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EUTROPHICATION, HABITAT DYNAMICS AND TROPHIC FEEDBACKS: UNDERSTANDING AND MANAGING COASTAL ECOSYSTEMS

W. M. Kemp, Professor⁽¹⁾ & W. R. Boynton, Professor⁽²⁾,

University of Maryland Center for Environmental Sciences,

⁽¹⁾ Horn Point Laboratory, P.O. Box 775, Cambridge, Maryland 21613, USA

⁽²⁾ Chesapeake Biological Lab. P.O. Box 38, Solomons, Maryland 20688, USA

Background and Introduction

As a consequence of natural hydrologic, meteorological and oceanographic processes, ecosystems at the land-sea interface tend to be focal points for delivery of water, sediments, nutrients, and organic matter derived from adjacent environments. This natural fertilization provides the life-blood which makes estuaries and other coastal ecosystems among the world's most highly productive biomes (Costanza et al. 1995). Inputs of these materials from watershed, atmosphere and ocean to coastal environments vary significantly across a wide spectrum of scales (days-to-decades), with fundamentally different variance spectra depending on the source. Coastal ecosystems are among the most heavily fertilized environments in the biosphere (LMER Coord. Comm.), and their associated populations and processes are highly responsive to variations in inputs and forces (Boynton and Kemp 1997). Overlain on the background variations of nutrient inputs to estuaries are global-scale eutrophication trends of increasing fertilization (Nixon 1995), arising in part from the demographic trends whereby human populations continue to be concentrated in coastal regions. Many detrimental ecological effects of eutrophication have been well documented; however, responses to over-fertilization often involve complex non-linear interactions, which are not well understood.

Chesapeake Bay Ecosystem. Here, we discuss the responses of coastal ecosystems to eutrophication in terms of changes in extent and structure of habitats and mitigating effects of ecological feedback processes. We draw largely from our experience in the study of Chesapeake Bay, which is a large estuarine ecosystem on the Atlantic coast of North America. This partially stratified estuary is approximately 300 km long and 3-30 km wide, with a drainage basin of 19,000 km² and a ratio of watershed-to-estuary areas of 17. Although the maximum depth of the estuary is some 60 m, its mean depth is only 9 m, with some 65% of its area less than that the mean. The Bay has numerous tributary estuaries, which have a range of differing sizes, shapes and circulation patterns. Chesapeake Bay is extremely productive, with annual mean rates of primary production between 400 and 600 g C m⁻² y⁻¹, and total fish harvest of 2 g fw m⁻² y⁻¹. In fact, compared with other coastal ecosystems worldwide, this estuary and its tributaries have among the highest rates of primary production per unit nutrient loading (Fig. 1a) and the highest fish yield per unit primary production (Fig. 1b). On the other hand, detrimental effects of eutrophication have been evident for the last two decades in Chesapeake Bay and its tributary ecosystems despite the fact that nutrient loading rates in these ecosystems are modest compared to other estuaries. Hence, the mechanisms which contribute to the Bay's high productivity may also be responsible for its relative sensitivity to eutrophication effects.

Nutrient Dynamics in Chesapeake Bay. Nutrients enter estuaries such as Chesapeake Bay through a variety of pathways, including **diffuse** (rivers, streams, groundwater) and point (sewage and industrial effluents) sources, and atmospheric deposition. Diffuse sources constitute 60 % of the total nitrogen (N) and phosphorus (P) loadings to the Bay, with the Susquehanna River delivering almost two-thirds of the total diffuse nutrient loading (Boynton et al. 1995). **Interannual** variations in river flow and associated nutrient and organic carbon (C) loading are relatively large, although secular trends of increasing N and decreasing C have been evident over the last fifteen years. Point sources deliver one-third or less of the N and P inputs to the Bay. Atmospheric deposition is another major source of N inputs to the Bay accounting for some 12-20% of the loading to the estuary's water surface (Boynton et al. 1995), with rainwater pH declining by 1.5 units in the decade of the 1970's (Ford and Correll, 1982). The major sinks for N are sediment burial (35%), transport to the ocean (30%) and denitrification (26%), with fisheries yield resulting in another 9% of the total removal of N from the Bay; in contrast, sediment burial accounts for the vast majority of all P losses (Boynton et al. 1995). It is remarkable that such a large fraction of the N entering the estuary is removed via trophic pathways to fish harvest.

