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Perspectives on The Chesapeake Bay: Recent Advances in Estuarine Sciences

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Chesapeake Bay Program

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PERSPECTIVES ON THE CHESAPEAKE BAY:

ADVANCES IN ESTUARINE SCIENCES

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December 1987

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PREFACE

The Chesapeake Bay Program began in the early 1970's as a research effort to uncover and define problems that had resulted in widely observed declines in harvestable resources and water quality in this great estuary. The Environmental Protection Agency published extensive reports on the results of this effort, which culminated in the Governors' Conference and the Chesapeake Bay Agreement of 1983.

The Chesapeake Bay Liaison Office was created as a result of that Conference and Agreement. Today the office is charged with coordinating extensive state and federal efforts to reverse the long downward trend and to restore and protect the Bay's living resources. The Office directs its resources and staff energy to implementing the Restoration and Protection Plan adopted by the Chesapeake Bay Executive Council in 1985. Our role was confirmed in a new basin-wide agreement signed December 15, 1987.

In this effort, however, far more needs to be known about the Chesapeake Bay, both to elucidate its problems and to inform managers making decisions about those problems. Accordingly, the Chesapeake Bay Program commissioned the Chesapeake Research Consortium to sponsor thorough literature searches in areas where management and the scientific community agreed our knowledge and understanding were incomplete.

This volume is directed at defining our needs in five major topic areas of inquiry:

1. Estuarine benthic-pelagic coupling and flow of materials
2. Changes in estuarine pelagic-trophic structure
3. Physical processes controlling estuarine circulation and mixing
4. The role of genetics in conservation of Bay plant and animal species
5. Estuarine chemical and physical processes and bioavailability of toxics

These areas were delineated by a steering committee of Bay scientists and science administrators (elsewhere acknowledged) convened on behalf of EPA by the Chesapeake Research Consortium. A full chapter is devoted to each topic area, with summaries of the available literature (both gray and refereed) and recommendations about direction and urgency for future work.

We have provided an executive summary, which follows this introduction. The summary is an important capsule view of the overall product, but I strongly commend to you the full text of each chapter. These writings represent some of the best and most comprehensive thinking available today, and especially in their "recommendations" sections, they point to areas of needed inquiry that are vital to the success of the Restoration and Protection Program. This publication and a major research conference in March 1988 will contribute to the foundation of a comprehensive—and annually updated—research plan mandated for delivery in July 1988 by the new Bay Agreement.

The perceptive reader will note that these topics do not directly include the important areas of living resource habitat requirements and modeling of the Bay system (some would say ecosystem modeling). While both these areas are referred to in the text of the following chapters, our substantial efforts in these areas will be found in the following documents:

-Habitat Requirements for Chesapeake Bay Living Resources, Report of the Living Resources Task Force, Chesapeake Bay Program Liaison Office, Annapolis, MD 21403, 63 pp plus appendices

-A Steady State Coupled Hydrodynamic Water Quality Model of the Eutrophication and Anoxia Process in Chesapeake Bay (Assignment #40, EPA Contract 68-03-3319) Prepared by Hydro-Qual, Inc., for Battelle Ocean Sciences, Duxbury, MA 21404, in 2 Volumes

This volume is intended as a starting point for dialogue in the Bay community on research needs. It has built upon several admirable past efforts including those of the Consortium, the National Oceanic and Atmospheric Administration, resource agencies in the states, and EPA itself. We expect this publication and the related research conference will help us define what research is necessary to advance the restoration and protection of the Bay's resources. All of us—government, scientific community, and concerned citizens—must cooperate to solve the dilemma of how we fund research in a world of limited budgets, without impeding the restoration and protection effort.

We look forward to the help and advice which you, the audience of this document, will bring us.

KENT MOUNTFORD, PHD
CHESAPEAKE BAY PROGRAM
ENVIRONMENTAL PROTECTION AGENCY

INTRODUCTION

Scientific knowledge and/or understanding is not static. The scientific community is continually advancing its understanding of fundamental principles or processes that will eventually have impact on decisions of societal importance. Our knowledge of the complex Chesapeake Bay system is no exception.

The scientific community has made marked progress in understanding fundamental processes underlying management approaches to the restoration of the Chesapeake Bay. Many of the individual studies have not, however, been synthesized with other studies in a context that disseminates their results to scientists or technical experts from other disciplines. In addition, as is to be expected in the study of complex systems or processes, the results raise additional questions.

This publication reviews five areas of estuarine research that we believe have critical importance to the protection and restoration of the Chesapeake Bay. The particular areas were selected because of their broad implications beyond the immediate disciplines in which the studies are conducted.

The Chesapeake Bay Program has already recognized the critical limitations in our knowledge of two of the areas: BENTHIC AND PELAGIC COUPLING IN THE CHESAPEAKE BAY and FACTORS DRIVING CHANGES IN THE PELAGIC TROPHIC STRUCTURES OF ESTUARIES, WITH IMPLICATIONS FOR THE CHESAPEAKE BAY, by initiating plans to develop new information on these areas for use in the next generation of models.

We have known for several decades that the life histories and distribution of living resources within the estuary are intimately tied to estuarine circulation, as is the distribution of toxic compounds introduced into these systems. It is only recently, however, that we have recognized that our general knowledge of circulation has not been sufficient to address the questions raised about many specific issues. It is hoped that the review of the topic: PHYSICAL PROCESSES THAT CONTROL CIRCULATION AND MIXING IN ESTUARINE SYSTEMS will assist in elucidating processes dependent on circulation and will stimulate much-needed additional research in this area.

The principal underlying goals of the Chesapeake Bay Program are to restore, protect, and ultimately manage the living resources of the Bay. The main thrust at present is to provide appropriate water quality to sustain these resources. A lesser thrust has been to develop a better assessment of stocks of commercial, recreational, and ecological importance to the system. Explosive advances in methodology applicable to genetic studies are now being applied to estuarine species.

The implications of the fourth review topic: GENETICS AND THE CONSERVATION OF ESTUARINE SPECIES may open new approaches to restoration and manipulation of stocks and must be considered in any emergent plans for living resource management.

The EPA-funded Chesapeake Bay Study provided us with the first complete benchmark inventory of toxic compounds in Chesapeake Bay. Additional efforts since the termination of the formal study have extended the inventory up the tributaries. Identification of toxic "hot spots" and our ability to measure compounds at ever lower concentrations have led to the realization that the simple presence of a compound may not be sufficient to define a toxic problem. Our final paper: CHEMICAL AND PHYSICAL PROCESSES INFLUENCING BIOAVAILABILITY OF TOXICS IN ESTUARIES addresses many of the complex phenomena that must be considered when trying to evaluate the impact of specific compounds or classes of compounds.

The following capsule summaries of the full reviews only touch upon the full ramifications of each topic. The reader is encouraged to read the reviews. The authors were requested to write the reviews for an audience of scientists in their own disciplines, scientists who require knowledge of the particular processes for understanding other phenomena, and technically conversant resource managers wishing to incorporate state-of-the-art scientific knowledge in their long-term planning. The authors were also requested to briefly touch on potential management implications and additional research needs related to their topics.

Summary of Chapter 1:
Benthic-Pelagic Coupling in the Chesapeake Bay

Although the importance of benthic-pelagic interactions in aquatic systems has been recognized for half a century, it is evident from this review that research in the field has been active for little more than a decade. Scientific studies in the Chesapeake Bay and elsewhere have provided initial descriptions of the complex patterns and mechanisms involved in connecting ecological processes in the water with those in the sediment. While many unresolved questions remain, a few preliminary conclusions can be drawn from this review.

Summary of Major Findings

Various methods have been employed for measuring both particle deposition and benthic fluxes of oxygen, ammonium, phosphate, and other metabolites across the sediment-water interface. It is encouraging to see that particle deposition rates estimated by geochemical (and paleobotanical) tracer techniques tend to converge with rates obtained from sediment-trap deployments, even though the two approaches measure this process on very different time scales. Direct measurements of benthic fluxes of nutrients and oxygen tend to agree well with observations made using in situ chambers and those involving intact sediment cores. Indirect estimates of nutrient flux based on diffusion modeling of pore-water concentrations are, however, often 2- to 10-fold lower than rates obtained from direct measurements, especially for productive systems with active macrofauna burrowing in sediments.

Seasonal cycles of particle deposition in the Chesapeake Bay and other coastal systems closely follow trends in phytoplankton production. Generally, 40-60% of the organic production by phytoplankton settles to the benthos. Much of the total mass of deposited material, however, appears to be terrigenous inorganic sediment, suggesting an important linkage between biotic processes and sedimentological transport.

The importance of particle deposition and burial in the overall input-output balance of nutrients (nitrogen, phosphorus, and silicon) for the Chesapeake Bay has recently been questioned. Whereas earlier reports indicated that most of the nutrient inputs from the Bay's watershed were retained and buried in its sediments, a revised analysis indicates that this may not be the case. This unresolved question has significant management implications for control of nutrient wastes.

Sediment oxygen consumption is an important sink for oxygen pools in the Chesapeake Bay and other estuaries. Over 50% of the total oxygen consumption in Bay regions less than 10 m deep occurs through benthic processes, which remove 10-20% of the water column oxygen pools per day in late spring. Nitrogen and phosphorus regenerated by benthic processes can satisfy about 20-50% of the phytoplankton demand in the main Bay and 50-100% in the shallower tributaries. These relative rates are similar to those reported for other coastal systems. Recent work in the Bay region has also indicated that benthic-pelagic interactions may provide a mechanism for temporary retention of nutrients delivered from the watershed in winter to support production in spring and summer.

Research efforts have identified a wide variety of physical, chemical and biological factors affecting benthic fluxes of nutrients and oxygen. Temperature and deposition of particulate organic matter are primary variables regulating benthic fluxes. Fluxes of nitrate and oxygen into sediments are directly related to concentrations and turbulent mixing in the overlying water. Oxygen concentration (especially as it approaches zero) also exerts profound, but as yet poorly described, effects on most benthic processes. Similarly, burrowing and feeding activities of macrofauna appear to significantly influence benthic fluxes, although exact mechanisms remain to be explained.

Relevance to Restoration and Protection Activities

Many of the processes involved in benthic-pelagic coupling will directly influence the outcome of proposed management actions to restore and protect water quality and living resources in the Chesapeake Bay. Several relevant questions are given below.

- Considerable evidence directly connects nutrient enrichment and increased anoxia in Bay waters. How is this relationship affected by deposition of plankton production to the bottom and subsequent oxygen consumption by benthic processes?
- How important is the nutrient regeneration capacity stored in Bay sediments, and to what extent would this result in continued large releases of nutrients even after inputs from the watershed were reduced, thereby delaying benefits of clean-up action?
- To what extent has the relative importance of benthic-pelagic processes such as denitrification and burial, which act as virtual sinks for nutrient inputs to

the Bay, been diminished due to eutrophication, and will management strategies restore these natural mechanisms of nutrient waste assimilation to effectively accelerate the benefits of clean-up actions?

- What is the role of benthic-pelagic coupling in the fate and transport of toxic substances entering the Bay?

In addition, if water quality modeling is to be a key component in management of Bay resources, it is particularly important that benthic-pelagic coupling processes be sufficiently well described to allow careful model calibration. The factors regulating these processes must also be understood and incorporated into such models to enable accurate projection and assessment of proposed strategies (e.g., 40% reduction in nutrient inputs) for restoration and protection of Bay water quality.

Future Directions

Conceptualization, calibration, and validation of rigorous mathematical water quality models will require an expanded scientific information base including improved descriptions of: (1) seasonal and spatial trends in benthic fluxes and metabolic processes; (2) the relationships among plankton production, particle deposition and benthic oxygen and nutrient fluxes; (3) specific metabolic processes (e.g., denitrification and sulfate reduction) that affect benthic fluxes of oxygen and nutrients; and (4) physical, chemical, and biological factors that regulate benthic fluxes. Data should be collected to resolve questions about Bay-wide budgets of nutrient inputs and outputs. In addition, the predictive capabilities of mathematical water quality models could be greatly supplemented by conducting parallel studies with estuarine mesocosms ("living models") to assess the potential outcome of major management decisions.

Ultimately, for these data collection activities to contribute to the development of effective Bay management strategies, an administrative mechanism must be established to communicate scientific findings to the managers and their constituents. Conversely, management questions and priorities must be articulated to the scientific community so that study designs and approaches can be adjusted to meet the management needs. The ongoing Bay monitoring program may offer a model for efficient bi-directional communication.

—W. Michael Kemp

Summary of Chapter 2
Factors Driving Changes in the Pelagic Trophic Structure of Estuaries, with Implications for the Chesapeake Bay

Processes governing the relative abundance of organisms ultimately determine the composition of biological communities and thus how energy and material is transferred among components of the ecosystem. In marine and estuarine environments, the pelagic food web plays a dominant role in these transfers. For this reason, changes in the composition of this trophic network, or in the direction or magnitude of flows, could have significant impacts on fishery yields, water quality, or other factors of concern to scientists and managers. This chapter reviews the factors that may influence the composition of the trophic network.

Summary of Major Findings

The biological success of any organism reflects both its physiological tolerances and controlling factors such as food supply. If growth is limited by quality or quantity of food, then population size may be regulated by factors controlling prey organisms in lower trophic levels; this has been termed "bottom-up" or source control. If nutrition is adequate, however, population size may be limited by predators in the next higher trophic level; this is "top-down" or sink control. The available evidence suggests that pelagic trophic structure in estuaries is controlled by a combination of these processes, the relative importance of which constantly changes in response to environmental fluctuations.

Estuaries such as the Chesapeake Bay are characterized by environmental variability of greater magnitude and frequency than other aquatic habitats; factors such as light, salinity, and nutrient availability change over time scales ranging from seconds to decades or more. This great variability is reflected in the system's biological components as well. Species composition and relative abundance typically change throughout the year, and, although repeating seasonal signals are strong and often important indicators, year-to-year variability may be significant. As a general rule of thumb, the effects of environmental change can be scaled to body size; that is, the smaller the organism and the faster its growth rate, the shorter the relevant time scale for response. Thus changes in phytoplankton community structure may occur within a few days, whereas those of fish communities may extend over years or decades. One of the most difficult tasks for managers is to separate changes due to natural variability from those due to human activity (which are potentially controllable), and to predict response to natural or anthropogenic environmental perturbation.

In most estuarine systems, phytoplankton are the dominant primary producers and the principal source of food for both the zooplankton-fish trophic chain and the bacterial-based microbial food web. For this reason, changes at the phytoplankton level can have wide-ranging effects on pelagic trophic structure. Elevated primary production stimulates increased microbial decomposition, with accompanying demands on dissolved oxygen. Resulting hypoxia and anoxia restricts habitat for plankton, fish, and shellfish, with consequent mortalities in many species, and enhances release of nutrients from the sediments. Reduction in water transparency due to increased algal biomass has also been linked to recent losses of submerged vegetation in the Chesapeake Bay.

Long-term changes in the relative dominance of various phytoplankton groups affect higher trophic levels and the direction (and efficiency) of transfers within food webs. Very small cells, which predominate in the Chesapeake Bay, cannot be readily ingested by many grazers (such as oysters or copepods). It has been hypothesized that nutrient enrichment may selectively enhance these small forms, and that this increased dominance by nanoplankton in turn favors gelatinous zooplankton (comb jellies and medusae). Because growth efficiencies of these "jellies" are so low, much of their ingested material is released as dissolved nutrients. In this respect they may represent a trophic "dead-end", with little material being passed on to higher levels. As eutrophication increases algal biomass and production while decreasing its usability by larger zooplankton or benthic species, more organic material will be cycled through the microbial loop. There is growing evidence that this process may now be operating in the Chesapeake Bay, but whether this represents a recent change in trophic structure is still uncertain.

When food limitation is less significant, predation may be the major process regulating population abundance. Predators ranging in size from small protozoans to large carnivorous fish have specific prey preferences. Selection can influence the species composition of prey communities, and thus the structure of pelagic food webs. Although the importance

of this process in marine ecosystems is uncertain, the concept of cascading trophic interaction as a dominant force regulating fresh water systems is well established. For example, removal of piscivorous fish can lead to increases in planktivorous species, declines in zooplankton biomass, enhanced phytoplankton densities, and decreased water clarity.

Relevance to Restoration and Protection Activities

There is a superficial similarity between this scenario and that of the Chesapeake Bay. Reduction in carnivorous species such as striped bass coupled with apparent increases in plankton-feeders such as menhaden is suggestive of top-down control. Estimates based on filtering capacity of both menhaden and benthic suspension feeders such as oysters indicate that at high population densities these planktivores can significantly alter phytoplankton abundance and even species composition. For example, oyster numbers present in the early 1900's may have been capable of filtering the entire volume of Chesapeake Bay in three days. During summer months, gelatinous predators significantly reduce zooplankton populations and may also affect larvae of species such as oysters. Because nutrients released by these forms can stimulate phytoplankton growth, their role in structuring pelagic food webs may be considerable. Selective predation by both crustacean and microzooplankton grazers also exerts control on abundance and composition of lower trophic levels.

Thus each marine pelagic trophic level is implicated in regulating the abundance and structure of one or more adjacent levels. Whether long-term changes observed (or postulated) in Bay pelagic communities are due to natural causes such as climate or to anthropogenic impacts is not readily determined, in part because of lack of sufficient long-term quantitative data. Human activities perturb natural controlling mechanisms from below through nutrient loading or from above by harvest of predatory or planktivorous species. It might therefore be hypothesized that eutrophication and a collapsed predator base are both driving changes in pelagic trophic structure of the Chesapeake Bay, and that these processes work in concert with natural fluctuations in the estuarine environment to produce observed trends.

Future Directions

These conclusions rely heavily on inference and emerging new ideas rather than rigorous scientific examination, and are thus best regarded as hypotheses in need of further testing. Important questions include:

- Do long-term changes in concentration and ratios of nutrient supplies cause changes in phytoplankton species composition?
- Are cascading trophic interactions significant in structuring estuarine communities?
- Does the relative importance of source vs. sink control vary as a function of productivity?
- In particular, what are the roles of gelatinous zooplankton, the microbial community, and fish trophic relationships in structuring the food web? How do these roles vary in response to nutrient supply and predator abundance?

Several of these questions represent generic research needs, but they are particularly applicable to processes regulating food webs in the Chesapeake Bay. The biota of the Bay will change as human beings continue to modify the environment. As management and restoration of the Bay proceeds, a unique opportunity exists to study and document the interactive effects of physical and biological factors controlling pelagic trophic structure. This will require a multifaceted approach incorporating data collection and modeling. Previous studies have demonstrated that results from one part of the estuary may not be valid in other portions. Intensive field sampling and in situ experimentation should be conducted on pertinent temporal and spatial scales to determine biological response to environmental variation. Bay-wide monitoring programs should continue to provide the long-term data necessary to identify the cause and significance of trends. Finally, these efforts should be coupled to multi-trophic level studies (e.g., mesocosms) and simulation models to test hypotheses in detail. This approach, which will require significant financial and managerial commitment, will quantify the functional relationships between nutrient supply and fish production. Thus we will increase our understanding of the factors that regulate pelagic trophic structure and improve our ability to predict changes in that structure.

—Gail MacKiernan

Summary of Chapter 3:
Physical Processes that Control Circulation and Mixing in Estuarine Systems

Summary of Major Findings

This chapter surveys the literature on circulation and mixing as it applies to the Chesapeake Bay. The approach is to consider processes in terms of their time scale: seasonal, short-term, or short-period. The seasonal processes are predominantly long-term fluctuations (greater than one month) in heating and fresh-water runoff. The short-term processes (from a tidal cycle up to one month) include fronts, wind, tides, and their variations, as well as the interactions with the shelf circulation. The short-period processes (less than a tidal period) are the dominant mixing mechanisms that effect the vertical exchange of properties in the estuary. There is a tendency for long-period processes to have large spatial scales and for short-period events to be smaller. Hence this organization by time scales also tends to sort by size as well. Often larger-scale, slower processes are easier to study, so we have more knowledge about the mean and seasonal circulation and some fairly good insight into the short-term processes. The short-period mixing has only recently been observed, and is still not quantified.

All the different processes interact. The mean circulation moves the fresh water down the estuary, setting up the stratification, which in turn affects the amount of vertical mixing. The vertical mixing is driven by the energy that is available from the tides, wind, internal waves, and mean circulation. The amount of vertical mixing helps determine the vertical density profile, which affects the downstream pressure gradient and hence the intensity of the mean circulation.

Relevance of Restoration and Protection Activities

Surprisingly little work has been performed in the Chesapeake proper. Although much of the fundamental work on estuarine circulation is associated with the Bay, it was predominantly performed in the tributaries. The Bay is large enough to have modes of motion that are not possible in the more restricted rivers. Our picture is incomplete, and we must understand the circulation and mixing in the Bay better before we can model the system satisfactorily. Even the classic two-layer circulation is now coming into question as better instrumentation becomes available to profile the currents.

Our needs for understanding of the circulation and mixing of the Bay are rather serious. We have the basic understanding of the circulation that was fundamental for the initial planning of the Bay cleanup. There is also a need to understand the causes and intensity of the fluctuations in the circulation. There is some insight into this problem, but we are a long way from being able to anticipate climatic variations and predict their effect in the Bay. Finally, the most stringent demand will be the coupling of the physical and biological systems to predict the fluctuations in both water quality and biological productivity.

Future research on the physical oceanography in the Chesapeake Bay must focus on identifying and understanding the processes that drive the circulation and mixing. Towards this end two types of work are needed.

Future Directions

Long-term measurements with modern remote sensing and profiling instruments are needed. New techniques for remotely measuring the surface currents with radar backscatter from shore-based stations should be combined with new acoustic profiling current meters mounted on the bottom of the Bay. This type of information, in conjunction with satellite remote sensing and data gathered on the many research cruises in the Bay, could start to quantify the physical processes over a wide range of scales.

