay. Any increases or decreases in nutrient inputs to the Bay are likely to significantly alter this process and result in shifts between the relative importance of fisheries production by demersal species (e.g., rockfish, weakfish, blue crabs) versus plankton based species (menhaden, bluefish). Any increases in particulate organic matter deposition will also contribute to greater depletion of oxygen from bottom waters.

In comparison with other coastal ecosystems, the relative production of benthic animals per unit algal production appears to be markedly inhibited in many regions of the Bay by the seasonal anoxia. Presumably, this process has affected also the production of key demersal fisheries, which are presently below their potential. Conversely, indirect evidence suggests that the exploitation of important suspension-feeding benthic animals (especially the oyster) may have contributed to the accumulation of phytoplankton biomass and the resulting reduction of Bay water clarity. This hypothetical relation needs further analysis before being translated into management strategies.

While nitrogen enrichment of Bay waters has contributed over recent decades to its eutrophication, this effect is mitigated by the natural bacterial processes of nitrification and denitrification, which transform nitrogen from useable forms (ammonium, nitrate) to unusable forms (dinitrogen gas) for estuarine phytoplankton. The coupled process of nitrification-denitrification is presently inhibited by hypoxic conditions during summer in many regions of the Bay. This amounts to a "positive feedback loop" in the Bay, where nitrogen enrichment leads to increased algal production, which leads to more anoxia which leads to less denitrification which leads to more nitrogen recycling, which leads to more algal production, which leads to more anoxia, and so on. Considering this relation in the inverse, even small reductions in nitrogen inputs to the Bay might lead to relatively large reversals of the eutrophication process by restoring nitrification-denitrification.

Strong evidence indicates that there is a residual effect of nutrient inputs to the Bay which operates on time scales of months to one or two years. In this case, physical processes of particle retention and relatively slow (compared to the water column) benthic processes of nutrient recycling combine to create a lag between nutrient inputs and some of the resulting primary production which is supported by those inputs. It appears that relatively high nutrient inputs during a high riverflow year support relatively high rates of primary production and benthic oxygen consumption in the following year. Most of these nutrients are not, however, retained in the estuary, such that ecological processes will respond rapidly to reductions in nutrient inputs. The question of whether a small residual effect can influence Bay ecology and for how long is central to predicting the impact of reducing nutrient loading to the estuary.

All of these mechanisms by which processes of benthic-pelagic coupling may affect the water quality and living resources of the Bay need to be taken into account in the development of models of water quality and ecosystem processes to predict the outcome of management strategies for improving environmental conditions in Chesapeake Bay.

Acknowledgments

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