Results and Discussions

Scaling Ecological Processes to Estuary Dimensions. In recent years ecologists have become acutely aware that measurements in natural and **experimental** systems vary with the temporal and spatial scales of observation, and that the **behaviour** of organisms and the structures of **communities** and ecosystems appear to vary also with scale. To an unquantified extent, the characteristics which we attribute to ecosystems are a function of the physical dimensions of the system and the scales of our observations. We are interested developing scaling principles for comparing observations among systems and subsystems to deepen our understanding of fundamental estuarine processes and to facilitate application of practical lessons learned from one scientific investigations in one system to address similar problems (e.g., eutrophication) in other coastal ecosystems.

Here we illustrate the importance of considering residence time and water depth as a key temporal and spatial scales for analysis of coastal ecosystems. Water residence time (T_r), provides a scaling variable which can be related to time-scales biological processes, fixed by physiological constraints. Phytoplankton **biomass** accumulation is directly related to nutrient delivery rate for many different estuaries with relatively long residence time. However, when T_r is short (relative to algal growth), phytoplankton biomass can be inversely related to river flow (Hagy 1996). Rates of benthic N recycling are directly related (with a seasonal time-lag) to N loading rates. However, there are slightly different relations for each of five estuarine tributaries of the Bay, with the ratio of N recycling per unit N loading **varying** from 1 to 3 and the ratio inversely related to water depth. A similar relation appears for data from different experimental ecosystems; however, the depth effect was more acute because of additional effects on light attenuation by mesocosm walls. It is critical that scaling relationships such as these be considered when extrapolating results obtained from experimental ecosystems to conditions in the natural environment. For example, recent experiments from mesocosms of differing depth (Fig. 2) revealed that volumetric rates of photosynthesis (PS) scaled inversely with depth in spring due to the prevalence of

light limitation, while areal rates scaled directly with depth during summer when rates were limited by nutrient availability (Petersen et al. 1997). In spring, other ecological processes including nutrient uptake rates and zooplankton growth and abundance appear to follow these patterns of PS scaling (Fig. 2). Although it appears that for all four data sets a single relation could be fit to observations from **mesocosms** and natural environment, attempts to extrapolate from mesocosm data provide poor predictions for natural estuaries.

Coastal Eutrophication and Habitat Loss. As a consequences of coastal eutrophication habitat for **demersal** and benthic is lost through two important mechanisms: oxygen depletion from **bottom** waters; declining **seagrass** populations. These eutrophication **effects**, which represent shifts from one toward another stable state (e.g., Scheffer 1989) are global in **their** scope.

Reports of seasonal depletion of oxygen (O_2) from bottom waters of Chesapeake Bay go back to the early 1930's. Each year natural processes contribute to springtime strengthening of density stratification (which isolated the **bottom** waters from potential atmospheric replenishment of O_2 , and deposition of the vernal algal bloom (Kemp et al. 1992). However, despite considerable interannual variation in bottom water O_2 conditions, it appears that there has been a secular increase in the spatial and temporal extent of hypoxic ($O_2 < 2$ mg/l) waters since the 1950's (Officer et al. 1984). Year to year variations in river flow lead to changes in two critical factors contributing to O_2 depletion: 1) buoyancy (associated with freshwater), which increases the strength of stratification, separating **bottom** waters from atmospheric sources of replenishment; 2) nutrients, which support algal growth, sinking and decay (and **microbial** O_2 consumption). In the mid 1980's the relation between volume of **summer-time** hypoxic water and river flow appears to have undergone a dramatic shift (Boicourt 1992). This shift is possibly related to a threshold at which hypoxic water starts to creep onto vast shoal areas of the Bay, affecting a range of biogeochemical processes, such as **nitrification-denitrification**, which have provided a feedback control on eutrophication (Kemp et al. 1990). It appears that small changes in nutrient delivery from year to year can lead to significant changes (3-5 weeks) in the timing of incipient hypoxic condition, which may **have** serious detrimental consequences for biogeochemical processes as well as for growth and survival of benthic animals.