Second, multi-disciplinary studies of specific processes should be performed. Specific experiments should focus on distinct problems such as the development of anoxia, the interaction of physical processes and larval recruitment, and the influence of wind on primary productivity.

Although much past work in this region has focused on estuarine circulation, there is at present insufficient work, and insufficient support, for the basic research into the physical processes in the Bay. Our ignorance will limit our ability to plan wisely, to monitor the situation, to interpret the observed variations, and hence to maximize the return on our investment in the Bay.

—Thomas Osborn

Summary of Chapter 4:
Genetics and the Conservation of Estuarine Species

Recent advances in scientific methodology, especially in the area of genetics, are providing researchers with the tools to analyze heritability of traits in greater detail than ever before. New technologies are also bringing the ability to modify, or "engineer", the genetic composition of organisms. These new sources of information are greatly expanding our understanding of the structures of populations, isolation or mixing of genetic materials, species complexes, the influence of environment upon genetic expression, and many other aspects of relationships at the organism and population level.

This chapter presents a comprehensive review and synthesis of the emerging place for molecular genetics as a fundamental tool in the evaluation and management of biotic systems such as the Chesapeake Bay. Of particular interest is the discussion of approaches to conservation and resource management through the application of genetics. The authors recognize the potential for protection and enhancement of stocks while citing the need for caution and consideration of the resulting impacts of such manipulations on the ecosystem. The use of genetic monitoring in hatchery or breeding programs can be effective in detecting deleterious changes or traits in organisms being developed for release into natural systems.

The chapter also addresses various aspects of methods for genetic assessment, including selective breeding and molecular techniques such as DNA sequencing and mitochondrial DNA analysis. Brief descriptions are given of the approach and rationale for using each of the methods presented.

Summary of Major Findings

The bulk of the chapter concerns the status of genetic knowledge for selected species of recognized importance to the Chesapeake Bay. Finfish examples stress the striped bass; invertebrates selected include the blue mussel, hard clam, and oyster. Notable by its absence is the blue crab, for which very little genetic analysis has been conducted.

The authors conclude that species in the Bay have apparently undergone some differentiation in response to varying conditions from the upper reaches to the Bay mouth but none of the species studied to date have produced highly localized populations. Thus it appears that the various species may be treated as single units for management purposes, and reliance on captive broodstock for enhancement programs should probably not introduce defective traits.

The authors suggest approaches for the enhancement of striped bass and oysters while emphasizing that less-recognized species provide food or other important ecological linkages.

Relevance to restoration and protection activities

Ultimately, genetic information and the technology for manipulating the genetic composition of organisms will be considered as tools for modifying the structure of aquatic communities, including the Chesapeake Bay. In fact, such modification is under way in the case of the striped bass and its hybrids, which are being created with either white bass or white perch.

The potential exists for resource managers to have both positive and negative effects upon the structure and functioning of a system such as the Chesapeake Bay. Because molecular geneticists have only recently begun to delve into genetic modifications on a large scale, there is much undiscovered information concerning the biotic and abiotic interactions of manipulated organisms, especially as they might affect the stability of an ecosystem. With this cautionary note in mind, we should nevertheless continue to explore the potentials presented by this emerging technology so that the ecosystem may be better able to withstand perturbations. Questions include:

- We are not able to determine how the Chesapeake Bay is responding to the decline in one of its top predators, the striped bass. Would the release of hybrids re-establish the necessary predator-prey dynamics?
- Would the engineering of an oyster that could withstand exposure to diseases or chemical pollution permit us to maintain the necessary links between primary producers and consumers?
- Would the restoration of oyster populations to their former levels have a positive impact on removal of primary producers that use excess nutrients and apparently drive the spread of areas low in dissolved oxygen?

The rapid expansion in genetic technology suggests that within the next decade we will be able to manipulate the genetic composition of most species found in the Bay. The manner and degree to which this capability is applied to managing the dynamics of the stocks is a matter of growing concern, which should be addressed in anticipation of the desire to use the emerging technology. At the very least, fisheries

management plans should begin to take into account the likelihood that genetically manipulated striped bass and oysters will be available for release into the Bay.

Necessary research and/or activities

The chapter authors point to the need for a variety of research efforts as well as genetic monitoring of hatchery-produced organisms. Also, readers of the chapter will readily recognize that the body of literature upon which the synthesis is based is not extensive. Thus it is obvious that genetic technology is opening many avenues of research and potential applications in management. Perhaps some of this chapter's readers will build upon its information to enhance their use of genetics in the development of Chesapeake Bay resources.

—William Rickards

Summary of Chapter 5:
Chemical and Physical Processes Influencing Bioavailability of Toxics in Estuaries

Summary of Major Findings

This chapter summarizes many of the processes in estuaries affecting bioavailability of compounds present in estuaries. Chemical factors discussed include ionic strength, inorganic and organic speciation and complexation, redox reactions, and production of organo-metallic compounds. A second area of discussion includes contaminant sources and processes affecting distribution including the microlayer, adsorption to particles, flocculation, sedimentation, and remobilization from sediments. A third area is biological processes affecting bioavailability, including uptake routes, food chain magnification, organism reaction through metallothionen production, biological transformation, degradation through biological processes, and chemical and physical modification of the environment by biota. The summary delineates six areas for further research including partitioning, the role of biota in transfer of pollutants, the effect of seasonal anoxia, sediment flux and movement, the role of communities, and descriptive studies of the effects of toxics.

Relevance to restoration and protection activities.

The subject of toxics in estuaries is controversial and complicated, and this chapter correctly states the difficulties of knowing all the factors affecting transport, availability, uptake and impact of pollutants. It answers in part the question why the many toxic materials detectable in estuaries are not more effective.

Because the areas of ignorance greatly exceed those of knowledge at present, restoration and protection activities concerning toxics in estuaries must be confined to the few specific cases where toxic effects have been found. Unfortunately, although chronic, sublethal, and synergistic effects of toxics on estuarine biota are suspected to be important, little is known about them. To be realistic and cost-effective we must take a scientifically broad approach towards deciphering the actual role of toxics in estuaries. This will require basic, biologically-oriented research by experts, which is not favored by managers but is the best way to discover the principles permitting effective detection and control of toxics in estuaries.

Necessary research and/or activities

Questions to be considered in future research activities include the definition of an estuarine toxic material. Are estuarine toxic materials those chemicals known to be toxic to humans who come into contact with them through food or water activities? Or are estuarine toxics defined through their effects on estuarine biota? This distinction is critical for determining the nature of the research and mediating activities to be done. If the definition is the latter, then the response of the biota (molluscs to organotin, fish to creosote, plankton communities to copper, etc.) must be examined in detail through sophisticated biomonitoring. Life cycles must be analyzed to detect impacts on early life-history stages. Physiological responses of estuarine animals must be studied to determine chronic and sublethal effects attributable to toxics. Monitoring of the health of estuarine biota must include the incidence of susceptibility to parasitism and other effects possibly synergistic with the presence of toxics.

If an estuarine contaminant is defined as that which is toxic to human beings, this initial research should establish the routes from the estuary to human populations and the probabilities of exposure as well as toxicological effects.

Once a substance has been defined as toxic in the estuarine system, the chemical and physical mechanisms governing bioavailability can be researched by using present or as-yet-undeveloped methods of chemical analysis. Natural mechanisms of reducing bioavailability and toxicity of the substance, such as capping of contaminated sediments, must be studied. Finally, laws should be drawn up and put into place to control or mediate the toxic. This has been the successful strategy in the past for handling of toxics in estuaries.

The full cost and time needed in the past for discovering and remedying problems due to estuarine toxics such as power plant chemicals, Kepone, TBT, and DDT must be examined and studied in detail if we are to make any serious recommendations about the handling of future and potential toxics.

With a careful combination of basic and applied research, admitting our ignorance and working from historical examples, perhaps we will achieve a successful strategy for detection and control of toxics in estuaries, our most impacted ecosystem.

—Harriette Phelps

CONCLUSION

In order for research activities in estuarine processes to contribute to the development of effective Chesapeake Bay management strategies, the scientific findings must be communicated to managers and the public. It is equally important that the scientific community understand management priorities and concerns.

The Chesapeake Bay Program is the most ambitious estuarine management program ever attempted. The Chesapeake Bay system is hydrologically complex and contains a wide diversity of habitats. The land uses of the watershed cover the full range of human activity. In addition, mangement is complicated by different political jurisdictions with differing philosophical approaches to resource management.

The scientific and management communities in the Bay region are faced with a strong public and political desire to "do something about the Bay." To respond to this desire, the scientific community must be prepared to address management questions with state-of-the-knowledge scientific insight. This series of papers, each in an area directly relevant to processes critical to our understanding Cheapeake Bay, should provide some of that required insight.

—MAURICE P. LYNCH

Benthic-Pelagic Coupling in the Chesapeake Bay

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INTRODUCTION

The Relevance of Benthic-Pelagic Processes to Water Quality Management in the Chesapeake Bay

The purpose of this review is to summarize past and ongoing research on the coupling of benthic and pelagic processes in the Chesapeake Bay and to place these studies in a context of work from other estuarine and coastal regions. Nutrient management continues to be one of the most pressing problems for agencies managing the resources of the Chesapeake Bay [135]. Current conceptual and mathematical models of estuarine nutrient dynamics, as well as recent monitoring data and experimental studies in estuarine mesocosms, suggest that the responses of estuarine ecosystems to eutrophication and nutrient control measures are influenced by the exchanges of organic matter and inorganic nutrients at the sediment-water interface. The tight coupling of benthic and pelagic nutrient flows in shallow bays sets the stage for a positive feedback loop [12, 91] of enhanced primary production, organic matter sedimentation, and deep water anoxia that is ultimately driven by an overabundance of inorganic nutrients.

Recent experiments at the Marine Ecosystems Research Laboratory (MERL) have shown that sediment-water exchanges of nutrients do indeed increase with increases in inorganic loading and primary production, but the increases are not directly proportional to the loading rate [65]. The results of a two-dimensional water quality model for the Chesapeake Bay [58] indicate that oxygen concentrations in bottom water could be significantly improved (on the order of 2 mg/l) if sediment oxygen demand and benthic nutrient fluxes were reduced by about 30%. However, the model's ability to simulate sediment-water exchanges was limited, and the effect of incremental changes in nutrient loading on water quality in the Bay remains unclear. There is, in fact, disagreement over the fundamental behavior of nutrients in the Bay system [83]. Accurate modeling and effective management of Bay water quality therefore depends on understanding the nature of the exchanges of organic matter, oxygen, and other constituents across the sediment-water interface.

The recent agreement of the states bordering the Chesapeake Bay to reduce nutrient loading of the Bay by 40% by the year 2000 (Draft Chesapeake Bay Agreement 1987) highlights the Bay managers' need to know how benthic-pelagic exchanges of oxygen and nutrients can assist or exacerbate clean-up efforts. Questions of immediate concern that fall within the scope of this review include:

(1) What is the quantitative relationship between nutrient loading of the Bay and sediment-water fluxes of oxygen and dissolved inorganic nutrients? For example, does a 40% reduction in allochthonous nutrient inputs produce an equivalent reduction in sediment oxygen demand and inorganic nitrogen and phosphorus release?

(2) What is the eutrophication memory of Bay sediments? Are they a nearly inexhaustible nutrient source and oxygen sink that will frustrate Bay clean-up efforts? Will sediment oxygen demand and nutrient fluxes respond rapidly (within a few years) or slowly (within decades or more) to changes in Bay nutrient loading and productivity?

More specific questions that need to be addressed to achieve better understanding of the relationship between sediment-water exchanges and Bay water quality include:

(1) What is the role of sediment oxygen demand in the onset and maintenance of deep water anoxia?

(2) What environmental factors control rates of sediment oxygen demand and nutrient releases?

(3) How important are remineralized nutrients in fueling the cycle of production, organic sedimentation, and oxygen depletion?

(4) How will increasing bottom water oxygen concentrations affect rates of nitrogen and phosphorus release from sediments?

(5) What controls the rates of specific nutrient transformations, such as nitrification, denitrification, and phosphorus sorption in Bay sediments? How are the rates of these reactions linked to observed sediment-water fluxes?

Historical Overview of Benthic-Pelagic Coupling

The important ecological consequences of shallowness in marine ecosystems were recognized over 30 years ago [94]. However, the first explicit references to the "coupling" of benthic and pelagic processes appeared in the marine and estuarine literature in the early and middle 1970's [49, 114]. Rowe et al. [114] claim to have made the "first successful attempts to measure directly the nutrient flux from nearshore sediments" in 1975. Hartwig [53] and Hale [46], however, had completed studies of sediment-water fluxes near Scripps Pier in California and in Narragansett Bay, respectively, the previous year. Direct measurements of organic matter sedimentation rates and sediment-water oxygen and nutrient exchanges were also being carried out in Narragansett Bay [88, 96] and the Patuxent River [16] during the same period.

These early references to benthic-pelagic coupling illustrate that quantitative work on sediments as functional components of coastal marine systems began relatively recently. The impact of these studies on conceptual models of estuarine nutrient cycles has nonetheless been dramatic. For example, Pomeroy's thoughtful and wide-ranging 1970 review entitled "The Strategy of Mineral Cycling" [107] contained almost no references to the functional role of sediment communities in nearshore nutrient dynamics. In contrast, more recent reviews [66, 85, 87, 89] have clearly identified nutrient transformations in sediments as an important feature of coastal ecosystems. The recent publication of two symposium volumes, one focused entirely on sediment oxygen demand [54] and the other reporting European studies of nutrient cycling and benthic-pelagic coupling [82], attest to the high level of activity in this field.

Current investigations of sediment-water exchanges in coastal waters and estuaries represent the drawing together of ideas and techniques that have been developed in fresh water over the last century. The first step in the progression toward the view of a body of water as a system with interacting benthic and pelagic components was the development of techniques to estimate and then to measure directly rates of oxygen consumption by river muds. Early efforts to determine "sediment oxygen demand" (SOD) can be found in the studies of polluted rivers carried out the late 1800's. These early investigations of sediment-water interactions, recently reviewed by Davis and Lathrop-Davis [32], were motivated by very practical concerns about the effects of sewage on municipal water supplies. The theme they sound—that oxygen-consuming processes in sediments influence the quality of the overlying water—is as timely in the Chesapeake Bay today as it was in the Illinois River a hundred years ago.

The first systematic study of the influence of sediments on overlying waters took place in stratified lakes [80] where the signal of sediment redox reactions and nutrient exchanges could be clearly followed in water column profiles. The early work in lakes showed the relationships between oxygen concentration, redox potential, and the release of nutrients from the sediment to the overlying water. Mortimer's summary [79] of his findings in stratified lakes is worth repeating here, because very similar events are now observed in regions of Chesapeake Bay. Mortimer [79] concluded that in aquatic systems

> ... where biological production or organic pollution is high, where the subthermocline volume is relatively small, or both ... a progressive decline in oxygen concentration from 2 mg/liter to analytical zero at the interface was ... correlated with mobilization of and transfer to the water first of manganese and later of iron. There is a concurrent transfer into the water of substantial quantities of phosphate, previously held in complex form.... Other changes include liberation into the water of ammonia and silicate. Further reduction of the sediment-water system permits microbial reduction of sulfate.

The interaction between the oxygen content of overlying water and inorganic nutrient releases from the sediment can therefore contribute to problems associated with eutrophication by providing positive feedback between enhanced organic matter production, low oxygen conditions, and release of fertilizing nutrients from the sediments to the overlying water.

The second stage in the evolution of ideas about the coupling of benthic and pelagic processes took place during the mid-1950's with the investigations of ecosystem-level energy flows in shallow aquatic

systems. Sediment chambers, or "bell jars", and their laboratory analogs, initially used to determine rates of sediment oxygen demand in river sediments [8, 38], were employed to determine benthic community production and respiration [23, 90, 103]. Although clearly related in their need to understand the mechanisms that control the exchanges of materials across the sediment-water interface, the efforts of water quality engineers and benthic ecologists proceeded along parallel but essentially independent lines. Engineers were concerned primarily with the role of sediments as an oxygen and pollution sink. Ecologists focused on the contribution of sediment communities to the material and energy flow budgets of the ecosystem. This distinction between the practical and scientific approaches to sediment-water exchanges persists today [cf. 35, 116].

The third important theme that weaves through the development of ideas about the coupling of benthic and pelagic systems is the powerful insight that the photosynthetic formation and decomposition of organic matter in marine systems follows more or less fixed elemental ratios [29, 41, 108, 109]. This stoichiometry permits interchangeable estimates of energy (as oxygen and carbon) and nutrient fluxes through pelagic and benthic systems; it stands squarely at the base of sophisticated models of organic matter diagenesis in sediments [4]. Analysis of deviations from Redfield's stoichiometries during the decomposition of organic matter in estuarine sediments has generated one of the very few explicit and testable hypotheses to emerge from studies of benthic-pelagic coupling [85]. Although more than half a century old, Redfield's Ratio remains one of the premier heuristic concepts in marine ecology.

Okuda's 1960 monograph [94] on nutrient dynamics of Matsushima Bay appears to have been the first quantitative work that clearly reflected the drawing together of these research themes in the context of coastal nutrient cycling. Early models of nutrient cycling in the open sea [130] and estuarine nutrient budgets [e.g., 52] emphasized the importance of nutrient regeneration in the water column and downplayed or ignored the functional role of the sediments. Okuda recognized the value of using Redfield-like stoichiometries to analyze the interactions between benthic and pelagic nutrient cycles. He clearly identified the important consequences of shallowness in marine systems:

> Since the organic matter produced in the shallow water may reach the bottom in a shorter time than that in the ocean, the sediments in shallow water may contain a greater fraction of undecomposed organic matter... Accordingly, it may be concluded that although the role of the ocean sediments in the metabolic circulation of organic matter is not important from the quantitative stand point [sic], the sediments in shallow water may play an important role qualitatively as well as quantitatively.

Okuda then demonstrated the functional role of sediments quantitatively by directly measuring primary productivity, sediment nutrient profiles, and rates of decomposition and sedimentation of organic matter. His analysis of the importance of detrital exports from seagrass beds and quantitative carbon and nitrogen budgets clearly points to the importance of sediment nutrient remineralization in the production economy of Matsushima Bay.

Current Models of Benthic-Pelagic Coupling

Today's conceptual model of the interactions between estuarine water sand sediments (Figure 1) took shape in the early and middle 1970's, as traditional descriptions of the seasonal cycles in the abundances of plankton and dissolved nutrients were combined with measurements of the rates at which organic matter and inorganic nutrients were added to, removed from, and transformed within estuarine systems. The shift from static to dynamic process-oriented measurements was driven by a search for the sources of the nutrients that supported phytoplankton production [e.g., 114] and the concurrent efforts to assemble quantitative estuarine nutrient budgets [e.g., 85].

Factors of importance in benthic-pelagic coupling (Figure 1) include: (1) the supply of "new" inorganic nutrients; (2) the rate at which organic matter is synthesized in and imported to the water column, i.e., the rates of primary production and allochthonous loading; (3) the rate at which organic matter sinks through the water column and is deposited as "new" sediment at the sediment surface; (4) the rates at which organic matter is consumed by various groups of organisms in the sediment community; (5) the rates at which nutrients remineralized in the sediment community are returned to the water column; and (6) the rate at which nutrients are permanently buried in sediment.