The **seagrass** populations of Chesapeake Bay **underwent** a dramatic decline in abundance starting in the early 1960's, coincident with major increases in nutrient loading and algal biomass and **decreases** in water clarity (Orth and Moore 1983). Although the decline of seagrasses was a bay wide phenomenon, it started in the **more** eutrophic regions (e.g., the upper Bay and western tributaries) and spread over the next decade to other areas of the estuary (Kemp et al. 1983). Ecosystem **simulation** models have been used to support and analyze inferences from **field** and laboratory **studies**--that nutrient enrichment was the primary cause (among others including increased suspended sediments and runoff of agricultural herbicides) of the **seagrass** losses (Kemp et al. 1995, Madden and Kemp 1996). **Seagrass** communities in this and other coastal systems provide important habitat for fish, invertebrates and waterfowl. Field observations indicate significantly higher abundance and diversity of **fish** and invertebrates in vegetated versus unvegetated shoal habitats (Lubbers et al. 1992), and fluctuations in valuable waterfowl populations are highly correlated with changes in

seagrass abundance over the last several decades (Kemp et al. 1984). Based on statistical analyses of data from current and former seagrass sites, indices were established to monitor the quality of environmental conditions for plant growth and survival (Dennison et al. 1993). Simulation models have been used to improve these indices and to develop effective strategies for restoration of seagrass habitats in relation to nutrient reduction and transplanting efforts (Madden and Kemp 1996).

Organic Carbon Balance & Net Ecosystem Metabolism As indicated above, inputs of inorganic nutrients are necessary to sustain fisheries harvest in coastal ecosystems. Inorganic nutrients are transformed into fish biomass through coupled primary and secondary production, with some nutrients being recycled, via respiration and other pathways of metabolic decomposition, back to inorganic forms. The net production of organic matter, over and above respiratory losses back to inorganic compounds, depends on nutrient inputs from external sources and sets constraints on the combined fluxes of export, burial and fish removal (Kemp et al. 1997). When density stratification is strong, photosynthesis and respiration are largely separated into upper and lower water layers, respectively. Hence, inputs of inorganic nutrients can lead to conditions of bottom O₂ depletion. Differences among adjacent regions in ecosystem structure, habitat quality and fisheries production may be directly related to decoupling of photosynthesis (PS) and respiration (R). We argue that the partitioning and net balance for metabolic processes ($NEM = PS - R$) provide useful indices of the health and productivity of coastal ecosystems (Kemp et al. 1997). The integrated NEM of coastal ecosystems appears to be directly related to the ratio of inorganic: organic nutrient inputs, suggesting that eutrophication trends are driving coastal ecosystems toward higher NEM (Fig. 3). In systems where PS and R are not separated significantly in time or space, such increases in NEM could be channeled into increased fish production. The opposite trend appears to be occurring in Chesapeake Bay where stratification and regionalization lead to separation of PS and R.