The conceptual model (Figure 1) also shows that in plankton-based systems such as the Chesapeake Bay, the coupling of pelagic and benthic processes reflects the spatial separation of predominantly autotrophic processes in the water column and heterotrophic processes in the sediments. This does not imply that heterotrophy does not occur in the

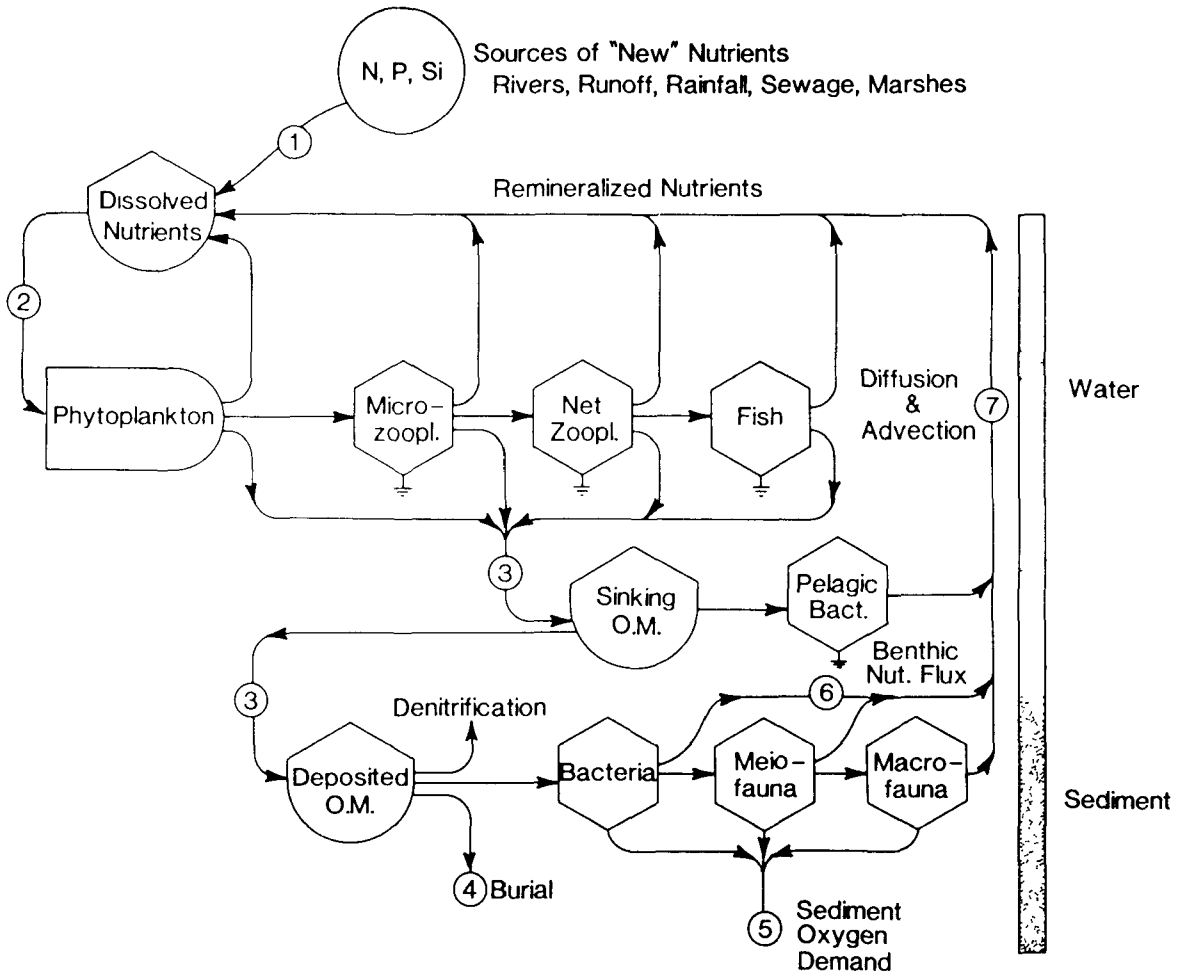


Figure 1. Conceptual model of nutrient element flows in plankton-based systems using Odum's energy flow symbols (modified from Nixon [85]). Pathways relevant to the coupling of benthic and pelagic systems are identified, with pertinent review papers, as follows: (1) inputs of nutrients from outside sources [33, 84, 87]; (2) uptake of nutrients by phytoplankton (not considered in this review); (3) sinking and deposition of particulate matter [6, 7, 19, 20, 78]; (4) burial and long-term diagenesis of organic matter [3, 55]; (5) oxygen consumption and other catabolic pathways [82, 102] (6) exchanges of oxygen, dissolved nutrients and other constitutents across the sediment-water interface [85, 86, 89, 140]; (7) upward diffusion and advection of remineralized nutrients (not considered in this review).

water column or autotrophy in the sediments. On the contrary, there is growing evidence that microheterotrophic "microbial loops" are responsible for very rapid cycling of nutrients in the water column [2, 136]. Autotrophy at the sediment surface by diatom mats, seaweeds, and seagrasses may also flourish where sufficient light reaches the bottom. However, there is generally a net production of organic matter in the euphotic zone of the water column and a net consumption of organic matter in the sediments.

As illustrated in Figure 1, the cycling of materials between Bay waters and sediments begins with the formation of organic matter and its deposition on the Bay bottom. Plankton production is the primary source of autochthonous (formed in situ) material; allochthonous (introduced from outside) sources of sediment include terrigenous material carried to the Bay by rivers, runoff, rain, wind, and shore erosion. Thorough discussions of plankton production in the Chesapeake Bay and particle sinking are beyond the scope of this review, and the reader is directed to the reviews of these topics cited in Figure 1.

The material deposited at the surface of estuarine sediments comprises a complex mixture of organic matter and inorganic minerals. Although inorganic phases are unquestionably involved in early sediment

diagenesis, the decomposition of organic matter is primarily responsible for the fluxes of oxygen and other constituents at the sediment-water interface. Organic matter is consumed in sediments via a sequence of energy-yielding biochemical reactions in which oxygen, nitrate, manganese, iron, and sulfate serve as progressively less efficient oxidizing agents. Sediment macrofauna may be the most conspicuous aerobic consumers of organic matter, but their contribution to the total metabolism of benthic communities is generally believed to be small [15]. More important to the sediment community metabolism is a diverse assemblage of bacteria and other microheterotrophs. Simplified equations for the microbially-mediated reactions of particular importance in estuarine sediments [3] are:

Aerobic metabolism

$$CH_2O + O_2 \longrightarrow CO_2 + H_2O$$

Nitrate reduction (denitrification)

$$5CH_2O + 4NO_3^- \longrightarrow 2N_2 + 4HCO_3^- + CO_2 + 3\,H_2O$$

Sulfate reduction

$$2CH_2O + SO_4^= \longrightarrow H_2S + 2HCO_3^-$$

Ammonium formation

$$CH_2NH_2COOH + 3(H^+) \longrightarrow CH_3COOH + NH_4^+$$

Methanogenesis

$$CO_2 + 8(H^+) \longrightarrow CH_4 + 2H_2O$$

The stoichiometry of nutrient remineralization during decomposition of organic matter in anoxic portions of estuarine sediments can also be described by a Redfield-like equation [111]:

$$6(CH_2O)_x\,(NH_3)_y\,(H_3PO_4)_z + 3_xSO_4^= \longrightarrow 6_xHCO_3^- + 3_xHS^- + 6_yNH_4^+ + 6_zHPO_4^= + (3_x + 12_z - 6_y)\,H^+$$

These reactions result in the consumption of oxygen, nitrate, and sulfate sequentially with depth in the sediment column. The reaction products—carbonate, di-nitrogen gas, hydrogen sulfide, ammonium, phosphate, and methane—accumulate in sediment pore waters, often in concentrations that far exceed those of the overlying water. Such accumulations are well documented in sediments from the Chesapeake Bay [18, 77] and elsewhere. The depletion of reactants and accumulation of reaction products drives a flux of dissolved constituents across the sediment-water interface. The rates at which constituents cross the sediment-water interface is influenced by many factors including the availability of reactants, the steepness of concentration gradient between the sediment and water, water currents over the sediments, physical resuspension of the sediments, sediment mixing by macrofauna (bioturbation), advection of pore waters by benthic fauna (biopumping), sediment compaction, and density-driven flushing of pore waters [3, 126].

The linkage or "coupling" between Bay waters and sediments can therefore be seen to consist of the downward flux of organic matter from the water to the sediment and the return flux of remineralized nutrients from the sediments to the water. That these exchanges should be taking place has been known for a very long time, and recent attention given them hardly signifies a revolution in ecological thinking. What is new, and what has become clearer over the past two decades, is that Okuda [94] was right: these exchanges are both quantitatively and qualitatively important in estuarine nutrient cycles. Nixon [85], for example, demonstrated that bottom communities, including two sites from the Patuxent River, consume 25-50% of the total organic matter produced in or imported to the system. Studies in a variety of coastal systems (reviewed in [85] and [140]) show that nutrients released from coastal sediments can supply a significant fraction, at times all, of the nutrients required for annual phytoplankton production.

The cycling of nutrients through the estuarine benthos may also profoundly affect estuarine productivity by altering the relative abundances of remineralized nitrogen and phosphorus. In his analysis of the Narragansett Bay nutrient budgets, Nixon [85] stated:

> The remarkable conclusion seems to be that much of the nitrogen limitation of primary production in coastal waters arises because of low inorganic N/P ratios brought about because some 25-50 percent of the organic matter fixed in these areas is remineralized on the bottom....[where] rates of denitrification....remove some 5-25 percent of the nitrogen orginally incorporated into organic matter.

Although couched as a conclusion, Nixon's statement [see also 120, 121] has been taken as an explicit hypothesis that denitrification in the sediments is responsible for the nitrogen limitation of production in coastal marine systems.

TECHNIQUES USED TO MEASURE EXCHANGES OF MATERIALS BETWEEN ESTUARINE WATERS AND SEDIMENTS

The Downward Flux of Particulate Matter

The rates at which sediments are deposited on the Bay bottom have been estimated in three ways:

(1) sediment mass transports [5, 10, 113, 118, 129]; (2) the distribution of particle-active radionuclides such as ^{210}Pb, ^{137}Cs, ^{239}Pu, ^{240}Pu, ^{234}Th, and ^{7}Be with depth in sediment cores [45, 56, 57, 92] and (3) sediment traps [12, 67]).

The time-resolutions of these techniques differ, and each is subject to its own set of technical limitations. Sediment mass balances integrate sediment inputs from various sources over a year or several years, geochemical tracers provide estimates of sediment deposition over periods of weeks (^{7}Be, ^{234}Th) to decades (^{210}Pb and ^{137}Cs); and sediment traps intercept the downward flux of materials over periods of hours to days. Mass balance approaches require intensive sampling of river-borne and aeolian fluxes, may underestimate episodic events such as floods, and are very sensitive to estimates of the area where active deposition is believed to take place [84]. Geochemical tracers are better at integrating short-term episodic depositional events into a longer-term sedimentation rate, but interpretation of isotope distributions in cores is complicated by bioturbation and non-uniform sediment deposition [92, 110]. Sediment traps, although the best method for obtaining direct measurements of short-term deposition, are subject to design and deployment problems [for reviews see 6, 7, 15, 20, 70], and collect a combination of resuspended and newly deposited material [67, 96].

Exchanges at the Sediment-Water Interface

Indirect techniques. The magnitude of fluxes across the sediment-water interface can be estimated indirectly, by modeling the gradient of pore water constituents near the sediment-water interface [3, 4, 73], or directly, by determining the rate of change of dissolved constituents in the water overlying the sediments [53, 88, 114, 140]. The modeling approach, essentially an application of Fick's first law of diffusion, requires accurate measurement of the concentration gradient and a good estimate of the constituent "diffusion coefficient" near the sediment-water interface [3]. This approach has therefore proved most useful in totally anoxic sediments and in the deep sea where sedimentation rates are low, physical mixing of the sediment and bioturbation are minimal, and deployment of in-situ chambers is impractical. Comparisons of fluxes determined by pore water modeling and intact sediment methods (described next) show that the modeling technique works best when fluxes at the sediment-water interface are dominated by diffusion [39]. The technique underestimates fluxes in situations where waves, tides, and benthic fauna stir the sediments and transport constituents across the interface [1, 22, 39, and others].

Direct in-situ and intact core techniques. Benthic fluxes can also be determined directly by various adaptations of "bell jar" chamber procedures [140] and the closely related "upstream-downstream" techniques [40, 61]. These techniques involve determining the change in concentration of dissolved constituents in a known volume of water trapped above or passing over a given area of the bottom. The flux of a dissolved constituent across the sediment-water interface in sediment chamber devices is then calculated using some form of the basic equation:

$$J_i = \frac{V\,(C_o - C_t)}{AT}$$

where J is the flux of constituent *i* in mols m^{-2} $time^{-1}$, V is the volume of water contained in the chamber (liters), C_o and C_t are the initial and final concentrations of constituent *i* (mols/liter) during an incubation of time T, and A is the area of bottom enclosed by the chamber (m^2).

In the absence of a standard method for carrying out direct flux determinations, a great variety of coring devices, chambers, tunnels, and free vehicles have been developed for in-situ, shipboard, and laboratory applications of the technique [54, 101, 140]. The advantage of this approach, in theory at least, is that it provides a better measure of fluxes in an intact sediment community, because chemical and biological contributions to the net fluxes are accurately reflected in the changes in concentration observed in the water. The simplicity and relative ease of this technique give it great appeal, and its application in all types of aquatic systems continues to grow. It must be noted, however, that this approach is not trouble-free. Fluxes determined in chambers are affected by disturbance of sediment surface during coring, transportation, and chamber deployments [64, 81], rates of water circulation [9, 15, 24, 76] and the associated boundary-layer effects [62], and groundwater flows [141]. Chemical and biological exchanges of dissolved nutrients generally increase as current velocity over the sediment increases, rising dramatically when current velocities are high enough to resuspend the sediment [9, 15, 59]. The problem of circulation in flux chambers is difficult to evaluate against the background of considerable spatial and temporal variability encountered in estuaries. It is, for example, very difficult to simulate the "correct" current speed during a 3-4 hour chamber experiment, in regions where near-bottom currents vary from zero to some tidal maximum.

Recently, Pamatmat [99] took issue with the uncritical use of oxygen flux determinations as indicators of "total sediment metabolism" and

advocated the direct measurement of heat production by sediment communities as a better measure of total energy flow through the benthos [100, 102, 104]. Although conceptually appealing, the technique appears fraught with technical difficulties, and with few exceptions [72, 133], direct calorimetry has been of limited use in benthic flux studies.

Microcosms and mesocosms. In addition to the empirical appoaches to the study of benthic fluxes described above, the exchanges of materials between estuarine waters and sediments have been examined in sediment-water microcosms ranging in size from small cores [42, 43, 63, 64] to the large mesocosm facilities in Kiel Bight [126] and the MERL tanks at the University of Rhode Island [65, 87, 95, 98, 115]. In contrast with the in-situ and most intact-core approaches described above, these experimental systems are primarily designed to examine how specific environmental factors or pollutants affect sediment-water exchanges. They permit a degree of environmental control and replicability not possible in field studies. The MERL tanks are particularly noteworthy because they were explicitly designed to facilitate the study of benthic-pelagic coupling: the sediment communities in the tanks can be isolated from the water column for benthic flux studies.

STUDIES OF SEDIMENT DEPOSITION AND BENTHIC NUTRIENT FLUXES IN THE CHESAPEAKE BAY

The Downward Flux of Particulate Matter

Annual rates and composition. Nixon [83] recently summarized estimates of the rates and patterns of total sediment (i.e., inorganic plus organic material) deposition in the Chesapeake Bay. These geological and geochemical studies have indicated that nearly all sediment entering the Bay from rivers and offshore is deposited within the Bay system [5, 113, 118]. Rates of total sediment deposition decrease from north to south along the main axis of the Bay, then increase again near the bay mouth [92]. Highest rates range from 1-5 kg dry wt $m^{-2} y^{-1}$ in the northern reaches of the Bay to about an order of magnitude less in the lower reaches. Estimates of annual sediment accumulation (dry weight) averaged over the area of the entire Bay range between 0.2 and 2 kg m^{-2} [5, 83, 92, 118].

Bay-wide budgets for nitrogen and phosphorus assembled during the first phase of the EPA-sponsored Chesapeake Bay Program [129] suggested that, like total sediment, essentially all the nitrogen and phosphorus entering the Bay from various sources is deposited on the Bay bottom. If this is true (and for the moment ignoring regional differences in deposition rates), ballpark estimates of the amounts of nitrogen and phosphorus deposited on the Bay bottom annually can be made by dividing the total amounts of nitrogen (160 x 10^6 kg/year) and phosphorus (30.3 x 10^6 kg/ year) entering the bay [129] by the area of Bay bottom (about 11 x 10^9 m^2, including tributaries [30]). These calculations suggest that Bay-wide annual average deposition rates of nitrogen and phosphorus should be on the order of 14 g/m^2 for nitrogen (1.0 g-at m^{-2} and 1.2 gm^{-2} for phosphorus (0.39 g-at m^{-2}). Similarly, the composition of particulate material deposited in the Bay should approximate the inputs divided by the total sediment load (3010 x 10^6 kg m^{-2} [129]). Material deposited on the Bay bottom, if it were unaltered by any biological or chemical processes, would therefore be expected to contain 5.3% nitrogen and 0.46% phosphorus by weight, and have an atomic N:P ratio of about 25.

It is now possible to compare the estimates of long-term sediment deposition with the short-term direct measurements of sediment deposition rates provided by sediment trap experiments. The only sediment trap data for the mainstem Chesapeake Bay available for this review were those provided by the Ecosystem Processes Component (EPC) of the Maryland Chesapeake Bay Monitoring Program ([12], W.R. Boynton et al., unpublished data); for an overview of the Maryland Monitoring Program see [74]. Sediment trap studies have also been carried out in some tributary estuaries including the Patuxent [17, 67], the Potomac (D. Shultz, pers. comm.), and Choptank River estuaries [139].

Mainstem Bay studies. Annual rates of the downward flux of sediment determined with sediment trap arrays located in the mainstem Bay at buoy R64 (Figure 2) by Boynton et al. [12 and unpublished data] were remarkably uniform over the period of July 1984 to June 1987. Time-weighted annual sedimentation rates of total seston to the traps located at a depth of 4-5 m averaged 1.70 ± 0.32 kg m^{-2} (mean ± SD). These rates are consistent with the estimate of Officer et al. [92] for the mid-Bay region, of 1.6 kg m^{-2} (dry weight). The shallowest traps were chosen for this comparison because they best integrate the amounts of material sinking through the euphotic zone [51, 122], and are likely to be the least biased by resuspended sediment. Traps located at mid-depths in the water column generally collected two to three times more material than the shallowest traps. The uncertainty in the net sedimentation rate determined with sediment traps is probably less than a factor of 2 or 3, well within the ranges of sedimentation rates found with

various transport and tracer approaches. The results of the trap studies also indicate that potentially labile components of the sedimenting particles (carbon, nitrogen, and phosphorus) comprised only 5-15% of the total mass of particulate matter sinking through the water column. Therefore, even if these labile constituents were totally remineralized before the particles reached the sediment surface, the sedimentation rates given by the traps would be high by only about 15%.

The annual flux of sediment collected in the near-surface traps of an array maintained in a 10-m water column on the Bay's mid-western flank (Station DB, Boynton et al., unpublished data) was four to five times greater than that found in deeper water near the central channel. The higher sedimentation rate found on the western flank can be attributed in part to sediment resuspension. In contrast with the material collected in deeper water, the elemental composition of the particulate matter collected on the flanks was fairly constant throughout the water column and more closely resembled that of near-surface sediments in the mid-Bay region (2-4% carbon, 0.2-0.5% nitrogen, 0.05-0.1% phosphorus) [12]. On the other hand, enhanced deposition of organic matter on the flanks of the Bay is consistent with recent findings of extraordinarily high summer chlorophyll levels and phytoplankton productivity on the Bay flanks [75, 124]. It is particularly intriguing that the annual deposition of carbon into the 3-m trap of some 400 g m^{-2} is consistent with daily net plankton production rates of 3-5 g m^{-2} found on the flanks in summer [75, 124]. The evidence from the mid-Bay sediment trap deployments shows that the rates of nitrogen and phosphorus deposition determined with sediment traps in the mid-Bay region are several times greater than would be predicted if all sediments and nutrients entering the Bay were deposited evenly over the Bay bottom. The simple deposition calculation made above also suggests that the nitrogen and phosphorus composition of sedimenting material should be about 5% and 0.5% by weight, respectively. The nitrogen and phosphorus content of particulate material collected in the traps, as a percentage of total material collected, is considerably less, averaging 1-2% nitrogen and 0.15-0.36% phosphorus. The N:P ratios averaged about 12, or about half the ratio predicted by the simple mass balance calculation.

Nixon [83] recently noted similar discrepancies between the expected and observed composition of Bay sediments and used these to challenge current interpretations of nutrient budgets assembled during the first seven-year phase of EPA's Chesapeake Bay Program. These budgets were initially interpreted as showing that sediments and nutrients behave similarly, i.e., "nearly all of the materials that enter the Bay remain there; nutrients trickle out of the Bay mouth at a very slow rate" [129]. Nixon has carefully constructed arguments using much of the same data to arrive at exactly the opposite conclusion. According to Nixon's calculations, only a small fraction of the nitrogen and phosphorus introduced into the Bay during non-flood years accumulates in the sediments. A fundamental disagreement therefore remains about the overall behavior of nutrients in the Bay. The sediment trap data support Nixon's interpretations, at least as far as indicating that the nitrogen and phosphorus composition of sedimenting particulate matter in the mid-mesohaline region of the Bay is considerably less than would be expected if nitrogen and phosphorus were being quantitatively removed from Bay water by sediment formation. Whether similar patterns of sediment and nutrient deposition hold for other regions of the mainstem Bay and tributary estuaries is not known.

Tributary estuaries. Boynton et al. [17] and Kemp and Boynton [67] described a series of sediment trap deployments carried out between August 1979 and July 1980 at five locations along the salinity gradient in the Patuxent River estuary. These studies indicated that net sediment deposition was highest in the low-salinity (0-5 ppt) regions of the estuary and decreased toward the mouth of the estuary. These authors suggest that differences in the timing of maximum dissolved nutrient inputs (winter and spring) and phytoplankton production (late spring and summer) result in a cycle of sediment formation, deposition, and nutrient remineralization that causes spatial and temporal separation of "new" and "regenerated" production in the estuary [37]. Their results suggest that nutrient deposition should be especially high in the transition zone between well-mixed, low-salinity water and the downstream region of two-layer estuarine circulation.

A budget for total sediment transports and deposition in the Choptank River estuary [139] demonstrated that nearly 20% of the sediment carried into the estuary was exported to the mainstem Bay. This fraction seems surprisingly large in view of the common notion that estuaries act as efficient sediment and nutrient traps. These results from the Choptank indicate that sediments derived from tributary basins, and presumably the particulate nutrients associated with them, are not necessarily deposited quantitatively in the Chesapeake's sub-estuaries.

Thus, although geological and geochemical evidence suggests that the inorganic component of the sediment load entering the Chesapeake Bay is

deposited and buried in Bay sediments, it is far from clear that nutrients behave similarly. Recent mass balance and sediment trap studies suggest that only a fraction of the nitrogen and phosphorus introduced into the Bay is permanently buried in the sediment.