Ecological Feedback Processes. There are many examples of non-linear, ecological feedback-processes lead to unexpected system responses to perturbations. The natural microbial process of denitrification (DN) removes approximately 25% of the N inputs to Chesapeake Bay under present conditions (Boynton et al. 1995). DN transforms the plant nutrient, nitrate, into nitrogen gas, which is unavailable for plant uptake. This value is low compared to the trend reported for other (non-stratified) estuaries, where denitrification removed some 50% of input N (Seitzinger 1988). In many estuaries, DN occurs primarily in sediments, directly coupled to nitrification, which is a process requiring O₂ to transform ammonium into nitrate. Hence, with eutrophication, the absence of O₂ inhibits nitrification, which in turn inhibits DN, which in turn allows concentrations of ammonium (a favored plant nutrient, typically limiting algal growth) to accumulate and support more growth and decomposition of algae which further reduces O₂ concentrations. The good news is that there is a similar self-enhancing effect when the process is reversed and eutrophication trends are mitigated. Prior to settlement by Europeans, the waters of Chesapeake Bay were filled with oyster populations which acquire food by filtering algae and other organic matter from the overlying water. When oysters and other benthic suspension-feeders are abundant, they may be capable of controlling algal biomass and reduce effects of eutrophication. As a result of human harvest and other factors, biomass of oysters has decreased 100-fold

since the middle of the nineteenth century, and it has been speculated that a restored oyster population would retard negative effects of eutrophication (Newell 1988). Ecosystem simulations suggest a more complex situation, because oyster feeding also enhances nutrient recycling. If oysters were placed in raft cultures above relatively deep (>8 m) waters, increased suspension-feeding results in greater hypoxic conditions. However, model experiments (Fig. 4) indicate that a 10-fold increase in oyster biomass concentrated in shoals would effect similar improvements in bottom water O₂ conditions as would a major reduction (40%) in nutrient loading to the Bay (Kemp and Bartleson 1991).

Conclusions

It is concluded that coastal eutrophication is a widespread problem of global proportions, arising from effects of humans. In estuaries like Chesapeake Bay, diffuse watershed and atmospheric sources of nutrients dominate, while the surprising importance of fisheries harvest as a N sink emphasizes the relation between nutrient loading, net production and trophic interactions leading to fish. A key consequence of eutrophication is loss of animal habitat in shallow and deep regions through declines in seagrasses and bottom oxygen, respectively. Ecosystem experiments and comparative analyses of data from different estuaries and different regions in a single system offer robust approaches to deepen our understanding of ecological processes and relations to human perturbations and to transfer lesson learned in one system to problems in another. Such analyses, however, require careful consideration of how differences in scale affect extrapolation. Effective strategies for restoring habitats destroyed by eutrophication can enhance natural feedback processes, which produce large improvements with small modifications.

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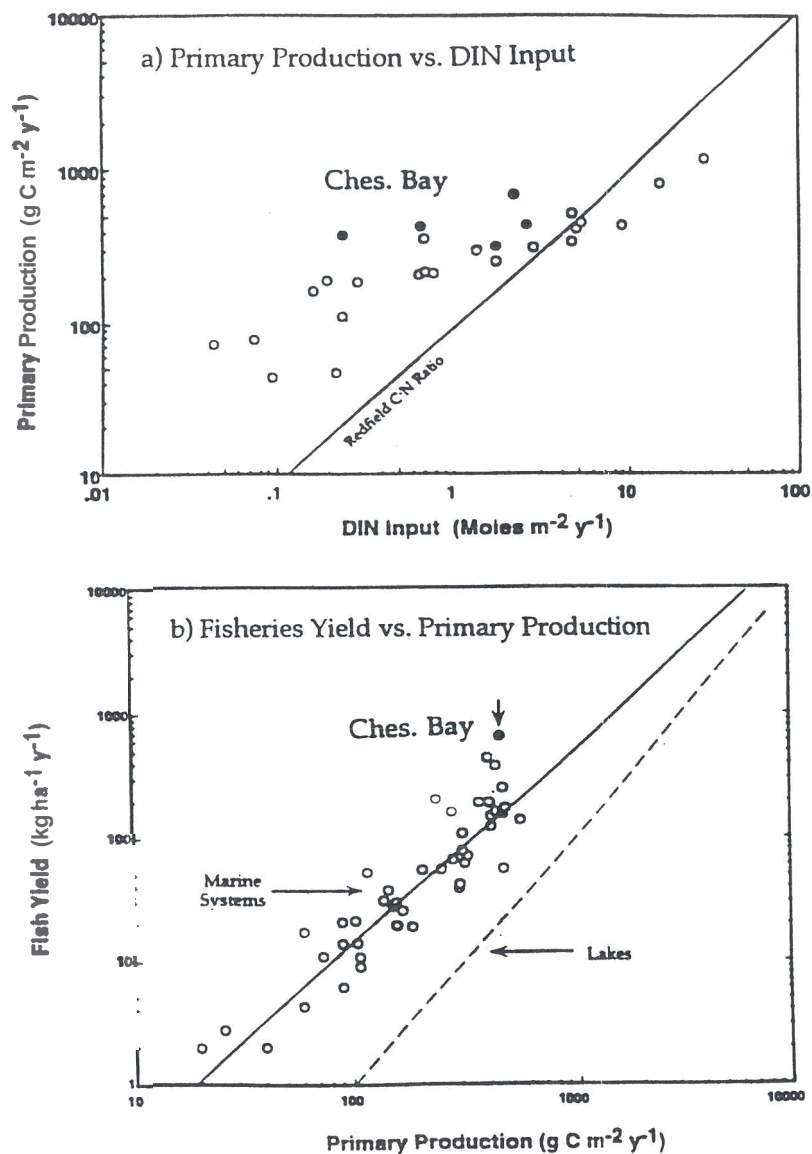