Seasonal patterns of sediment deposition. Sediment resuspension unquestionably adds an as yet unresolvable dimension to sediment trap data from shallow systems [51, 96]. Nevertheless, sediment fluxes recorded by the trap arrays in the mainstem Bay [12] followed seasonal cycles that are ecologically interpretable and, except for the near-bottom traps, do not appear to be so completely biased by sediment resuspension that the signal from the deposition of new material is lost. The three-year record [12] of particulate carbon deposition to the near-surface traps showed that the period from March to October could be divided into three sedimentation regimes. The spring period began in March, or perhaps earlier, when sedimentation rates increased; they peaked in late April or May at about 1 g C m^{-2} daily. This extended depositional event was followed by a steep decline in May. The summer regime was characterized by an overall trend of increasing deposition rates punctuated with strong depositional events of short duration (1-2 weeks). A third period of high deposition occurred in mid- to late fall (October-November). The deposition of total seston, particulate nitrogen, particulate phosphorus, and total chlorophyll followed patterns nearly identical to those of particulate carbon [12]. The seasonal pattern of particulate carbon deposition observed in shallower water on the western flank followed a similar overall pattern, but peak deposition rates were as much as two- to fivefold greater than those found in deeper water.

Year-to-year differences occur in the magnitudes and timing of major depositional events, particularly during summer, but the overall pattern of sediment deposition to traps in the mid-mainstem Bay is consistent with seasonal patterns of integrated area-based primary production for the Maryland Monitoring Station MCB4.3C [123], which is located near the trap array at station R64 of Boynton et al. The high and sustained deposition rates observed in spring can therefore be attributed to the "sink-out" of the spring phytoplankton bloom, and the peaks of carbon and other nutrient deposition observed in summer and fall can be attributed to the periodic but irregularly timed bloom-and-crash nature of summer phytoplankton blooms. This seasonal pattern of sediment deposition in the Chesapeake Bay differs somewhat from that found in other coastal waters [31, 51, 105, 127] in showing the effect of the spring diatom bloom and the long period of high summer production rates on the sedimentation of organic matter. Deposition in other systems, such as Kiel Bight, is even more strongly seasonally pulsed, with the major depositional event of the year taking place in the spring. One of the important implications of these findings is that a large fraction of the spring bloom may not be grazed by zooplankton and may sink to the bottom directly as intact cells. The sinking of the bloom therefore represents an important source of high-quality organic matter to the benthos, and fuels high rates of sediment oxygen demand in deep waters and the sediment as the season progresses into summer.

A final point demonstrated by the results of recent sediment trap deployments in the Bay is that the composition of inorganic and organic particulate material suspended in the water column generally shows little resemblance to the particulate matter collected in traps, and the concentration of suspended seston does not provide a good indication of the amount of material sinking through the water. The theoretical basis for this difference is now well known [78]: large, fast-sinking particles are relatively rare in the water column and are therefore not adequately sampled by water bottles and low-volume pumps. It is therefore not surprising to find differences in the elemental compositions of suspended particulate matter (sampled with bottles or pumps) and the sinking particles collected in sediment traps. Functionally, these represent two rather distinct populations of particles. Boynton et al. [12], for example, found that the atomic C:N:P ratios for suspended particulate matter at station R64 averaged 250: 24: 1 during two years of observations. During the same period, the composition of material collected in the sediment traps located within or just below the seasonal oxycline (about 9 m) averaged 95: 12: 1. In terms of both the C:N ratio and N:P ratio, the material collected in the traps represented significantly higher-quality organic matter than that suspended in the water.

Factors influencing the downward flux of particulate organic matter. Systematic analysis of physical and biological factors that contribute to seasonal and shorter-term rates of sediment formation, deposition, and resuspension is not available for any region of the mainstem Chesapeake Bay. Studies from other coastal areas [48, 96, 105, 127] suggest that physical factors including currents, wave action, and water column stratification influence rates of sedimentation and sediment resuspension. The relative importance of sediment that originates from aeolian and other atmospheric sources is also not known. There are no reports of attempts to determine the origin of particulate material collected in the recent sediment trap

Table 1. Benthic flux studies in the Chesapeake Bay. Map code numbers correspond to the locations shown in Figure 3.

Map ref. number	Study reference	Study period From	Study period To	No. stations or areas	No. obs. per year	Method	Fluxes reported O_2	NH_4	N+N	NO_2	DON	DIP	DOP	Si	Other	Sponsor
MAINSTEM BAY																
A	Bricker & Troup [18]	Aug 1972		12	NG	PW						X			Various anions and cations	AEC
B	Matisoff et al. [77]	Jun 1971	Sep 1973	2	13	PW		X				X		X	Cl^-, S^-, Fe^-, Mg^{++}	AEC
	Matisoff et al. [77]	Apr 1974		4												
C	Boynton et al. [14]	Jun 1977	May 1978	5	4	BC	X								Total community metabolism	MdDNR
D	Smullen et al. [129]	NG		5-8	3	PW		X				X				EPA
E	D'Elia et al. [34]	Aug 1980	May 1981	4	2	BC								X		EPA, MdSGC
F	Boynton & Kemp [11]	Jul 1980	May 1981	5	2	BC	X		X			X			Sediment C, N, P	EPA, MdDNR
G	Boynton et al. [12]	Jul 1984	May 1986	4	4	BC	X	X	X	X		X		X	Surf. sediment C, N, P	
WESTERN SHORE TRIBUTARIES																
Patuxent River Estuary																
H	Boynton et al. [13]	May 1978	Jun 1979	2	6	BC	X	X	X		X	X	X		Water column studies	MdPPSP
I	Boynton et al. [16]	May 1978	Jun 1979	2	6	BC	X	X	X		X	X	X		Analysis of data reported in H	MdPPSP
J	Boynton et al. [15]	Jul 1978	Aug 1978	3	2	BC	X								Effect of water circulation	None
K	Boynton et al. [17]	Jul 1979	May 1980	4	6	BC	X	X	X	X	X	X	X	X	Sediment traps	MdDNR-PPSP
E	D'Elia et al. [34]	Aug 1980	May 1981	1	2	BC								X	See E	
L	Kemp & Boynton [67]	May 1978	May 1980	5	6	BC		X							Further analysis of data in K	MdDNR-PPSP
M	Yamada & D'Elia [138]	Late Summer		1	NG	LC								X		MdSGC
N	J. Boynton [9]	June NG	Sept NG	3	1	BC	X	X		X		X		X	Sed. and pore water profiles	
G	Boynton et al. [12]	Jul 1984	May 1986	2	4	BC	X	X	X	X		X		X	See G	
O	Lantrip et al. In Press [71]	Jun 1982	Nov 1983	11	3-4	BC	X	X	X	X	X	X	X			
Potomac River Estuary																
P	Callender [21]	Aug 1979		12	1	BC	X	X	X			X		X	Only DIP data reported	USGS, NSF
P	Callender & Hammond [22]	Aug 1979		12	1	BC, PW	X	X	X			X		X	Compared BC, PW methods	USGS, NSF
Q	Cerco [25]	Jul 1984	Oct 1984	1	NG	LC	X	X	X			X			Effect of temp. and O_2 on fluxes	NSF
R	Seitzinger [119]	Sep 1985	Dec 1985	8	1	LC		X	X			X			Effect of pH on DIP flux	EPA, MWCOG
G	Boynton et al. [12]	Jul 1984	May 1986	2	4	BC	X	X	X	X		X		X	Continuing study	MdOEP
S	Cerco [24]	Nov 1986				LC	X		X							NSF
T	Cerco [27]	Jul 1984	Oct 1984	1	weekly	LC	X	X	X			X			Effect of temp., DO on fluxes	
York River Estuary																
U	Phoel et al. [106]	NG		3	1	BC	X	X	X							NG
V	Rizzo [112]	Mar 1983	Dec 1983			BC	X	X	X			X			Sandy shoal site, <2 m deep	
James and Appomattox Estuary																
W	Cerco [25]	Jul 1983	Oct 1984	23	2	BC	X	X	X			X	X			RRDPC
EASTERN SHORE																
Choptank River																
X	Smith & Fisher [128]	Jun 1982	Jul 1983	1	8	BC	X	X	X			X		X		NSF
G	Boynton et al. [12]	Jul 1984	May 1986	2	4	BC	X	X	X	X		X		X	See G	
Pocomoke Sound																
E	D'Elia et al. [34]	Aug 1980	May 1981	1	2	BC								X	See E	
F	Boynton & Kemp [11]	Jul 1980	May 1981	1	2	BC	X		X			X			See F	

deployments, or to quantify the relative abundances of sedimenting particles that entered the water column from either the air-water or sediment-water interface.

As in other coastal plankton-based systems, there appears to be some coupling between plankton production and the deposition of organic carbon in the mainstem Bay. Carbon budgets assembled by Kemp and Boynton [68] for the water column and benthos of the western shore communities near Calvert Cliffs have suggested that 20-40% of annual plankton production reaches the Bay benthos. These estimates are consistent with Nixon's [85] correlation between sediment community metabolism and organic matter input rates if, as shown by Kemp and Boynton's budgets, nearly all the carbon deposited on the bottom is respired by the bottom community.

Another factor that has not yet been adequately evaluated in the Bay is whether the deposition of particulate matter could be significantly altered by the abundance of filter-feeding benthic animals, as has been suggested for San Francisco Bay [28] and other systems [93].

Sediment Oxygen Uptake and Nutrient Fluxes

Identification and description of studies from the Bay region. A search of the primary and grey literature turned up some two dozen reports that deal at some level of detail with sediment-water exchanges of oxygen or nutrients in the Chesapeake Bay and its tributaries (Table 1). These reports are of three types: (1) characterizations of spatial and temporal variability in pore water profiles [e.g., 18, 77, 129]; (2) direct determinations of sediment-water fluxes using in-situ or shipboard benthic chambers [10, 12, 22]; and (3) laboratory studies of the effects of various environmental conditions on rates of sediment oxygen demand and dissolved nutrient exchanges [e.g., 25, 26, 119, 138].

NOTES for Table 1 (facing page): AEC = Atomic Energy Commission; BC = benthic chamber; DIP = dissolved inorganic phosphorus; DON = dissolved organic nitrogen; DOP = dissolved organic phosphorus; EPA = Environmental Protection Agency; LC = laboratory core; MdDNR = Maryland Department of Natural Resources; MdOEP = Maryland Office of Environmental Protection; MdPPSP = Maryland Power Plant Siting Program; MdSGC = Maryland Sea Grant College; MWCOG = Maryland-Washington Council of Governments; NG = not given; N + N = nitrate = nitrite; NSF = National Science Foundation; PW = pore-water profiles; RRDPC = Richmond Regional District Planning Committee; USGS = United States Geological Service.

The early studies of sediment pore waters indicated that the observed profiles could support fluxes of ammonium and phosphate to the overlying water but did not report such calculations per se [18, 79]. Fluxes of ammonium and phosphate based on sediment profiles were, however, combined with a limited suite of in-situ chamber determinations of ammonium and phosphate fluxes [131] and used by Smullen et al. [129] to estimate the contribution of sediment-water exchanges to the Bay's nutrient budgets.

The compilation of reports presented in Table 1 revealed two important features of the benthic flux work that has been carried out in the Chesapeake Bay. First, in terms of both techniques and insights into fundamental controlling mechanisms, research on sediment-water exchanges in Chesapeake Bay began relatively recently. Benthic oxygen fluxes in the Chesapeake Bay were first directly measured a little over 10 years ago [14] near the Calvert Cliffs nuclear power plant, and the first in-situ determinations of sediment-water nutrient fluxes (again in relation to power plant operations), were done about a year later near the Chalk Point power plant in the low-salinity region of the Patuxent River estuary [16]. As mentioned in the Introduction, similar work had been underway in other coastal and estuarine regions in the early 1970's.

The second feature emerging from the summary in Table 1 is that benthic flux work in the Chesapeake Bay was initially supported almost entirely by "mission-oriented" sponsors, particularly those concerned with assessing the environmental inpacts of power plant operations. Direct determinations of nutrient fluxes across the sediment-water interface was apparently not perceived as a major research objective during the first phase of the Chesapeake Bay Program. As a consequence, the nutrient-sediment flux data reported in the Program Synthesis by Taft [131] and Smullen et al. [129] were, by the authors' own admission, very limited. The temporal and spatial design of these studies often makes little ecological sense, and much of the data generated are available only in grey literature reports. Of the studies listed in Table 1, fewer than half have appeared in peer-reviewed journals or books. Only four areas (the western flank of the mainstem Bay near Calvert Cliffs [17], the Patuxent [67], a shoal near Gloucester Point in the York estuary [112], and a site near Horn Point in the Choptank [128]) were sampled often enough over an annual cycle to permit some reasonable estimate of annually-integrated sediment flux rates.

When the locations of study sites gleaned from the works listed in Table 1 are brought together

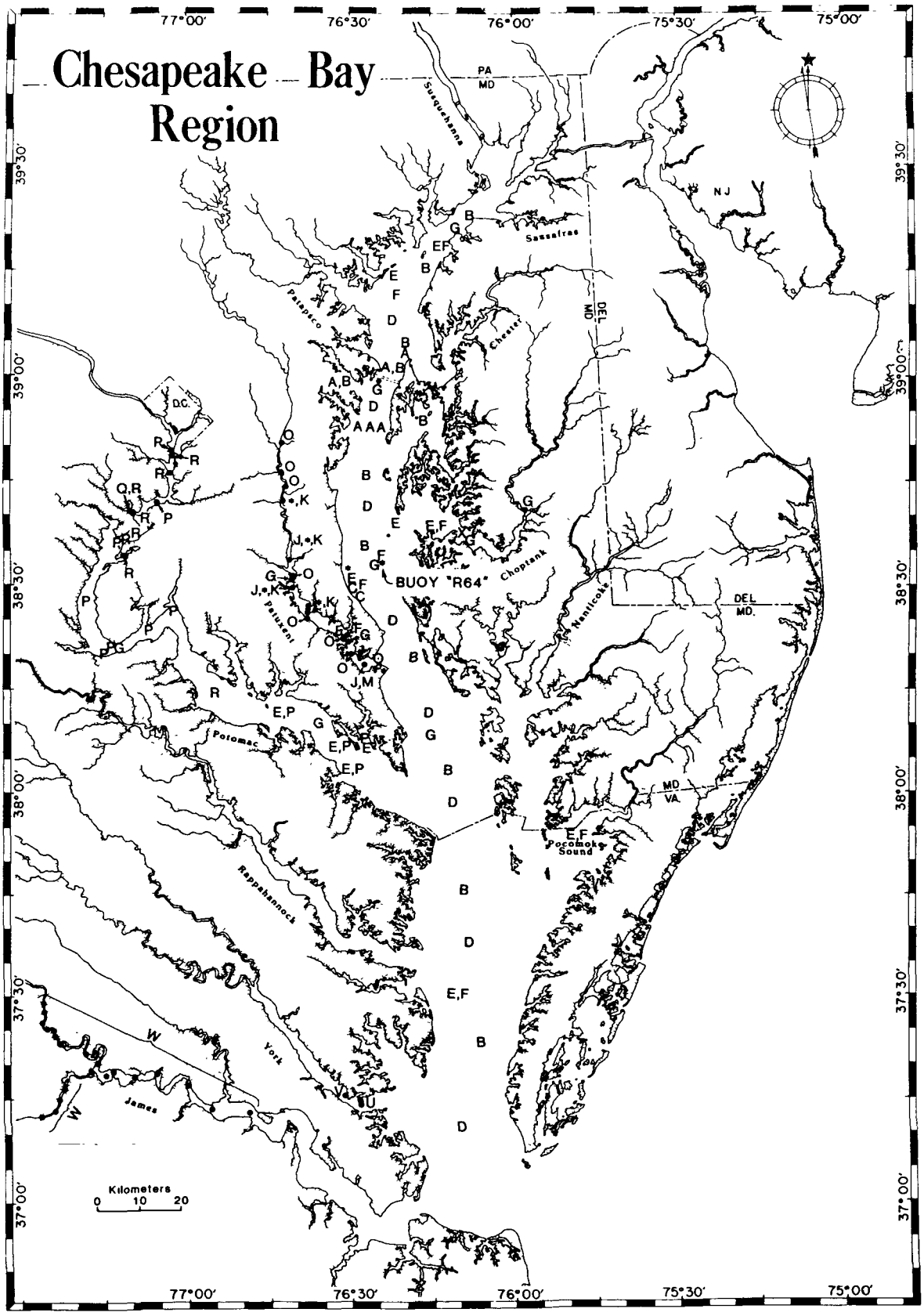


Figure 2. Map of the Chesapeake Bay showing locations of sediment-flux studies (letters) and sediment trap deployments (asterisks). Letters correspond to studies listed in Table 1.

(Figure 2), it becomes clear that work on sediment-water exchanges in the Chesapeake system has been concentrated in the Maryland portion of the mainstem Bay and in the Patuxent, Potomac, and the upper reaches of the James River tributaries. Studies along the mainstem are almost entirely restricted to the relatively deep mid-Bay channel. No data on sediment-water fluxes are available for the Rappahannock, York, lower James, and eastern shore tributaries (except the Choptank) or for most of the lower mainstem Bay or shoal regions throughout the Bay. It is also important to note that coverage of the sites shown in Figure 3 is far from even. Most studies report fewer than four measurements per year, and very few report fluxes for oxygen and a complete suite of inorganic nutrients.

Spatial and seasonal patterns of sediment-water fluxes in the Patuxent River and mid-mainstem Bay. Two regions of the Bay for which substantial amounts of sediment flux data are available are the Patuxent River estuary [17, 67, 71] and the mid-mainstem Bay [10], especially the portion north of the Maryland-Virginia state line [12].

Patuxent River Estuary. Lantrip et al. [71] reported the results of benthic chamber determinations carried out more or less seasonally for two years at 11 stations along the length of the tidal-fresh and estuarine portions of the Patuxent River. In contrast with earlier work [17, 67, 69] which indicated rather clear temporal and spatial patterns in sediment fluxes along the estuarine portion of the Patuxent, the preliminary analysis of these data by Lantrip et al. [71] failed to reveal any consistent patterns in the flux data. Data from the two OEP monitoring stations in the Patuxent [12] also exhibit considerably less variability and fall squarely on the means of the fluxes reported by Lantrip et al. [71]. In both of these studies, however, sampling designs were heavily weighted toward the spring and summer months. The lack of measurements throughout the winter may account for the overall lack of a temperature signal in the flux data. Skewing the flux measurements toward the summer months also obviously biases the overall mean, as summer fluxes may well be higher and more variable than other seasons (see, e.g., [88]).

Mid-Mainstem Bay. Longitudinal transects summarizing spatial and seasonal patterns of benthic oxygen and nutrient fluxes along the axis of the mainstem Bay are shown in Figure 3 (overleaf). These figures were assembled by comparing data for May and August for stations located along the main axis of the Bay [12, 67] with data for the shallow mainstem stations near Calvert Cliffs [17]. Variability of the mainstem flux data has been minimized by showing standard deviations around each mean. These data from the mainstem Bay point to significant seasonal and spatial patterns in nutrient fluxes. Benthic oxygen fluxes were relatively high near the head of the Bay in the spring and summer. The spike in oxygen fluxes in the mid-Bay region was attributable to the shallow stations near Calvert Cliffs in May and the deeper mainstem stations in August. Variability in the mid-Bay oxygen fluxes increased in August as bottom waters alternated between oxic and hypoxic conditions. Almost no spatial pattern was evident in nutrient fluxes along the main axis of the Bay in May. In summer, however, fluxes of ammonium, phosphate, and silicate increased dramatically in the mid-Bay region, probably in response to the combination of high temperatures and low oxygen in the bottom water. Seasonal differences in nitrate + nitrite (N+N) fluxes were also apparent, shifting from Bay-wide sediment uptake in May to strong release of nitrate in the upper Bay in August.

THE NATURE OF BENTHIC-PELAGIC COUPLING IN THE CHESAPEAKE BAY

Factors That Influence Rates of Sediment-Water Exchanges

The exchanges of oxygen and inorganic nutrients between sediments and waters in the Chesapeake Bay appear to vary with time and space in ways that defy simple explanation. Understanding the sources of this variability therefore remains an important research goal. The approach most often taken has been to search for correlations between benthic fluxes of chemical constituents and various environmental parameters, such as water temperature, depth, sediment characteristics, mixed layer depth, and rates of organic loading [47, 50, 65, 86, 88]. Although this approach may eventually lead to an empirical model of sediment-water nutrient exchanges in the Bay region, it sheds little light on the mechanisms responsible for the observed correlations.

Water temperature and water column stratification. An early summary of sediment oxygen fluxes from a variety of aquatic systems [50] suggested that the flux of oxygen across the sediment-water interface was correlated with temperature. As more data from marine systems became available, the model was modified [49] to show that annual rates of sediment oxygen uptake could be related to a parameter arrived at by dividing annual primary production by the depth of the mixed layer of the water column. More recently, Rudnick and Oviatt [115] reported that temperature and oxygen uptake by the sediment

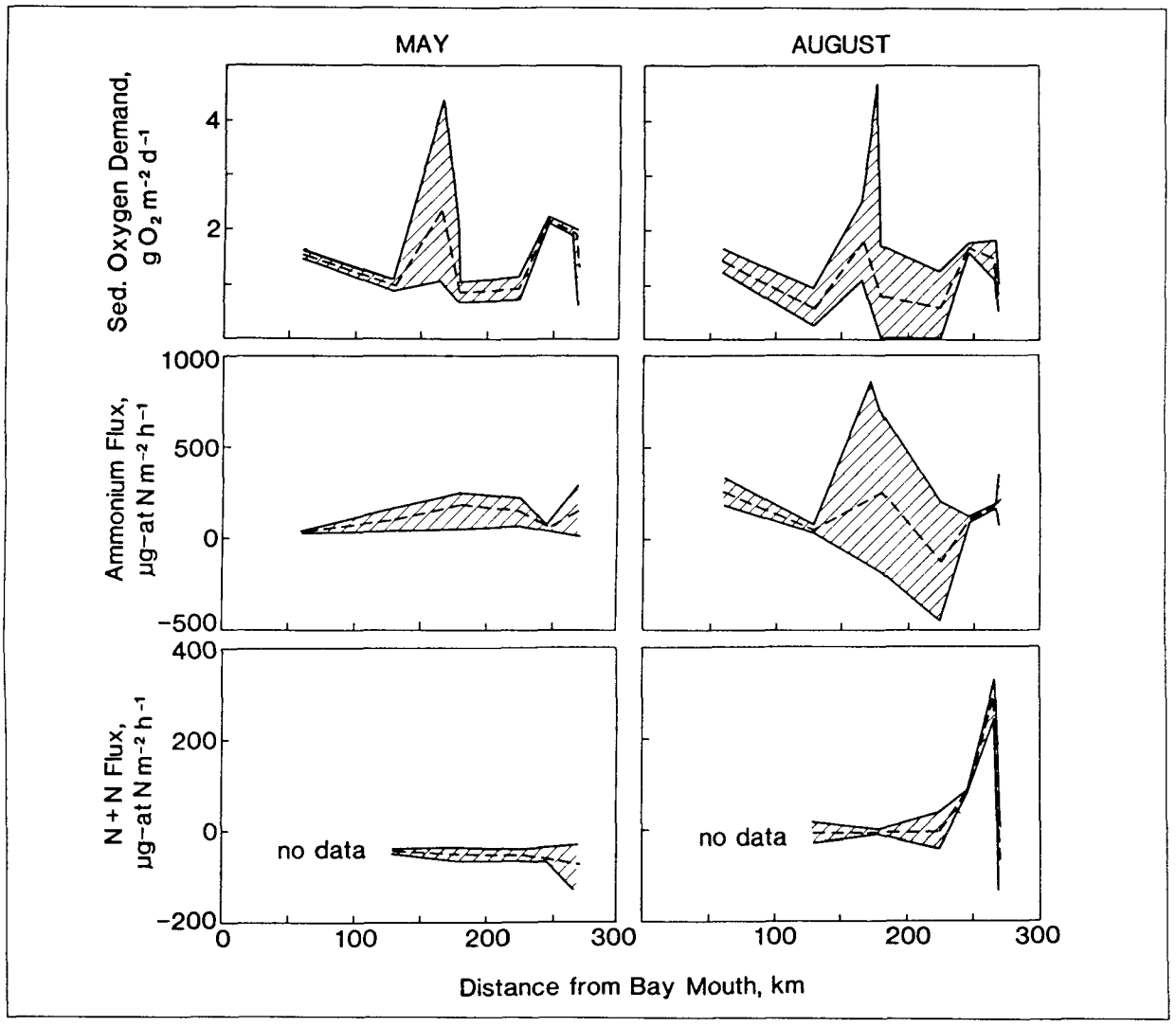
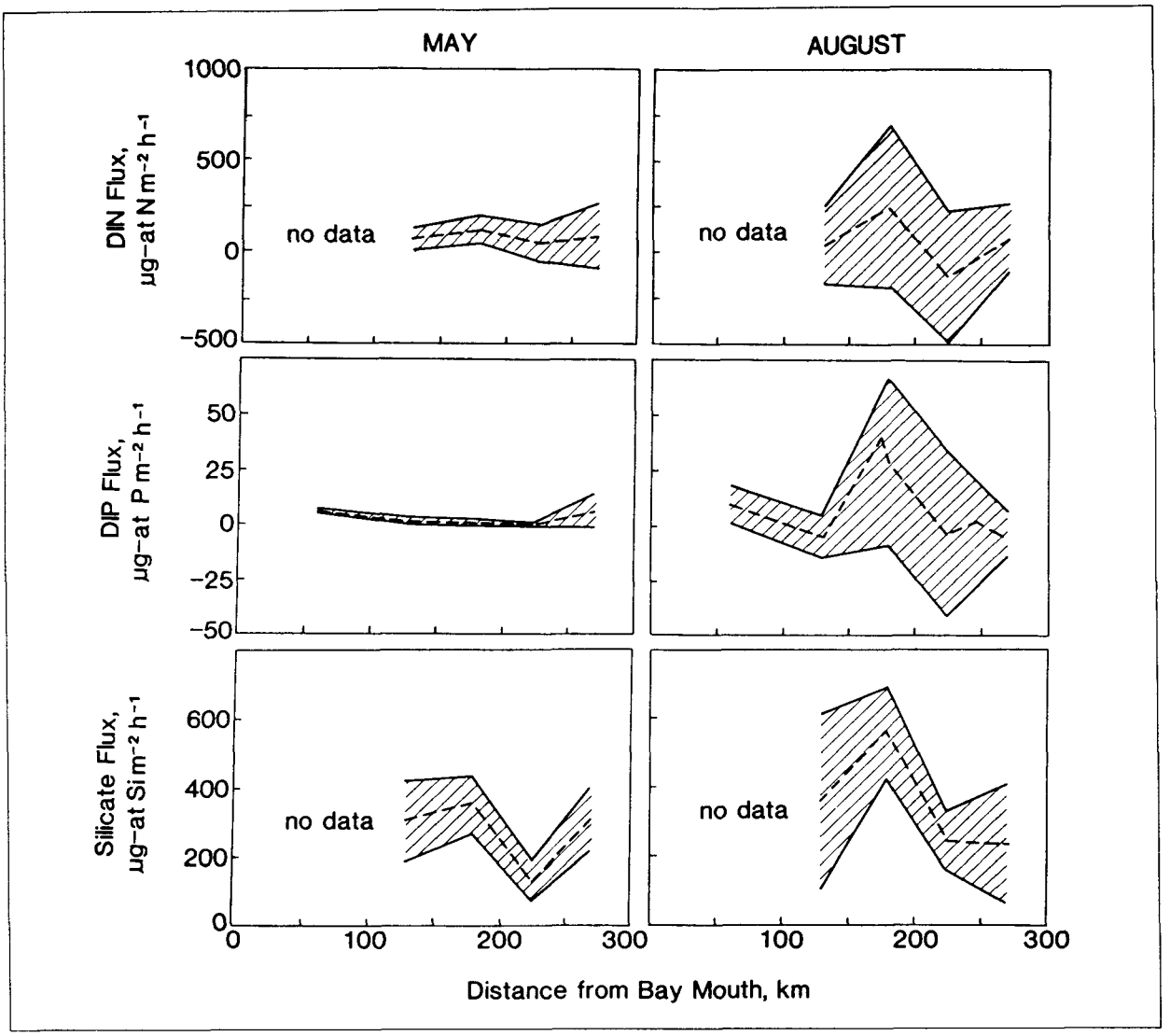


Figure 3 (above and next page). Seasonal and spatial patterns of oxygen and inorganic nutrient fluxes in the mainstem Chesapeake Bay. The mean and standard deviations of data [10, 12, 14, Boynton et al., unpublished data] for the months of May (left series of panels) and August (right series) are shown at stations located by the distance from the mouth of the Bay.

communities in the MERL mesocosms were highly correlated (r=0.927) and could be described over a temperature range of 0-25°C by the simple exponential equation O_2 flux = $e^{0.0991+2.118}$. Similar relationships between temperature and benthic nutrient fluxes have also been described recently for the mesohaline region of the mainstem Bay [44]. But in general, Boynton et al. [12] were unable (with some exceptions discussed below) to demonstrate significant single-variable correlation between sediment-water fluxes determined at 10 stations in the Maryland portion of the Bay (sampled four times per year) and most environmental parameters, including bottom water temperature.

Sediment characteristics. The conceptual model of nutrient cycling presented in the INTRODUCTION (Figure 1) shows that the amounts of particulate carbon, nitrogen, and phosphorus accumulating in estuarine sediments represent the net effects of organic matter deposition and nutrient remineralization. Although it seems likely that some relationship exists between organic deposition rates, benthic nutrient fluxes, and the resulting carbon, nitrogen, and phosphorus content of the sediment, most studies in estuaries have reported no clear relationships between sediment characteristics and sediment fluxes. This lack of clear relationships was also reported by Boynton et al. [12] with one important exception: a significant positive correlation exists between the total nitrogen content and the flux of total dissolved inorganic nitrogen from the sediment. They attributed this relationship to the effects of oxygen concentration



on the products of microbial nitrogen transformations in the sediment column or at the sediment-water interface. For reasons that are not fully understood but are probably linked to factors that regulate microbially mediated-mediated nitrification and denitrification reactions in Bay sediments [60, 120, 121, 134], nitrogen remineralization tends to be less complete under anoxic conditions; thus nitrogen accumulates in the regions of the Bay where the sediment tends to be more reduced.

Dissolved oxygen. The influence of oxygen concentration and water temperature on sediment-water exchanges of oxygen and nutrients has been examined in laboratory-maintained cores [25] and empirically from field data [e.g., 12, 26]. The studies carried out by Cerco [25, 26] have shown that the fluxes of ammonium, nitrate, and phosphate increase with decreasing oxygen concentration. The rate of sediment oxygen uptake also increases with temperature, but decreases as oxygen concentrations drop in the overlying water.

Data collected by Boynton et al. [12 and unpublished data] also show that rates of sediment oxygen demand drop more or less linearly (O_2 flux = 0.11 $[O_2]$ + 0.44, r=0.54) with the oxygen concentration of the overlying water. Their field data exhibit considerable scatter, particularly at higher oxygen concentrations, which indicates that additional factors are involved in regulating rates of sediment oxygen consumption.

In the passage quoted in the INTRODUCTION, Mortimer [79] predicted that the release of inorganic phosphorus from sediments would increase when the oxygen concentration of the overlying water dropped below 2 mg/l. The studies of Boynton et al. [12 and unpublished data] indicate that this prediction holds in

the Maryland portion of the bay. Their data showed that at oxygen concentrations above 2 mg/l the phosphate flux from the sediment was low and erratic. When oxygen concentrations in the overlying water dropped below 2 mg/l, the flux of phosphate from the sediment increased dramatically. Webb and D'Elia [137] had described a nearly identical relationship between phosphate and oxygen concentrations during an investigation of neap-tide stratification in the York River estuary. They observed significant increases in dissolved phosphate concentrations when the oxygen content of the water dropped below 2 mg/l and attributed both the phosphate source and oxygen sink to benthic fluxes of these constituents. The relationship between sediment-water exchange of phosphate, sediment redox conditions, and the formation of phosphate-containing amorphous ferric oxyhydroxides was also examined in the Potomac River estuary by Callender and Hammond [22].

pH. Seitzinger [119] recently demonstrated that the release of phosphate from sediments from the upper Potomac estuary increased when the pH of the overlying water rose above 9. Estuarine waters with salinities above about 5 ppt are fairly well buffered against increases in pH to these levels. The pH-mediated release of sediment phosphate would therefore be most likely to occur in the tidal-fresh and low-salinity regions, such as the upper Potomac, that are subject to intense algal blooms.

Rates of organic matter deposition. The concept of benthic-pelagic coupling assumes a functional relationship between the deposition of organic matter at the sediment-water interface and benthic nutrient remineralization. There is good reason to believe this model is basically correct; the relationship between annual rates of organic matter supply and benthic carbon consumption described by Nixon [85] is very compelling. Nevertheless, direct evidence for the model requires simultaneous (or contemporaneous) short-term determinations of organic deposition rates and dissolved nutrient fluxes at the sediment water interface. This has rarely been attempted in estuaries (see Boynton's work on the Patuxent [16]), and only recently have such data become available for the mainstem Chesapeake Bay. The preliminary analysis of the data from sediment trap deployments and benthic flux determinations in the mid-mainstem Bay [12] indicates that there may indeed be a linear relationship between the amounts of particulate carbon sinking to the Bay bottom and the rates of oxygen fluxes at the sediment water interface. As predicted by the model of benthic-pelagic coupling introduced earlier, the rate of oxygen consumption in the sediment generally increased with higher rates of organic carbon deposition. Boynton et al. [12] are careful to point out that these relationships may not hold as more data become available. Nevertheless, they provide at least preliminary support for the view that sediment-water exchanges respond relatively rapidly (i.e., within a few months) to changing organic loading rates.

The Stoichiometry of Nutrient Fluxes

Boynton and Kemp [10] have described seasonal changes in stoichiometry of nutrient fluxes along the length of the mainstem Bay. In summer, the ratio of the benthic fluxes of inorganic nitrogen and oxygen was 18.5:1, similar to the Redfield ratio of 16:1. A more complete stoichiometric model for the formation, deposition, and remineralization of organic matter in the central Bay [12] included nutrient ratios of suspended particulate matter, material collected in sediment traps, surficial sediments, and benthic fluxes. The results of this analysis revealed that particles suspended in the water column generally have relatively high C:P and N:P ratios. The similarity between the C:N:P ratios of suspended seston and surficial sediment was striking and suggested that the sediments suspended in the water column may contain a considerable fraction of resuspended sediment. Differences between nutrient ratios of suspended seston and the particulate matter collected in the top and middle sediment traps were also striking. Unlike the material suspended in the water column, material collected in the traps followed Redfield's ratios almost exactly in early spring and late summer, but also exhibited significant phosphorus depletion relative to nitrogen and carbon just before the major depositional events in mid-spring and mid-summer. This difference suggested that suspended and sinking particles comprised two rather distinct populations of particles, the former more similar to resuspended sediment, the latter apparently reflecting the nutritional state of the plankton, which undergo significant seasonal changes. This analysis also suggested that when sediment fluxes from all stations and all sampling times were combined (mainstem plus tributaries), the fluxes of inorganic nitrogen and inorganic phosphorus across the sediment-water interface averaged 15.7:1, almost exactly Redfield's ratio for marine plankton. I have recently recalculated this ratio using three years of flux data from only the four mainstem stations and found the N:P ratio (5.7:1) to be significantly less than the previous estimate. This calculation for the mainstem stations is consistent with reports (summarized by Nixon [85]) of relatively low inorganic N:P ratios of estuarine benthic fluxes. However, the benthic fluxes from the

Bay's tributaries appear to be characterized by N:P ratios that are close to Redfield's ratio or higher.

Benthic-Pelagic Coupling in the Chesapeake Bay

Data available at present allow an examination of the interactions of primary production, organic deposition, and nutrient remineralization on a seasonal (rather than annual) basis for regions of the mainstem Bay and Patuxent River. For example, Kemp and Boynton [68] reported daily rates of benthic respiration (sediment oxygen uptake) for the shallow-water communities near Calvert Cliffs ranging from 0.24 to 3.4 g O_2 m^{-2}. Converted to carbon equivalents, these rates of benthic community respiration represented 30-40% of gross phytoplankton productivity in summer, and 50-100% of plankton productivity in winter. The annual carbon budgets assembled for this community show that essentially all the carbon available for deposition on the bottom could be consumed in the benthos.

Boynton and Kemp [10] also determined spring and summer benthic fluxes of oxygen and nutrients at five locations along the axis of the mainstem Bay and three locations in tributary systems. They estimated that ammonium flux from the sediment could usually meet 20-40% of the nitrogen requirement for phytoplankton production along the mainstem, and perhaps 10-25% of the plankton nitrogen requirement in tributary estuaries. The more extensive data from the Patuxent River estuary reported by Boynton et al. [16] and Lantrip et al. [71] indicated that the fluxes of ammonium and phosphate from the sediments of this tributary are often more than sufficient (sometimes by factors of two or three) to supply the daily production requirments of the phytoplankton. Lantrip et al. [71] showed that the flux of ammonium and phosphate from the sediments represents a significant source of inorganic nutrients in the estuary at all times of the year except winter. During spring, summer, and fall, the sediment release of ammonium was two to three times greater than the inorganic nitrogen loading of the estuary from runoff and other sources.

Returning to the mainstem Bay, Boynton et al. [12] estimated the consumption of oxygen by mid-Bay sediment communities could remove 2-16% of the oxygen inventory of the water column per day. Their estimates suggested that during periods of water column stratification, sediment oxygen demand alone could drive deep waters into anoxia in 10-13 days. They also calculated that the amounts of carbon, nitrogen, and phosphorus sinking out of the upper waters of the mid-mainstem Bay represented a significant fraction (3-63%) of plankton production. The data also indicated that when oxygen levels in the overlying water are > 1 mg/l, oxygen-consuming processes in the sediments can account for the consumption of 70-100% of the organic carbon sinking to the bottom. Sediment oxygen demand drops to zero when the overlying water becomes anoxic, and the fraction of organic deposition consumed by aerobic respiration in the sediment decreases during anoxic events. It is important to note that the decomposition of organic matter can (and undoubtedly does) continue in the sediment during anoxic events via various metabolic pathways, especially sulfate reduction. These reactions result in the buildup of reduced products, such as sulfides, that can contribute to sediment oxygen demand when the deep waters of the Bay are reoxygenated. The rates of these anaerobic processes in the Bay are poorly known and need to be better characterized.

Finally, the seasonal budgets for the mid-Bay region asssembled by Boynton et al. [12] indicated once again that nutrients remineralized in Bay sediments represent a significant fraction of the amounts of inorganic nitrogen and phosphorus needed to support primary production in the water column. For nitrogen this fraction appears to fall in the range of 15-40%. The fraction of phytoplankton phosphorus demand met by the benthic flux of dissolved inorganic phosphorus is more difficult to determine from these seasonal measurements because the release of phosphate from the sediments is highly sensitive to the oxygen content of the overlying water. As Mortimer [79] predicted, the fraction of phytoplankton phosphorus demand met by benthic fluxes in oxic regions of the Bay is probably measurable but small (the data of Boynton et al. suggest between 0 and 40%). Phosphate flux from the sediments increases during hypoxic and anoxic events in the mainstem Bay and tributaries. During these events the daily rate of phosphate release from the sediments may exceed phytoplankton demand by as much as 200%.

SUMMARY AND RECOMMENDATIONS

The purpose of this review has been to examine the interactions between the waters and sediment of the Chesapeake Bay relevant to problems associated with changes in nutrient loading of the estuary. Studies to date have unequivocally demonstrated that organic matter sinks through the water column, that oxygen is consumed by Bay sediments, and that inorganic nutrients are returned to the overlying water. Two problems, however, complicate the task of assembling a comprehensive quantitative model of these processes in the Chesapeake Bay. First, no

reasonably tightly-constrained estimates of annual rates of sediment oxygen demand or benthic nutrient fluxes are available for any region of the mainstem Chesapeake Bay. This lack of annually-integrated flux data makes it difficult to assess the contribution of sediment fluxes to the annual Bay-wide budgets of nutrient loadings and primary production. Second, considerable amounts of pertinent data remain in essentially raw form in grey-literature reports or have been collected so recently that data reduction and synthesis has not yet been possible.

The other findings of this review are: (1) A survey of the white and grey scientific literature uncovered only about two dozen reports (about half of which are not available as peer-reviewed reports in primary literature) that deal directly or indirectly with the processes of sediment deposition or the exchanges of oxygen and nutrients across the sediment-water interface in the Chesapeake Bay. These reports represent a small fraction of literature generated on these subjects over the past two decades.

(2) Geographical distribution of the studies of sediment deposition and benthic fluxes in the Chesapeake Bay is very uneven. While extensive data sets on these processes are available (and continue to grow) for the Patuxent River and the Maryland portion of the mainstem Bay, virtually no data could be found for the Rappahannock, York, lower James, and eastern shore tributaries (except the Choptank River). Very little information on these processes is available for most of the Virginia portion of the mainstem Bay. Studies of the mainstem Bay have generally been conducted in relatively deep water along the central axis, and almost no information is available for vast shallow portions of the mainstem Bay on the eastern and western flanks of the central channel.

(3) Few of the studies of sediment-water exchanges undertaken in the Bay region have provided data suitable for tightly-constrained estimates of annual rates of sediment deposition or sediment nutrient fluxes. Seasonal sampling strategies have revealed a great deal about benthic-pelagic noise in the Chesapeake Bay and very little about the signal. The problem of periodic anoxia in regions of the Bay exacerbates the problems associated with seasonal sampling by introducing yet another important variable in the suite of conditions that regulate benthic-pelagic exchanges.

Recommendations for Future Work

(1) Field research aimed at determining annual rates of sediment deposition, sediment oxygen demand, and benthic nutrient fluxes, based on weekly or bi-weekly sampling schedules, is needed to adequately quantify these processes and assess their importance in the budgets of nutrient loadings and productivity in the Bay.

(2) Estimates of sediment deposition, sediment oxygen demand, and benthic nutrient fluxes are needed for more tributary estuaries on both the eastern and western shores of the Bay. Similar work needs to be extended into the Virginia portion of the mainstem Bay and in shoal regions throughout the mainstem Bay.

(3) Research needs to be undertaken to re-examine whether, and how, various regions of the estuary act to trap sediments and nutrients.

(4) Data from past and current monitoring programs and modeling efforts need to be synthesized and published in the peer-reviewed literature.

(5) Although this review was not aimed at summarizing work on specific benthic processes that generate the fluxes of constituents across the sediment-water interface, it is clear that further research on reaction pathways such as nitrification, denitrification, and sulfate reduction will lead to a better quantitative understanding of oxygen and nutrient dynamics in the Bay.

The Need For Experimental Work in Mesocosms

Investigations of sediment formation, deposition, and benthic nutrient remineralization in the Chesapeake Bay have to date been limited to field-oriented, essentially descriptive studies. These have provided, and will continue to provide, important data on the magnitude of these processes in various parts of the Bay system. Progress in understanding these processes will be slow, however, if this essentially phenomenological approach is not complemented with experimental work. This is because controlled experiments cannot be carried out in the field. However, an ecological experiment of mind-boggling scale is already under way, as attempts are made to regulate the amounts of inorganic nutrients that enter the Chesapeake system of estuaries. Our ability to predict the results of this experiment is extremely limited.