Fig. 1. Comparative analysis among coastal ecosystems relating (a) annual mean primary production (PP) to variations in nitrogen (DIN) loading & (b) annual mean fisheries yield to variations in PP. Redrawn from (a) Nixon (1992) and (b) Nixon (1988); filled circles for Chesapeake Bay values.

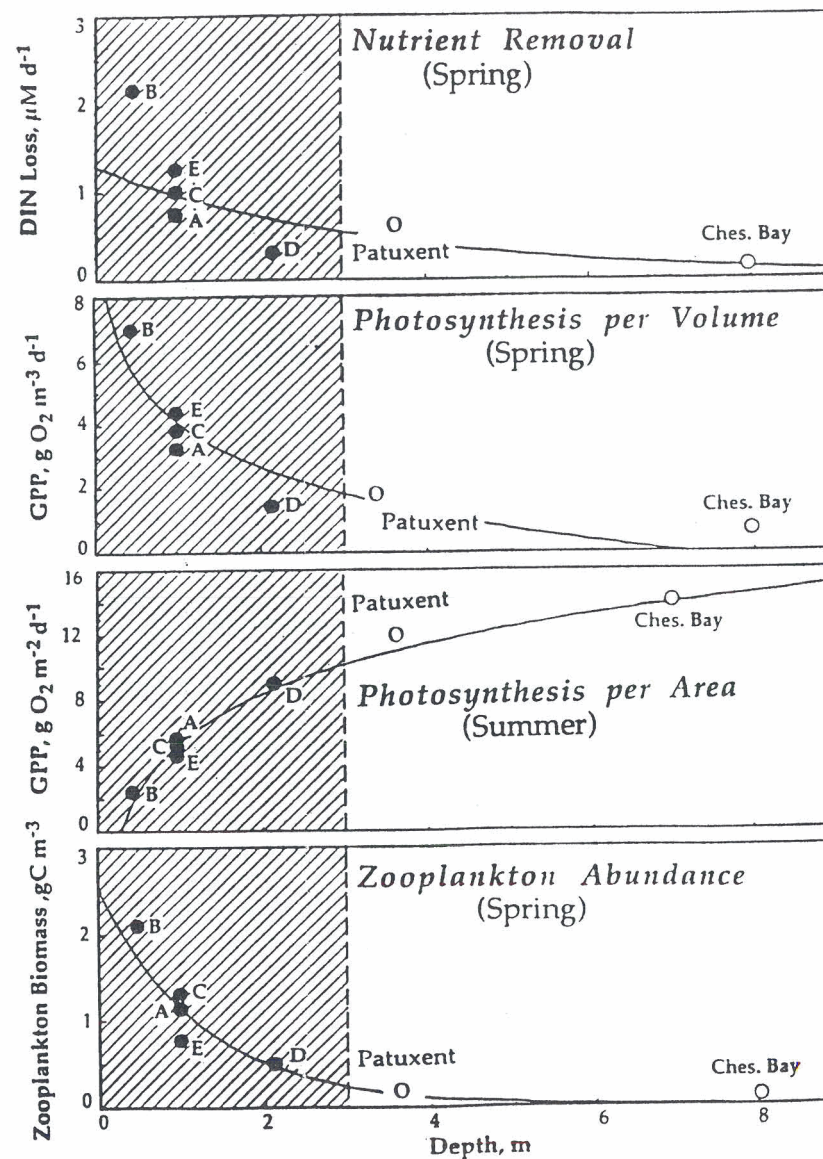


Fig. 2. Scaling properties & processes in experimental (filled circles) and natural (open circles) ecosystems versus water depth for: (a) nitrogen (DIN) uptake in spring; (b) photosynthesis (PS) per water volume in spring; (c) PS per area in summer; (d) zooplankton abundance in spring.

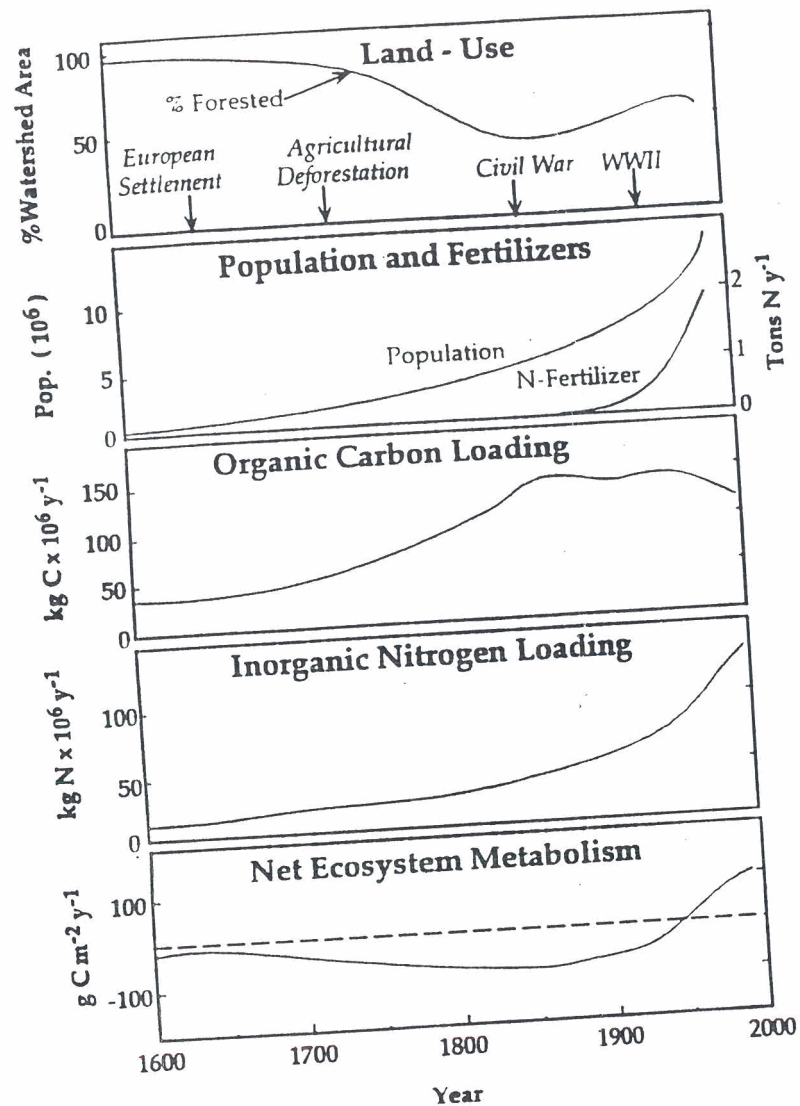


Fig. 3. Reconstructed history of: (a) land-use plus (b) human population and nitrogen fertilizer use in Chesapeake Bay watershed; (c, d) inputs of organic carbon and inorganic nitrogen to the estuary; and (e) net ecosystem metabolism (photosynthesis minus respiration) of estuarine ecosystem.

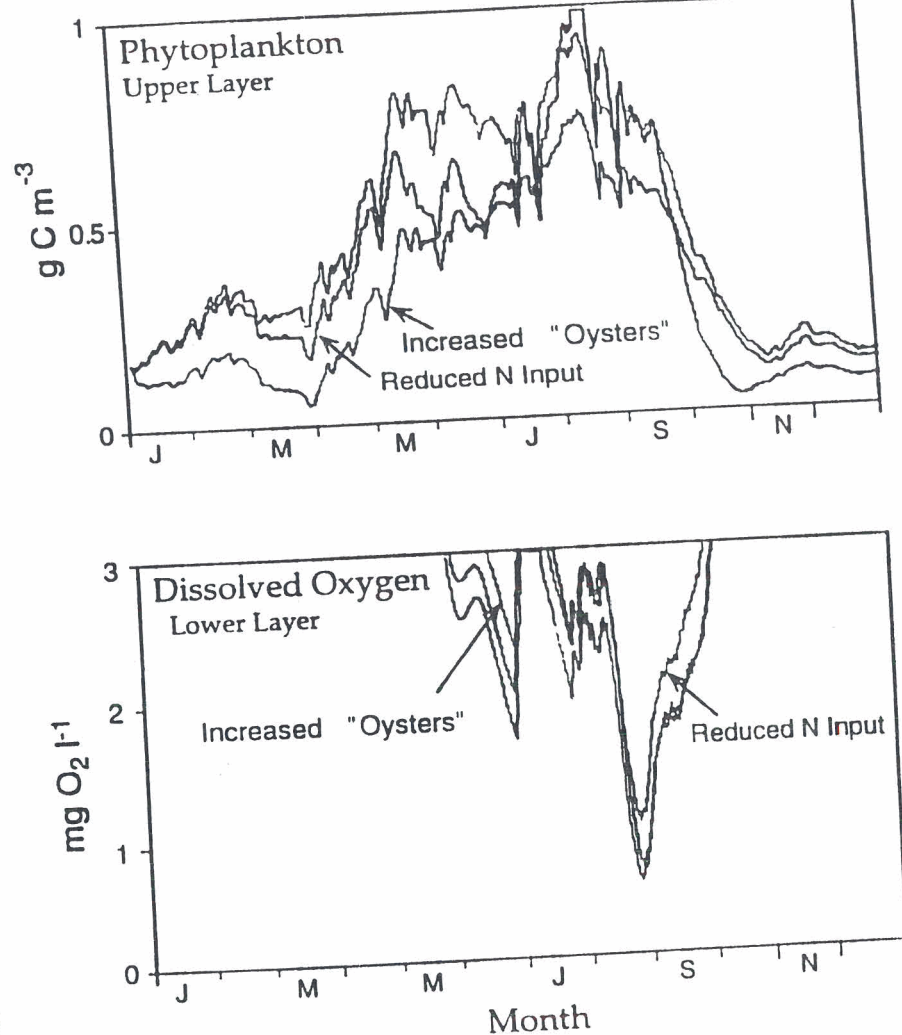


Fig. 4. Model simulations comparing effects of reducing nutrient loading to Chesapeake Bay by 40 % of present values versus restoring biomass of suspension-feeding oysters to former levels; ecosystem responses measured in terms of (a) phytoplankton abundance and (b) bottom layer dissolved oxygen.