I end this review by recommending that monitoring and modeling efforts currently aimed at understanding nutrient dynamics in the Chesapeake Bay be augmented with experimental studies in sediment-water mesocosms. The power of mesocosm-based research in addressing pollution-related problems has been amply demonstrated by experiments in the plankton-based systems at Benedict [36, 117], and the MERL facilities in Rhode Island [63, 65, 95, 98, 115]. I close on this note because, as this review came

together, it became apparent to me that the Chesapeake Bay yields its secrets very reluctantly. A combination of monitoring, modeling, and experimental work is needed to make rapid strides in understanding its dynamics.

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Factors Driving Changes in the Pelagic Trophic Structure of Estuaries, with Implications for the Chesapeake Bay

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INTRODUCTION

Physiological tolerances and food supply determine the potential success of an individual organism. If growth is limited by the quantity or quality of food, then population size, and therefore community composition, is determined by factors regulating the dynamics of prey organisms in the next "lower" trophic level: "bottom-up" or source control. If, however, adequate nutrition is available such that growth is resource-independent, then population size may be governed by predators comprising the next "higher" trophic level: "top-down" or sink control.

Estuaries are characterized by environmental stresses of greater amplitude and frequency than most other aquatic habitats. Although environmental variability occurs over broad temporal scales, the most significant component is scaled to body size: the smaller the organism, the faster the growth rate, the shorter the relevant time scale. Thus, the importance of source vs. sink control of trophic structure changes as a function of processes determining the availability of food and susceptibility to predation. Imbalances between these processes cause population oscillations, which are damped as balance is restored. However, long-term environmental changes superimposed on this short-term variability, whether climatic (e.g., temperature) or anthropogenic (e.g., eutrophication), can significantly alter the structure of pelagic food webs. This review considers factors regulating source and sink control of pelagic food webs, and the role of long-term environmental modifications in altering these relationships. Potentially significant ramifications for trophic structure in the Chesapeake Bay are highlighted in Figure 1.

SOURCE CONTROL

Early research in biological oceanography [88-90] was fueled primarily by incentives to be derived from understanding, predicting, and improving the production of fish in the sea. Such attempts to predict commercial yield from data on primary or secondary production have met with little success. One reason is that the quantity of production may not be nearly as important as the number of steps in the food chain [179]. Trophic dynamic theory proposes that major energy losses, perhaps as high as 90% [200], accompany each transfer between trophic levels. Such rapid attenuation prohibits long food chains with predator stacked upon predator. This scenario also implies that food chains may increase in length in more productive regions or under more eutrophic conditions [160]. Moreover, systems dominated by small primary producers should exhibit reduced terminal production, because of the increased length of the food chain [179]. An alternative hypothesis states that top predators subsisting on long food chains have lower metabolic expenditures that balance the decrease in available food, so that yield is constant [109]. Common to both propositions is the assumption that changes in the size distribution or community composition at lower trophic levels have little impact on succeeding trophic levels; that is, production is production, and all prey are consumed with equal efficiency and gusto.

More recent models recognize that size structure is at least as important as biomass or production in understanding the exchange of energy between trophic levels [205]. Greve and Parsons' very provocative hypothesis, which has received surprisingly little

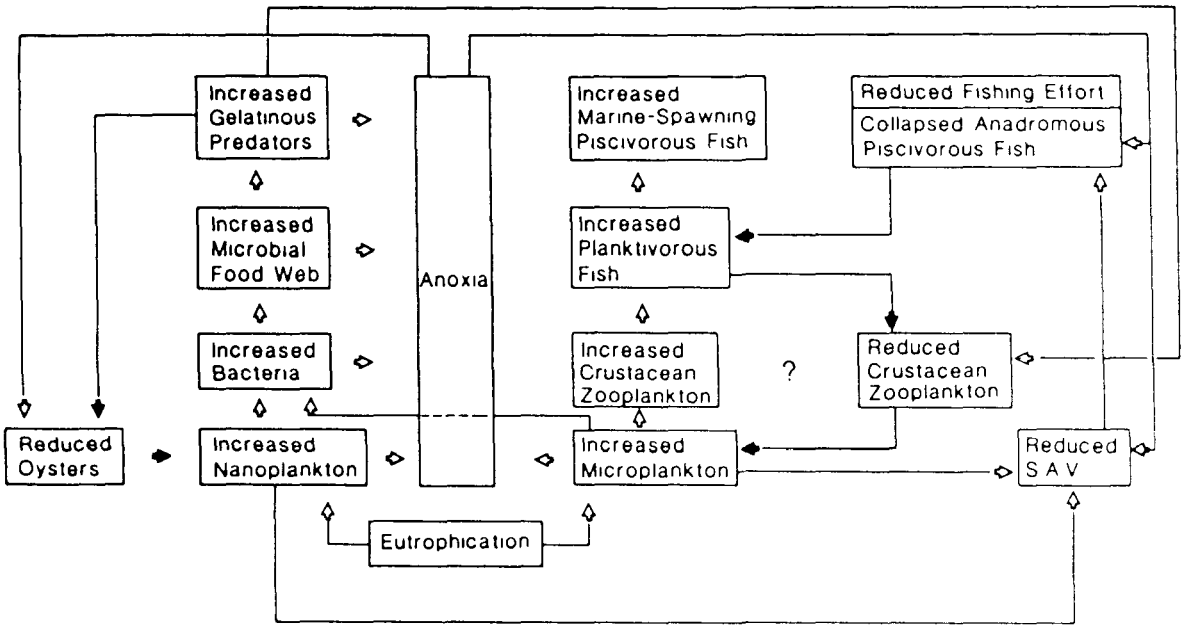

Figure 1. Flow chart illustrating some of the hypothetical trophic linkages which may be significant in Chesapeake Bay. Clear arrows define pathways that appear to be strongly influenced by "bottom-up" or source control. Bold arrows show trophic interactions in which "top-down" or sink control appears dominant. Pathways that appear to be less significant are not illustrated for purposes of clarity. Note that most of the changes in stock sizes to the right of the anoxia compartment have been documented, while those to the left await confirmation. SAV = submerged aquatic vegetation.

attention, speculates that dominance by phytoflagellates results in ctenophores and other gelatinous organisms as top predators, compared with systems dominated by diatoms, which support teleosts as top predators [80]. Thus, a shift from fish to jellyfish is predicted where eutrophication, pollutants, or other conditions induce shifts in dominance from diatoms to flagellates. The implications of such a shift are underscored by the general notion that gelatinous predators are "a dead end in the energy transfer" [110]. Greve and Parsons' hypothesis contrasts starkly with previous considerations of plankton trophic interactions by implying that changes in community composition within one trophic level, for whatever reasons, reverberate through the food web and result in significant alterations in the structure of the entire food web. Evaluation of this general concept is a focal point of this review.

Phytoplankton

Phytoplankton are the dominant primary producers in most marine environments, including estuaries, and are the principal food supply for both the bacteria-based microbial food web and the more traditional zooplanktonic food web. Thus changes at this level may have significant effects on pelagic trophic structure. Growth rate (i.e., primary production) and community composition may be altered independently or concurrently. There is little evidence that long-term changes in the magnitude of production have a direct effect on trophic structure; the indirect effects, however, may be considerable. For example, ample support from mesocosm studies [91, 149] and from the Chesapeake Bay [15, 222] indicates that increased primary production, resulting in elevated organic loading of the water column and benthos, stimulates microbial utilization of most or all of the available oxygen. The development of hypoxia and anoxia restricts habitat space of phytoplankton and zooplankton [195, 224] reducing access to nutrients and food, and perhaps increasing exposure to predation. Anoxia also inhibits the germination of resting spores of phytoplankton [44] and resting eggs of zooplankton [105, 231, 232], potentially altering the composition of both groups. Anoxia reduces the habitat space of fish and shellfish [39, 165, 186] and has been hypothesized to induce mortality of larvae, juveniles, and adults unable to locate oxygenated waters. In addition to anoxia, chronic increased primary production is responsible for decreased water transparency, which has been associated with major declines in submerged aquatic vegetation in the Chesapeake Bay

[13, 147]. These macrophytes provide important nursery areas for juvenile fish [86, 165], and their disappearance may have significant implications for predator-prey relationships among pelagic organisms [69, 146].

In contrast to changes in the rate of primary production, long-term alterations in the relative dominance of phytoplankton species may directly affect the structure of higher trophic levels and the efficiency of transfer within food webs. The literature is replete with data describing the nutritional value of diatoms and their preferred status in the diets of herbivores; however, two taxonomic groups of phytoplankton, dinoflagellates and cyanobacteria, are highly variable in their susceptibility to predation and their contribution to diets of grazers. Species of dinoflagellates differ considerably in their quality as food for ciliates [207, 240], crustacean zooplankton [93], and fish larvae [185]. Some dinoflagellates are acceptable at low concentrations but are less attractive at bloom densities [210]. It has been suggested that certain species' lethal or inhibitory effects on grazers are partially responsible for development and maintenance of their significant blooms [61, 93]. Dinoflagellates are apparently a poor food for oyster larvae [45], a characteristic attributed to interference with larval feeding by dinoflagellate trichocysts [227]. At least one dinoflagellate passes undigested from the guts of adult oysters [70]. Dinoflagellate blooms have also been implicated in mortality of larval fish [163], perhaps because of exudates that clog their gills [100].

The effect of cyanobacteria on pelagic food webs appears to be due more to small size or lack of nutritional quality than to direct toxicity. Cyanobacteria are ingested by both heterotrophic nanoplankton and ciliates [25, 98, 157], but their nutritional value remains in doubt. They do not satisfy the dietary requirements of numerous planktonic ciliates [172, 240, 246], although one species was maintained in culture for an extended period on a pure diet of cyanobacteria [102]. Crustacean zooplankton clearly do not utilize cyanobacteria, which pass undigested through their guts [102, 198]. Cyanobacteria are also inadequate food for oyster larvae and significantly decrease their feeding on other, more nutritious food [46, 227].

Thus changes in both the magnitude of primary production and the dominant algae can significantly affect pelagic trophic structure. From the perspective of source control, the major factors driving changes in phytoplankton growth and community composition include temperature, the quantity and quality of subsurface irradiance, the supply rates and ratios of nutrients, and the influence of physical processes on their distributions in time and space. Temperature influences the growth rates and seasonal occurrence patterns of phytoplankton, although primary production and species succession do not appear to be regulated by temperature [57, 104]. The role of temperature in seasonal patterns is beyond the scope of this review, but the effects of long-term changes in temperature on biological variability are considered in a later section. In addition to the physical and chemical factors outlined above, a considerable body of evidence indicates that phytoplankton growth and community composition are affected by the availability, toxicity, and interactions between various trace metals and other chemical compounds that originate from anthropogenic sources [17, 62, 136]. Acute and sublethal effects have also been documented in higher trophic levels [170, 219]. The influence of toxic compounds on biological communities of estuaries is reviewed in detail in Chapter 5 of this publication [182].

The intensity and spectral distribution of in situ irradiance affects the growth rates of phytoplankton. Irradiance is attenuated in estuarine waters primarily by phytoplankton pigments and mineral suspensates [159]. Light transmittance in the Chesapeake Bay has decreased historically as eutrophication has proceeded [243], to the point that primary production in portions of the Bay and the adjacent Delaware estuary appears to be regulated by light limitation [83, 155, 156]. Reductions in the proportion of light in the photosynthetically important regions of the spectrum, which have been documented in the Bay [32, 243], also contribute to light regulation of phytoplankton growth. In laboratory studies, such changes in the light regime can affect nutrient requirements and relationships among phytoplankton species by altering their optimal ratios of cellular constituents [248]. Whether the temporal trends in light availability in the Chesapeake Bay are responsible for driving changes in the composition of phytoplankton communities has not been demonstrated. Theoretical considerations imply that reductions in irradiance might favor enhanced growth of cyanobacteria and equally small eucaryotic phytoplankton [64, 74].

Increased attenuation of irradiance may also favor motile taxa that can readily adjust their vertical position in the water column. The migratory ability of bloom-forming dinoflagellates, which permits them to concentrate in upper sunlit layers during the day and to utilize the higher nutrient concentrations found in deeper layers during the night, was proposed to account for their numerical superiority over diatoms and non-motile species in the Southern California Bight [58]. A similar scenario may explain the

continued occurrence of dinoflagellate blooms in the nutrient-poor surface waters of the Chesapeake Bay during the summer [226]. Blooms of at least one dinoflagellate, *Prorocentrum mariae-lebouriae*, apparently develop in the northern Bay from the introduction of "seed" populations derived from the southern Bay via subsurface transport during high spring streamflow [225, 226]. As a result, interannual variability in blooms of this species [223] and others [224] may be correlated with fluctuations in streamflow [184], locations of associated frontal regions [188], and pycnocline-tilting events [123]. Thus seasonal, interannual, and longer-term variability in physical transport mechanisms, described in detail by Itsweire and Phillips [97], may change the composition of plankton communities. The effects on higher trophic levels may be direct [101] or magnified through trophic interactions [247].

Extensive field evidence has demonstrated that annual nutrient inputs from the surrounding watershed into the Chesapeake Bay have increased and have resulted in enhanced primary production [15, 22, 142]. Mesocosm studies have confirmed the positive correlation between eutrophication and primary production [51, 141, 149]. Similar enclosure experiments have also demonstrated that nutrient enrichment may alter phytoplankton community composition over periods of days to weeks [77, 181], with the limiting nutrient and the extent of limitation varying seasonally. Changes in phytoplankton composition would be expected as nutrient fluxes and ratios change, because each species has different requirements [111, 217]. However, evidence demonstrating significant long-term changes in community structure in response to eutrophication remains equivocal. The effects of progressive eutrophication on trophic structure in Moriches Bay and Great South Bay (New York) are examples often cited. Extremely dense populations of a chlorophyte and a cyanobacterium developed in waters heavily fertilized by effluent from duck farms, and these blooms coincided with collapse of an extensive oyster fishery [178]. These, and other similar occurrences of dense blooms of phytoflagellates in hypereutrophic waters [122], imply that elevated nutrient supplies alter phytoplankton community composition toward prevalence of small, less desirable species [201]. Dominance by flagellates and other nanoplankton, however, is not predicated upon an excessive supply of nutrients [59]. Rather, the ratio of silicon to other limiting nutrients appears critical in determining species dominance in phytoplankton communities [143]. Contemporary calculations based on the supply rate of silicon suggest that diatom production may represent one half of the total annual primary production [50]. Much of this apparently occurs during the spring diatom bloom. Silicate limitation of diatom growth has been proposed as a contributing factor in the collapse of their blooms in some years [192], although this hypothesis remains to be experimentally verified.

Summer communities in the Bay are dominated by flagellates, dinoflagellates, and cyanobacteria [125]. These taxa have the "least desirable" characteristics according to Ryther and Officer [180], prompting some investigators to suggest that eutrophication has resulted in changes from diatom- to flagellate-dominated communities [142]. Analysis of historical data indicates that the contemporary Bay has a longer growth period, more diversity, and a greater total abundance of phytoplankton than in the past [125]. Although the importance of photosynthetic nanoplankton has received increased recognition [128, 189, 235], significant changes in techniques of sampling, preservation, and enumeration preclude quantitative interpretation of long-term trends in abundance of nanoplankton, including cyanobacteria. To the extent that historical changes towards dominance by various nanoplankton taxa have occurred, the structure of higher trophic levels may have been influenced as previously outlined.

Bacteria and Heterotrophic Nanoplankton

Models of freshwater trophic relationships predict that eutrophication increases the proportion of inedible phytoplankton, and that "inedible algae serve as a buffer against variations in nutrient supply" [19]. Primary production, however, provides the major substrate for bacterial growth, and therefore enhanced primary production can be expected to stimulate microbial production. Such a cause-effect relationship was observed along a eutrophication gradient in mesocosms [91]. Historical data are not available from the Chesapeake Bay, but present bacterial communities are extremely abundant and metabolically active [123, 222, H. Ducklow, pers. comm.]. Bacterial density is positively correlated with chlorophyll concentration in the Chesapeake Bay [222] and elsewhere [9]. Data are not available to determine if phytoplankton composition directly influences bacterial metabolism, but indirect effects are potentially significant, as that proportion of primary production not consumed or assimilated by grazers is available to support bacterial production. The magnitude of the spring bloom is sufficient to account for development of summer anoxia in the Chesapeake Bay, where bacterial abundance is a good predictor of oxygen concentration in the water column [222]. Thus, shifts in pelagic trophic structure toward

dominance by inedible or less desirable phytoplankton do not necessarily serve as a nutrient buffer, but rather may divert the flow of energy from "higher" trophic levels to the microbial food web.

In addition to utilization of dissolved oxygen, the production of new biomass by bacteria has significant implications for the structure of pelagic communities. Observations of relatively constant bacterial biomass despite rapid growth rates [47, 162, 244], which suggests that bacterial production is approximately balanced by losses to microzooplankton, form the conceptual basis for a microbial food web [5, 161]. Experimental studies indicate that bacterial mortality is mostly due to predation by heterotrophic nanoplankton, primarily colorless flagellates [2, 48, 82]. Other components of the heterotrophic nanoplankton, such as heterotrophic dinoflagellates, feed primarily on eucaryotic cells. Field investigations showed that the dynamics of nanoplankton were coupled to those of bacteria, albeit lagging by a few days [3], suggesting that the heterotrophic nanoplankton were initially resource-limited. The abundance and production of bacteria in the Chesapeake Bay imply that heterotrophic nanoplankton may not be food-limited, at least during the late spring and summer, indicating that this trophic link may be significant. This conclusion may require modification to the extent that small phytoplankton are an important component in the diets of heterotrophic nanoplankton [76, 152, 214]. Phototrophic nanoplankton are abundant in the Chesapeake Bay; however, the previously discussed uncertain food quality of many of these cells may limit their contribution to the diets of heterotrophic nanoplankton.

The role of nanoplankton in the development of anoxia may be especially important. As noted above, field studies have demonstrated a strong relationship between bacterial abundance and oxygen consumption. The latter measurement includes respiration by all plankton, most of which are assumed to be bacterial. Laboratory experiments have demonstrated that the contribution of colorless flagellates to oxygen consumption, carbon mineralization, and nutrient regeneration may equal or exceed that of bacteria [1, 29, 75]. Assuming that an average nanoplankton, approximated by a 4-μm sphere, respires at a mean rate of 2.7×10^{-5} nl O_2 μm^{-3} h^{-1} [29], a community of nanoplankton present at 5×10^6 cells/l [47, 241] would consume 0.1 ml $O_2 l^{-1}$ d^{-1}. The closeness of this value to measured utilization rates in the Chesapeake Bay [142, 215] suggests that an operational microbial food web, rather than simply bacterial metabolism, may be responsible for the onset of anoxia. This hypothesis, however, has not been experimentally tested in the field.

Ciliates

Planktonic ciliates also prey on bacteria [175, 220], but their primary role is thought to be as grazers of photosynthetic [73, 236] and heterotrophic [3, 196] nanoplankton. Ciliates are a food source for suspension and filter feeders ranging from other ciliates to adult menhaden (see summary in [239]), and this trophic connection was hypothesized to be a significant pathway influencing the recruitment of larval fish [154]. In this regard, network analysis suggests that food passing through ciliates is an important component in the diet of striped bass in the Chesapeake Bay [6]. There is a paucity of information on the abundance and temporal distribution of both protozoan and metazoan microzooplankton in the Bay [21], although limited data suggest abundant ciliate populations in spring and summer [190]. The arguments concerning the effects of food quantity and quality on heterotrophic nanoplankton production in the Bay are equally applicable to ciliated protozoans. The growth and production rates of ciliates in Narragansett Bay over an annual cycle were strong functions of the quantity and size distribution of phytoplankton [237, 239]. In comparison, chlorophyll concentrations and production of nanoplankton appear to be higher in the Chesapeake Bay [128, 235], so that limitation of ciliate production by food quantity may be less significant. In Narragansett Bay, however, food quality was a major factor regulating the structure and abundance of ciliate populations, and it is likely to be important elsewhere.

When abundant, ciliates can be a significant source of nutrition for copepods [176, 221] and fish larvae [92], especially when edible or preferred food is scarce. They are also a critical food source during the development of larval ctenophores, and represent an important component in the diets of adult ctenophores and coelenterate medusae when stocks of macrozooplankton are low [209, 211]. This trophic relationship is consistent with the coincident importance of small phytoplankton and gelatinous predators in the Chesapeake Bay, and provides a documented mechanism in support of the hypothesized dominance of ctenophores and coelenterate medusae under such conditions.

Crustacean Zooplankton

Copepods generally dominate crustacean zooplankton communities in estuaries [21, 24], although cladocerans may be seasonally important. Both groups, particularly copepods, depend on phytoplankton for their primary nutrition; bacteria are too small for copepods to collect efficiently [11]. Thus changes in phytoplankton production and community composi-

tion represent the major source of potential food limitation. Field studies in Narragansett Bay [55], Puget Sound [115], and the Southern California Bight [33] indicate that copepods are often food-limited. Because the quantity of daily primary production in these waters far exceeds the copepod's requirements, the poor quality of food is generally implicated. Specifically, ingestion of nutrient-limited phytoplankton [34], interference by or low nutritional value of non-living suspended particulates [177], and occurrence of toxic or inedible species [94] are thought to contribute to food limitation .

In contrast, elevated nutrient levels in the Chesapeake Bay imply that phytoplankton should be in excellent physiological state for much of the year, except perhaps during the collapse of the spring diatom bloom. Contemporary levels of suspended sediment in the Bay do not significantly interfere with copepod feeding [191]. Comparison of present chlorophyll concentrations (which may be similar to those in previous years [123, 128, 192, 235]) with egg production rates of *Acartia tonsa* [55] suggests that the quantity of phytoplankton may not limit macrozooplankton production. These considerations imply a nutritionally satisfactory environment for crustacean zooplankton in Chesapeake Bay. Comparisons with 20 years ago indicate a possible increase in zooplankton standing stocks in the Patuxent River [24], but it is unknown whether these data are representative of the entire Bay. Moreover, the different techniques of data collection preclude definitive conclusions of historical trends in zooplankton abundance. Indeed, copepod production in the Chesapeake Bay may be food-limited because of the poor nutritional value, small size, toxicity, or low preference for the dominant phytoplankton species. The most abundant copepods in the bay, *Acartia tonsa* and *Eurytemora affinis*, do not actively feed on the dominant co-occurring dinoflagellates and avoid vertically migrating populations [193]. Blooms of inedible dinoflagellates have been implicated in regulating copepod populations in Swedish waters [118], and may be similarly influential in the Chesapeake Bay.

Gelatinous Zooplankton

Ctenophores and coelenterate medusae are generally the most abundant gelatinous zooplankton in estuaries. Characterized by voracious appetites and rapid growth rates [166, 171], these organisms are capable of decimating prey populations. This aspect is discussed in detail in the next section. These organisms, however, have high metabolic rates that require a constant food supply, and they lack storage reserves; thus they are very susceptible to food limitation. Elsewhere, the seasonal disappearance or collapse of blooms of both medusae and ctenophores has been attributed to starvation [94, 135]. In the Chesapeake Bay, ctenophores *(Mnemiopsis)* and scyphomedusae *(Aurelia, Chrysaora)* co-occur and dominate gelatinous zooplankton communities in spring and summer [21, 23, 60]. All three species prey on crustacean zooplankton as adults, but *Chrysaora* also eats *Mnemiopsis* and other gelatinous organisms [27, 36, 133], indicating that food limitation, competition, and predation may interact to regulate their population dynamics. In one study [60], the mid-summer decline in ctenophores coincided with low levels of crustacean zooplankton and increasing concentrations of *Chrysaora*, implying regulation from above and below. *Chrysaora* declined after the collapse of its primary food sources, ctenophores and copepods. This seasonal appearance and disappearance of gelatinous zooplankton was likely influenced by several factors in addition to food limitation, but the availability of food may be a strong determinant of standing stocks. In Narragansett Bay, interannual variations in the seasonal biomass of ctenophores was significantly correlated with the standing stocks of crustacean zooplankton: years with large zooplankton populations were also years with large ctenophore populations [49]. If this correlation is applicable to the Chesapeake Bay, the possible increase in copepod biomass during the past 20 years could support larger populations of gelatinous zooplankton. Quantitative data are not available to evaluate this hypothesis.

Teleosts

The considerable motility of fish compared to plankton complicates evaluation of the potential role of resource limitation in structuring fish communities. Moreover, abundance data are generally derived from commercial statistics, which must be adjusted for fishing effort to resolve historical trends. Finally, there is the uncertain relationship of parental stock size to larval survival and recruitment. Cushing [40] and Lasker [116], among others, give detailed consideration to these processes. A few relevant points are offered here on the role of environmental and nutritional influences in the success of three important fishes in the Chesapeake Bay: menhaden, anchovy, and striped bass.

First-feeding menhaden larvae prey visually on individual dinoflagellates and ciliates [208]. They select larger prey as they grow, concentrating on crustacean zooplankton [103]. Development of gill rakers upon metamorphosis permits switching by juveniles to a filter-feeding mode that retains phyto-

plankton cells as small as 7-8 μm [67]. Cells of 2-8 μm are also collected, but with very low efficiency [35, 67]. Larger adults remove particles ranging in size from 16 μm to 1200 μm with increasing efficiency; cells much smaller than 16 μm are not retained [54]. Their feeding is linked to zooplankton and larger species of phytoplankton, i.e., to particle size rather than concentration. In contrast, the survival of first-feeding larvae depends upon encountering sufficient numbers of dinoflagellates and ciliates during the critical first few days. Copepod nauplii may also be important in larval nutrition by providing a rarer but considerably larger ration (E. Houde, pers. comm.), as they do for growth of ctenophore larvae [211]. Spatial variability in prey composition and concentrations is likely important, as adults spawn and larvae develop predominantly outside the Chesapeake Bay. The apparent historical increase in menhaden stocks within the Bay, supported by both catch statistics and juvenile indices [63], suggests that good conditions exist for all life history stages, perhaps due to the increased standing stocks of both phytoplankton and zooplankton, and to the ability of juveniles to utilize detritus [117]. In the tributaries of the Chesapeake Bay and North Carolina, the abundance of juvenile menhaden was highly correlated with that of diatoms and microflagellates, but poorly correlated with large dinoflagellates and cyanobacteria [66]. These data suggest that menhaden have specific prey preferences and use chemical cues associated with phytoplankton to alter their distribution patterns.

Bay anchovies are zooplanktivores throughout their lives [52] and are therefore dependent on factors regulating the abundance of crustacean zooplankton. Zooplankton stocks, if they have increased with eutrophication, could support larger populations of anchovies. Anchovies have declined in certain portions of the Bay [63], but long-term trends have not been documented Bay-wide. The major period of spawning, May through August [145], coincides with the annual maximum in copepod biomass [24, 87], but also with the maximum abundance of gelatinous zooplankton. Independent of possible predation on larvae by gelatinous zooplankton, the similarity in their food preferences suggests that interannual variations in anchovy stock size might be inversely related to the biomass of gelatinous zooplankton because of competition for food. This hypothesis is speculative and awaits experimental investigation.

Juvenile and adult striped bass are piscivorous, while larvae feed on crustacean zooplankton. Field surveys have implicated food density in influencing the survival of larvae [108, 194], and significant positive correlations have been found between biochemical indices of nutritional state and the abundance of copepods and cladocerans [126]. These relationships may be coincidental, but greater survival of larvae would be expected if zooplankton densities have increased accompanying eutrophication. Recent laboratory experiments have suggested that striped bass are more prey-insensitive than many fish larvae, and contemporary plankton concentrations in Chesapeake Bay tributaries appear to be sufficient to support good survival of larvae (E. Houde, pers. comm.). Adult populations have decreased in recent years, apparently because of diminished spawning stocks or poor survival of juveniles [78]. This declining trend may partially reflect loss of deep-water habitat space for adults, caused by anoxia, and loss of shallow-water habitats for juveniles, due to declines in submerged aquatic vegetation [39, 165]. Thus, paradoxically, conditions that may promote survival of larvae (enhanced primary and secondary production) may indirectly contribute to declines in parent stocks.

SINK CONTROL

The previous section considered the role of resource limitation in structuring pelagic food webs. Where limitation of growth rate is less significant, predation may be a major process regulating population abundance. Predators ranging in size from small protozoan grazers to large vertebrate carnivores have specific preferences for prey, implying that selective predation influences the species composition of prey communities. Thus changes in the magnitude and distribution of predation pressure can alter the structure of pelagic food webs. "Feeding is such a universal and commonplace business that we are inclined to forget its importance. The primary driving force of all animals is the necessity of finding the right type of food and enough of it" [56].

The nature of predation in marine ecosystems has generally been investigated as limited trophic interactions, e.g., jellyfish preying on fish larvae, copepods preying on diatoms. Armed with such data, investigators have used theoretical and deterministic models to examine the roles of various trophic levels in structuring marine food webs [112, 203], often concluding that "observed changes in ecosystem structure may be caused as much by changes at higher trophic levels as by environmental factors" [205]. The extent to which pelagic trophic structure in marine ecosystems is regulated by primary production, herbivory, or predation remains uncertain [114, 204].

In contrast, cascading trophic interactions induced by predation have been proposed as a dominant force

regulating freshwater ecosystems [31]. Case studies in artificial pools [96], lake enclosures [121], reservoirs [8], and the Great Lakes [20] have consistently shown that addition of piscivorous fish (or removal of planktivorous fish) results in increased zooplankton populations, reduced phytoplankton biomass, and increased optical transmission in the water column. Conversely, removal of piscivores leads to an increase of planktivores, which results in decreased zooplankton biomass, enhanced phyto-plankton, and reduced water clarity.

The superficial similarity between the latter scenario and the present status of the Chesapeake Bay implies that cascading trophic interactions induced by predation may be operating in the Bay. Evaluation of this hypothesis is complicated, however, by apparent discrepancies and inadequate data bases. For example, zooplankton populations do not appear to have declined, and may actually have increased in response to the higher phytoplankton biomass accompanying eutrophication. This apparent trend conflicts with cascading trophic theory; but it agrees with observations that top-down regulation of lower trophic levels weakens as productivity increases, and is supplanted by bottom-up control [130]. The effects of predator control and nutrient addition on trophic structure are independent, but may be synergistic [4, 20, 121]. *Acartia tonsa,* which remains the dominant copepod in Chesapeake Bay, is particularly well-adapted to utilizing productive estuaries [55, 87]. The enhancement of *Acartia* dominance by elevated nutrients [68] suggests that losses to predators may become less significant because of increased growth under more eutrophic conditions. The potential role of predation in structuring other components of pelagic food webs in estuarine systems is considered below.

Teleosts

The relative importance of source and sink controls in driving changes in marine piscivorous and planktivorous fish stocks is uncertain. For example, stocks of striped bass have decreased in the Chesapeake Bay and along the entire Atlantic seaboard [12]. The Bay is a major spawning and nursery area, and the decline has been attributed to reduced spawning stocks or first-year survival [78]. The relative contributions of environmental stress [165] and fishing mortality [78] have not been resolved, although previous collapses in pelagic fisheries were attributed to environmental and climatic changes [40]. Interestingly, all major anadromous fish stocks have declined in recent years, while recruitments of marine-spawning stocks have increased or fluctuated with little apparent long-term trend [63]. These data suggest that aspects of water quality or resource control within the Bay may be more important in determining stock sizes than cascading trophic interactions. The theory of top-down control predicts that larger menhaden stocks should accompany the collapse in striped bass. Menhaden abundance has increased, but much of the increase has been attributed to reduced fishing mortality. Provocatively, other predators on menhaden, such as bluefish and weakfish, have increased in abundance concurrently with their prey. This relationship implies that resource control may be dominant even at the top of the food web. Irrespective of the cause, the increase in forage fish has significant implications for the Chesapeake Bay. Additional evidence suggests that predation may substantially affect pelagic trophic structure, and these data are summarized below.

Adult menhaden preferentially collect large phytoplankton cells and zooplankton [54] and filter nanoplankton inefficiently. If the elevated primary production in the Chesapeake Bay is chiefly due to small cells, then apparent increases in menhaden stocks [63] may reflect processes such as reduced predation on adults or increased survival of recruits. The increase in menhaden stocks along the entire Eastern seaboard is at least partially due to reduced fishing mortality. The increase might be even greater if present fishing effort were not focused on fish aged 0-1 year (E. Houde, pers. comm.). In Narragansett Bay, the occurrence of menhaden schools is associated with reductions in phytoplankton biomass (and oxygen concentration) and increases in NH_4 [148]. Thus, adult menhaden theoretically contribute to the dominance of nanoplankton by removing large cells and herbivores, while releasing nutrients that support the continued growth of small cells. The effects of juveniles [67] may partially ameliorate size-selective predation pressure. The potential importance of menhaden predation in the Chesapeake Bay was underscored by McHugh [129], who calculated that, if all the menhaden landed annually were present at one time, they could filter a volume of water equivalent to the Virginia portion of the Bay in 12 hours.

In a simulation model of Narragansett Bay [112], menhaden exerted a controlling influence on food web stability, particularly in damping herbivore-phytoplankton interactions. Increases in menhaden stocks caused reductions in zooplankton populations, leading to larger phytoplankton standing stocks. Menhaden schools allowed to migrate freely around the Bay, seeking the highest food concentrations, depleted the zooplankton stocks by the end of each day. Mixing from adjacent areas was almost sufficient to replenish the zooplankton stocks. A provocative observation

was that the menhaden in the model avoided areas with abundant ctenophore populations. Although similar models have not been constructed for the Chesapeake Bay, these observations suggest that interannual variations and long-term changes in menhaden stocks may significantly alter the abundance, size distribution, and spatial patterns of phytoplankton and zooplankton communities.

Benthos

From the perspective of top-down control, benthic suspension feeders are potentially capable of translocating significant quantities of organic matter from the water column to the sediment, and may be a major factor regulating plankton populations in certain regions [43]. Garber [72] and others [14, 109, 140] have discussed the seminal role of benthic-pelagic coupling in influencing water column processes. The regulatory nature of benthic grazing has been demonstrated in mesocosms [53] and implicated in North and South San Francisco Bay and in Pamlico, Core, and Bogue Sounds [37, 138, 144]. Oyster reefs [42] and mudflats dominated by blue mussels and soft-shell clams [28] removed significant quantities of phytoplankton during tidal excursions.

Environmental conditions over much of the shallow flanks and in the tributaries of the Chesapeake Bay meet the criteria required for benthic control of plankton populations [144]. For example, suspension-feeding by recently-settled meroplanktonic larvae was estimated to remove 70-100% of particles in a 7-m water column in June during 1978-1980 [85]. In the Potomac River, a mid-stream depression in phytoplankton biomass was correlated with high densities of the Asiatic clam, *Corbicula* [38]. Experimental and field abundance data indicated that *Corbicula* could filter the volume of water contained in the phytoplankton "sag" in three to four days, suggesting that benthic grazing was responsible for the removal of phytoplankton.

In the Bay proper, Malone et al. [123] observed distinct differences in primary production and phytoplankton biomass along lateral transects in 1984. High productivity and low standing stocks of phytoplankton, coupled with an apparent absence of planktonic suspension feeders, suggested that benthic grazing may have controlled phytoplankton biomass along the eastern shore, where dense aggregations of oysters occurred. Much of the mainstream of the Bay appears to be too deep for benthic grazing to exert substantial influence on water column structure. Moreover, the shallow flanks apparently experience frequent exposures to hypoxic and anoxic waters via lateral displacements of the pycnocline [123, 192], which could reduce their grazing impact. Thus benthic regulation of planktonic abundance and composition is likely to exhibit considerable spatial and temporal variability.

In the past such effects may have occurred over larger spatial areas, as oyster populations in the early 1900's may have been capable of filtering a volume equivalent to the entire bay in three days [106]. Current estimates suggest that the oyster population may be ≤4 million bushels, compared to 80 million bushels as recently as 1985 [183, cited in 222]. Oysters prey primarily on phytoplankton of 1-10 μm in size [84, 245], indicating that their collapse might have contributed substantially to the current dominance of nanoplankton in the Chesapeake Bay. While speculative, such an effect would be exacerbated by the selective removal of large phytoplankton and zooplankton by menhaden.

Gelatinous Zooplankton

Gelatinous zooplankton are notorious predators that can rapidly crop prey populations. In estuaries, the dominant ctenophores and medusae both ingest fish larvae [36, 167, 233], although this is particularly well-documented for medusae such as *Aurelia* [134, 234]. In Mississippi Sound, ctenophores were reported to ingest larval menhaden and anchovies [158]. The most frequently documented predation, however, is on crustacean zooplankton, which has significant implications for other trophic levels. Predation by gelatinous zooplankton may drastically reduce stocks of crustacean zooplankton, resulting in diminished survival of fish larvae and reduced recruitment of herring [133], plaice [81], haddock [65], and salmon [153]. Other investigations have demonstrated that predatory removal of zooplankton by leptomedusae [94], scyphomedusae [118, 132], and ctenophores [49] reduces grazing pressure on phytoplankton and results in their blooms. Thus, in other estuarine systems [49, 113], interannual variability in stock sizes of gelatinous zooplankton regulates the dynamics of organisms one or more trophic levels removed. Changes in phytoplankton and zooplankton composition may also accompany variations in the abundance of gelatinous predators [71, 134].

In the Chesapeake Bay, the ctenophore *Mnemiopsis* and the medusae *Chrysaora* and *Aurelia* are the dominant gelatinous zooplankton. Calculations based on laboratory feeding rates and field abundances suggest that ctenophores may remove a substantial fraction of copepod production in the Bay [10, 23]. In other estuaries, where they have few natural predators

or predation pressure on them exhibits significant interannual variability [49, 135], there are extensive oscillations in the abundance of herbivores and phytoplankton. In the Chesapeake Bay, *Chrysaora* predation on ctenophores and other, presumably young, medusae such as *Aurelia* (cited in [36]) induces seasonal fluctuations in community structure suggestive of alternate control by food limitation and predation [60]. In that study, increasing densities of *Mnemiopsis* and *Aurelia* were associated with decreasing crustacean zooplankton and higher phytoplankton stocks, presumably reflecting predation and release from grazing, respectively. Declines in *Mnemiopsis* and *Aurelia* coincided with pulses of *Chrysaora*, resulting in rebounds of herbivore populations, which then reduced phytoplankton biomass. *Chrysaora* collapsed after the decline of its prey populations, suggesting starvation. Predation by butterfish and harvestfish on *Chrysaora* and ctenophores, although not quantified in the Chesapeake Bay, may be significant there and elsewhere [124, 150]. Predation by the atentaculate ctenophore *Beroe* on *Mnemiopsis* may also be important in the lower Bay [23].

There is another mechanism, in addition to regulation of prey abundance, by which gelatinous zooplankton may affect pelagic trophic structure. Growth efficiencies of ctenophores are <10% [171], and those of medusae are likely similar in view of their low carbon content [197]. The bulk of their assimilated food is required for energy metabolism, and therefore much of their particulate ration is returned to the water column in the form of regenerated nutrients. Phytoplankton production is enhanced directly by this remineralization and indirectly by removal of herbivores. Mass mortality of medusae apparently occurs after spawning; it may also be related to starvation or declining temperatures in autumn [60, 124]. This input of biomass, plus that derived from enhanced primary production, was implicated as the cause of repeated anoxia in Swedish waters [118], and may possibly contribute to hypoxia or anoxia in the Chesapeake Bay. Quantitative, long-term data on standing stocks of gelatinous zooplankton are required to address this hypothesis.

These studies suggest that predation by gelatinous zooplankton may have significant implications for the structure of pelagic communities in the Chesapeake Bay during the summer months, a possibility supported by network analysis [6]. In addition to cascading effects caused by changes in abundance, predation may substantially affect recruitment of oyster larvae. Strong inverse correlations were reported between interannual variations in oyster spat set and ctenophore abundance in Barnegat Bay [137]. The guts of ctenophores there contained an average of 14 larvae, which is equivalent to daily ingestion of 168-336 larvae/ctenophore, using gut residence times of 1-2 hr [169, 212]. This calculation assumes constant feeding, which is probably valid since wild animals consume more food in situ than is predicted from estimates of clearance rate and apparent food concentration [212]. They do not necessarily feed constantly, but apparently find adequate food. The mean summer concentration of larvae in the Choptank River over a two-year period was 12 larvae/liter (range 2-55 [187]), or 12×10^3 m^{-3} The average concentration of ctenophores during their blooms is 10-100/m^3 [113, 131]. At lower abundances, ctenophores might ingest 14-28% of the standing stock of larvae each day. Higher but still ecologically relevant densities could rapidly eliminate oyster larvae and thus dramatically affect oyster spat set. These data, if representative of the Chesapeake Bay, suggest that the coincident occurrence of large populations of gelatinous zooplankton and reduced oyster stocks [63] may not be accidental.

Interannual variability in the density of oyster spat is positively correlated with salinity [230], resulting in the prediction that oyster spat sets would be poor in years of low salinity. Low salinity also induces cyst formation and mortality in the polyp stage of the sea nettle *Chrysaora* [26, 27], whose abundance as adults appears negatively correlated with streamflow (D. Cargo, pers. comm.). Since sea nettles are hypothesized to be major predators on ctenophores, and ctenophores may be significant predators on oyster larvae, there is the provocative implication that the positive relationship between salinity and oyster set may be stimulated by predator-prey interactions. Moreover, the decline of oysters may contribute to the dominance of nanoplankton, which is postulated to favor gelatinous zooplankton through an enhanced microzooplankton food web. These relationships remain to be documented, but they suggest that, once initiated, biological feedback may serve to reinforce changes in pelagic trophic structure.

Crustacean Zooplankton

Understanding of the potential role of copepods and other crustacean zooplankton in structuring pelagic food webs has recently undergone a conceptual revolution. An enlarging body of evidence indicates that herbivorous zooplankton do not use simple mechanical means to collect food particles, but that they use complex mechanosensory and chemosensory behavior to identify, select, capture, ingest, and reject individual prey items [151, 164]. Such

selective grazing may regulate the size structure of plankton communities [205]; it also has significant implications for, and is dramatically influenced by, species composition of the phytoplankton. *Acartia tonsa* is the major crustacean grazer in the meso- and polyhaline portions of the Chesapeake Bay during the summer [87]. It apparently prefers large particles, gradually switching to small ones as those are removed [173]. However, the smallest particle that it can collect is 3-5 μm [139]. Thus the grazing activities of *Acartia* remove large cells and regenerate nutrients to enhance the growth of competing nanoplankton, promoting their dominance of phytoplankton communities during the summer [128]. In addition to modifying the size distribution of phytoplankton, selective grazing by *Acartia* and other zooplankton may alter phytoplankton species composition. Lack of feeding on, or direct avoidance of, certain dinoflagellates [193] and microflagellates [218], combined with selective predation on other edible species, may contribute to development and maintenance of monospecific phytoplankton blooms [95]. These accumulations of algae, if ungrazed, may eventually fuel continued anoxia. In addition, the documented regulation of crustacean zooplankton by gelatinous zooplankton suggests that interannual variability or long-term changes in the abundance of ctenophores and jellyfish may influence the structure of phytoplankton communities.

Protozoan Zooplankton

Ciliates and heterotrophic nanoplankton are both capable of growth rates faster than those of their prey [7, 30], implying that their in situ population dynamics are controlled by predation. In agreement with these theoretical considerations, laboratory and field studies have demonstrated that predation by ciliates regulates nanoplankton abundance [3, 168], while grazing by nanoplankton controls bacterial numbers [48, 119]. The applicability of these conclusions to the Chesapeake Bay is uncertain because of the paucity of data on these protozoans [21]. Preliminary calculations based on radiolabel experiments and abundance data suggest that microzooplankton (excluding heterotrophic nanoplankton) may remove 13-55% of phytoplankton biomass during the spring and summer [190]. Similar data are not available for heterotrophic nanoplankton, but grazing rates (200 bacteria nanoplankton^{-1} hr^{-1} at ecologically relevant densities (2×10^3 nanoplankton ml^{-1}) suggest potential removal of 10^7 bacteria ml^{-1} d^{-1}, which approximates the standing stock [123]. Clearly, predation by ciliates and heterotrophic nanoplankton may significantly affect the abundance of their prey, and modeling efforts support this hypothesis in the Chesapeake Bay [6].

Elsewhere, grazing by microzooplankton also influences seasonal variations in the size structure of phytoplankton [238] and bacterial [220] communities. Moreover, ciliates can regulate the timing and magnitude of dinoflagellate blooms in coastal New England embayments [242]. Although similar data do not exist for the Chesapeake Bay, the apparent availability of underutilized dinoflagellate populations in the Chesapeake Bay provides a substantial food source for microherbivores, whose grazing may reduce the contribution of such blooms to anoxia. The growth efficiencies of ciliates and heterotrophic nanoplankton, however, indicate that a large proportion of ingested food is remineralized [75, 236]. Since bacteria are efficient competitors with phytoplankton for nutrients [18], an abundant and active microbial food web may function to sequester and recycle nutrients.

Thus, each marine pelagic trophic level is implicated in regulating the abundance and structure of one or more adjacent levels. The theory of cascading trophic interactions predicts that changes at higher trophic levels should be transferred sequentially to lower levels. This "domino effect" has recently been demonstrated, in freshwater enclosures, to extend from fish to bacteria [174]. The addition of planktivorous fish reduced crustacean zooplankton, resulting in higher phytoplankton biomass. Release of dissolved organic carbon by algae stimulated bacterial productivity and biomass, which supported elevated populations of heterotrophic nanoplankton. Provocatively, nutrient additions, which had no direct effect on fish and crustacean zooplankton, further stimulated primary production and hence bacterial production, resulting in even higher biomass of bacteria and heterotrophic nanoplankton. These results, if applicable to more complex marine ecosystems, suggest that eutrophication and a collapsed predator base, whether visualized as diminished piscivore stocks or reduced fishing effort on planktivores, may *both* be driving changes in the pelagic trophic structure in Chesapeake Bay.

LONG-TERM CHANGES AND PATTERNS

Changes are discerned by comparing differences over time, with more data or longer periods conferring greater significance or certainty in describing a trend. The time period over which changes are effected is proportional to the generation time of the pertinent organism, with larger organisms integrating over longer periods. Thus, changes from the bottom up

and from the top down will interact on different time scales to determine pelagic trophic structure. The potential effects of eutrophication have been considered throughout this review, because of documented effects on food web interactions and ample data demonstrating nutrification in the Chesapeake Bay; however, other long-term changes, principally those in climatic patterns, significantly affect trophic structure and likely are integrated with changes induced by eutrophication.

Climatic changes over large spatial and temporal scales have been recognized for some time [216]. Of these, changes in temperature and solar radiation appear to have the greatest impact on pelagic communities. For example, steady declines in incident irradiance due to increased cloud cover over the Northeast Atlantic Ocean from 1948 to 1965 were responsible for progressive delays in the inception of the spring phytoplankton bloom [41]. Similar, more recent meteorological events (e.g., the "dark decade" of the 1970's [202]) may also have influenced the timing and magnitude of phytoplankton blooms.

Long-term data sets show a consistent pattern of declining temperatures during the late 1800's, followed by increasingly warmer years from ca. 1905 to 1950, and decreases again from 1950 to the late 1960's. These trends occurred in the waters of the Chesapeake Bay [16], Narragansett Bay [99, 202], and the Gulf of Maine [213], and appear to be representative of the eastern seaboard [216] and perhaps the entire northern hemisphere [41].

Such climatic variability is associated with substantial changes in the timing, magnitude, and duration of phytoplankton blooms and zooplankton responses [41, 202]. Perhaps more important, significant alterations in community structure of both groups accompany these climatic patterns. Fluctuations in recruitment and year-class strength of planktivorous and piscivorous fish, particularly clupeids, may be related to climatically-driven changes in their food supply [41]. Interannual variations in the yield of commercial fisheries have been linked to long-term fluctuations in the physical environment [213]. Climatic changes may also influence commercial stocks in the Chesapeake Bay [228], although potential relationships are complicated by long-term trends in fishing effort. The mechanisms proposed to account for these biological responses include the match or mismatch in timing of predator and prey populations [41], and changes in dominance between subordinate and dominant organisms due to intraspecific and interspecific competition [199]. Evidence suggests that both mechanisms are likely operational. Interannual variability in sea surface temperatures may have altered the structure of predator communities on the Scotian Shelf, where unusually warm years were associated with increased overwintering survival of ctenophores, whose depredation of zooplankton stocks was hypothesized as the agent of extensive mortality of haddock larvae [65]. Increased occurrence of dinoflagellate blooms and shifts in dominance from fish to gelatinous predators have also been attributed to climatic fluctuations [118]. Thus long-term changes in the physical environment may be responsible for driving complex changes in pelagic trophic structure, and must be considered when evaluating biological trends and their significance.

SUMMARY AND IMPLICATIONS

Clearly, there is no simple answer to the question implicit in the title of this article. The nutrition of one organism requires the death of another. In the absence of predation, a population is eventually limited by resource availability, and the decline is seldom gradual. Predation acts to minimize such oscillations. In the century since Darwin identified the mechanisms behind the origin of species, research has resolved a number of details concerning relationships among organisms. We still do not know, however, how food webs are structured [127]. The available data on marine ecosystems indicate that pelagic trophic structure in estuaries is a synergistic product of source and sink control. Attempts to model the structure and function of pelagic trophic levels in the Chesapeake Bay [6, 229] and elsewhere [112, 205] have identified potentially important linkages and controlling mechanisms. Consideration of the relationship between the temporal scales of change and the size-dependent generation times of organisms suggests that the relative importance of predation and resource limitation shifts continually in response to perturbations in an unstable environment, seasonality in physical forcing functions, and system productivity. In the Chesapeake Bay, the crash of the spring diatom bloom may indicate a lack of predation control at that time. In contrast, the resulting high production but constant biomass of bacteria implies significant control from above. Over longer time scales, the apparent increase in menhaden stocks suggests diminished effects of both resource limitation and predation.

Human activities perturb both mechanisms, and these perturbations apparently act in concert and may be autocatalytic (see Figure 1). From below, nutrification enhances primary production. From above, predation, disease, and anoxia decimate oyster popu-

lations, while decreased fishing effort, reduced anadromous piscivore stocks, and increased food availability promote menhaden stocks. These changes may alter trophic structure by size-selective stimulation of nanoplankton growth in excess of sufficient regulation. This shift to small plankton, combined with enhanced bacterial production, apparently supports an active microbial food web that retains and shunts nutrients away from the "traditional" predators.

Such an ecosystem off balance may select for gelatinous zooplankton as important top carnivores. Paradoxically, their growth efficiencies are so low that they would seem to be trophic cul-de-sacs. It remains uncertain whether their hypothesized relationship with nanoplankton food chains is supported experimentally and, if so, whether it reflects cause or effect. Once the dominance is established, however, the food preferences and metabolic rates of ctenophores and coelenterate medusae appear to reinforce their predominance. As significant predators and inconsequential prey, perhaps they represent a cybernetic response by an ecosystem attempting to restore stability [120]. Much more information is needed to fully understand their role in system energetics.

These general conclusions rely heavily on inference and emerging new ideas rather than rigorous scientific examination, and are best viewed as hypotheses. Three questions are particularly salient and appear amenable to field examination in a testing ground such as the Chesapeake Bay: (1) Do long-term changes in the concentrations and ratios of nutrient supplies cause changes in phytoplankton species composition? (2) Are cascading trophic interactions significant in structuring estuarine communities? (3) Does the relative importance of source vs. sink control vary as a function of productivity? Clearly, these questions are at the core of understanding the processes responsible for structuring pelagic food webs and thus the steps necessary to restructure and properly manage the Chesapeake Bay. Addressing these questions requires substantially more information on several specific trophic links. In addition to the absence of information on gelatinous predators, two other food web components require further investigation.

The potential importance of bacteria and the associated microbial food web is now well established, but relatively little is known about its function (i.e., as a link to higher trophic levels or as a nutrient sink), its importance in processing cyanobacteria and phytoflagellate production, its relationship to metazoan food webs, and its role in maintaining or promoting the establishment of ctenophores and medusae as significant carnivores. Does the role of the microbial food web vary seasonally and spatially, and are its effects amplified or minimized by changes in nutrient supply and predator structure?

Fisheries is another component of pelagic food webs for which there is inadequate information. Studies in fresh water suggest that cascading trophic interactions can structure pelagic food webs through predation, and that adequate stocks of top piscivores can ameliorate the effects of eutrophication. To evaluate these relationships in estuarine environments, we will need data on the forage base and food habits of predators, age and growth studies of prey, predator-based mortality data, and fishery-independent stock assessments.

Several of these represent generic research needs, but they are particularly applicable to understanding processes regulating food webs in the Chesapeake Bay. The biota of the Chesapeake Bay represent a balance, however tenuous, between those that would prosper under "pristine"'or natural environmental conditions, and those whose tolerances encompass effects due to anthropogenic inputs. This suite of organisms and their interrelationships will change with continuing human modification of the environment. This review indicates the difficulties in ascribing cause and effect in the absence of long-term, quantitative data. As management of the Bay proceeds, a unique opportunity exists to study and document the interactive effects of the physical and physiological factors that drive changes in pelagic trophic structure. This will require a multi-faceted approach incorporating data collection and modeling. The Bay is very large and chemically, physically, and biologically diverse. Previous studies have demonstrated that results from one portion of the Bay may not be valid in other portions. Part of the challenge for the future is to continue documentation of spatial and temporal variability, as exemplified by Malone et al. [123]. Intensive field sampling and in situ experimentation should be conducted on pertinent temporal and spatial scales to determine biological responses to environmental variation. Bay-wide monitoring programs should be continued to provide the long time series of data necessary to identify the cause and significance of trends. Finally, these efforts should be coupled to multitrophic level studies (e.g., mesocosms) and simulation models to test hypotheses in detail. This approach will require a substantial funding and management commitment; however, it will quantify the functional relationships between nutrient supply and fish production, and increase our understanding of, and therefore our ability to predict changes in, the factors that regulate pelagic trophic structure.

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Physical Processes that Control Circulation and Mixing in Estuarine Systems

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INTRODUCTION

The Chesapeake Bay and its tributary rivers form the largest and most productive estuarine system in the continental United States. The Bay stretches 315 km from the Susquehanna River south to Norfolk, VA. At a depth of 20 m the average width is 3.5 km, while at 10 m the width varies from 5 to 20 km. The Bay's general circulation has been studied over the past 35 years by means of short- to long-term current meter moorings, tide gauges, wind observations, surveys of water column properties, and dye tracing studies [15, 20, 59, 61, 85, 86].

The physical processes driving the circulation and stratification in a partially stratified estuary, such as the Chesapeake Bay, can be classified according to three time scales [10]: (1) seasonal processes (time scale larger than a month); (2) short-term processes (time scale of a tidal period to a month); and (3) short-period, small-scale mixing processes (time scale less than a tidal period). Seasonal and short-term processes control horizontal distribution, transport, and diffusion of water properties, while small-scale mixing processes dominate the vertical exchanges of properties across the pycnocline (density step between two layers of different density).

Solar heating and fresh water inflow drive the seasonal processes that generate the general, two-layer estuarine circulation and the mean stratification [60, 61]. In turn, this circulation controls the subsurface, longitudinal transport of nutrients and non-motile organisms [81, 82]. The strength of the mean stratification created by solar heating and freshwater inflow affects the amount of vertical mixing between the two layers. A sharp pycnocline effectively isolates the deeper layer from downward mixing of dissolved oxygen and therefore contributes to the creation of anoxic basins [50, 72]. On the other hand, wind storms in the fall and winter, when the stratification is at a minimum, can produce top-to-bottom mixing over large portions of the Chesapeake Bay [31, 34].

The short-term processes, which include wind forcing, tidal variations, long-period internal waves, cross-bay seiching, fronts and plumes, ocean coupling, and shelf interaction, and diurnal variation in heat flux affect the sub-tidal circulation. Only the overall effect of these processes on the circulation and stratification has been studied [51, 84-86, 88]. The spatial and temporal resolution of the past studies was rather coarse. Typical current meter moorings had two meters, with one meter presumably in each layer of the water column, and the current data were averaged over periods of 15 minutes to an hour. Higher-resolution current profiles have been obtained only in the tributary rivers, either with profiling current meters (e.g., the James River [58], the Potomac River [20], and Baltimore Harbor [15]) or with a bottom-mounted Acoustic Doppler Current Profiler (in the Patuxent River [66]).

Finally, short-period internal waves and turbulent mixing control the vertical distribution and exchange of water column properties, nutrients and organisms. Very little is known about turbulent mixing mechanisms: what are the predominant mechanisms, how often do mixing events occur during the tidal cycle, how long do they last, what is their intensity, and what are the resulting vertical fluxes? Only one attempt has been made at measuring the turbulent kinetic energy and turbulent fluxes in the Patuxent River estuary [70]. The identification of possible mixing mechanisms in the Chesapeake Bay has resulted from field work in other partially stratified estuaries [27, 48, 49, 54, 81] and the open ocean [36, 76], laboratory experiments [11, 57, 76], and observations of small-scale internal waves in the upper Chesapeake Bay [10].

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SEASONAL PROCESSES: GRAVITATIONAL CIRCULATION

Pritchard [59-61] characterized the Chesapeake Bay and its tributary rivers as moderately or partially stratified estuaries. At the peak of the freshwater runoff, the major tributaries can be classified as salt-wedge estuaries (the river flow is much larger than the tidal oscillations). In partially mixed estuaries, a mean two-layer flow system exists (after removal of the tidal components) in which the freshwater upper layer flows towards the sea, while the bottom saltier layer travels from the ocean to the head of the estuary. This mean estuarine circulation is commonly termed gravitational or non-tidal circulation.

The tidal current amplitude in the mid-channel of the Chesapeake Bay ranges from 0.5 to 2 knots (0.25 to 1 m/sec), with the strongest currents at the mouth and the head of the Bay. The mean horizontal velocity in each layer is about 20% of the maximum tidal velocity [63]. In order to conserve mass, the saltier water that flows up the Bay in the bottom layer returns to the sea in the upper layer, thus creating a net upward flow from the bottom layer to the upper layer. The large ratio between the area of the Bay and its cross-section implies that the velocity of this upward flow is small compared with the horizontal currents [65]. Finally, in fairly straight estuaries like the Chesapeake Bay proper, the Coriolis force is balanced by lateral pressure gradients resulting from lateral variations in mass and acceleration [61]. In the tributaries, like the James River, where curvature effects are important, the centrifugal force contributes significantly to the lateral balance [17, 73].

The National Ocean Service of the National Oceanographic and Atmospheric Administration (NOAA) conducted a large-scale current meter study of the Chesapeake Bay involving over 130 current meters deployed for periods of a few weeks to a year. The study covered the entire Bay in three phases, with four long-term stations occupied year-round throughout the entire survey. In addition to current meter data, conductivity, temperature, and depth (CTD) data, tidal data, and meteorological data were recorded. Some of the data have been analyzed by Goodrich and his co-workers [31-34], but global scientific results from the survey report [12] have yet to be assessed.

Mean Equations of Motion

Pritchard [61] and Cameron and Pritchard [14] wrote out the mean equations of motion (equations averaged over at least one tidal cycle) for a geometrically simple estuary. They considered a long, comparatively narrow estuary with a single source of fresh water at its head. This is a good representation of the Chesapeake Bay, except for the multiple freshwater sources in the Lower Chesapeake Bay. The choice of a rectilinear, right-hand coordinate system is as follows: the x-axis is along the estuary, starting at its head and going towards the ocean; the y-axis is in the transverse direction, along the width of the estuary, and the z-axis is directed vertically, with the positive direction upward. The corresponding velocity components are denoted as U, V, and W, respectively.

The classical Reynolds decomposition of the flow field into a mean flow (over the averaging period) and a fluctuating velocity can be modified to include periodic flow oscillations such as waves and tides. The three components of the instantaneous velocity field can be expressed as:

$$\begin{aligned} U &= \overline{U} + \tilde{U} + u \\ V &= \overline{V} + \tilde{V} + v \\ W &= \overline{W} + \tilde{W} + w \end{aligned} \qquad (1)$$

where the (—) represents a time average over one or more tidal period. ($\tilde{U}, \tilde{V}, \tilde{W}$) denotes the tidal flow (averaging to zero over the averaging period) and (u, v, w) the fluctuating flow field (with time scales less than a tidal period).

Following Cameron and Pritchard [14] and Bowden [7], the evolution equations for the mean longitudinal and transverse velocity components in an elongated, partially mixed estuary are:

$$\frac{\partial \overline{U}}{\partial t} + \overline{U}\frac{\partial \overline{U}}{\partial x} + \overline{W}\frac{\partial \overline{U}}{\partial z} + \frac{\partial}{\partial x}\overline{\tilde{U}\tilde{U}} + \frac{\partial}{\partial z}\overline{\tilde{U}\tilde{W}} = -\alpha\overline{\frac{\partial p}{\partial x}} - \frac{\partial}{\partial x}\overline{uu} - \frac{\partial}{\partial y}\overline{uv} - \frac{\partial}{\partial z}\overline{uw} \qquad (2)$$

and

$$0 = -\alpha\overline{\frac{\partial p}{\partial y}} - f\overline{U} - \frac{\partial}{\partial x}\overline{uv} - \frac{\partial}{\partial y}\overline{vv} - \frac{\partial}{\partial z}\overline{vw} \qquad (3)$$

where α is the specific volume of water and f the Coriolis parameter. The molecular terms can be neglected compared with the turbulent stress terms (except very near the boundaries), and the mean transverse velocities $\overline{V}$ and $\tilde{V}$ are assumed to be small compared with their longitudinal counterparts, so that the acceleration terms involving them can be neglected. Finally, the Coriolis term involving the transverse mean velocity is neglected in the longitudinal velocity equation. Similar assumptions apply to the vertical velocity component so that the mean vertical equation reduces to the hydrostatic equation involving a balance between gravity and vertical pressure gradient.

In the case of the Chesapeake Bay, Cameron and Pritchard [14] expressed the tidal velocity in terms of a single harmonic function representing the dominant semi-diurnal tide M2 (period 12.4 hours). For better accuracy two other semi-diurnal tidal components (S2 and N2) and three diurnal tidal components (K1, O1 and P1) should be considered. The tidal amplitudes should also be modulated to include the spring-neap variations when the averaging period is greater than a week. In the case of a single harmonic and a short averaging period, the tidal flow can be written as:

$$\begin{aligned} \tilde{U} &= U_o \cos\phi_u \\ \tilde{V} &= V_o \cos\phi_v \\ \tilde{W} &= W_o \cos\phi_w \end{aligned} \tag{4}$$

In elongated estuaries, the longitudinal tidal component $\tilde{U}$ is the most important. The transverse component $\tilde{V}$ reflects changes in width of the estuary and the vertical component $\tilde{W}$ results from the tidal changes in water depth. The ϕ_i are the tidal phases for the three velocity components. They include the time-varying part and a constant-phase reference.

Cameron and Pritchard [14] made several assumptions based on observations from the James River estuary study [57] to simplify the mean equations. Pritchard [60] argued that the horizontal Reynolds stress terms (involving u and v) were small compared to $\partial(\overline{uw})/\partial z$ and $\partial(\overline{vw})/\partial z$. Furthermore, in the Chesapeake Bay and its tributaries, the tidal wave is a progressive wave, so that $\tilde{U}$ and $\tilde{W}$ are 90° out of phase.) For a steady state, equations 2 and 3 reduce to:

$$\bar{U}\frac{\partial \bar{U}}{\partial x} + \bar{W}\frac{\partial \bar{U}}{\partial z} + \overline{\tilde{U}\frac{\partial \tilde{U}}{\partial x}} = -\alpha\overline{\frac{\partial p}{\partial x}} - \frac{\partial}{\partial z}\overline{uw} \tag{5}$$

and

$$f\bar{U} = -\alpha\overline{\frac{\partial p}{\partial y}} - \frac{\partial}{\partial z}\overline{vw} \tag{6}$$

Pritchard [61] found that, in the James River estuary, the main balance along the estuary was between the pressure gradient and the vertical gradient of the turbulent stress $\partial\overline{uw}/\partial z$ but that the non-linear tidal term $\overline{\tilde{U}\partial\tilde{U}/\partial x}$ could be important. The acceleration terms due to the non-tidal, mean motion were negligible. In the Chesapeake Bay, the tidal term could be significant near the mouth and the head of the estuary where tidal amplitudes are large (about 0.6 m) and at spring tides when the tidal amplitudes are maximal. The transverse velocity component was found to be in geostrophic balance, with the lateral pressure gradient nearly balanced by the Coriolis force. The turbulent shear stress was of secondary importance. Pritchard [61] speculated that this term might be more significant in highly curved estuaries. Stewart [73] used the James River data of Pritchard [61] and Pritchard and Kent [64] to show that the imbalance between the Coriolis force and the lateral pressure gradient could be due to the centrifugal force (mostly in the tidal fluctuations $-\tilde{U}^2/R$) created by a curvature of radius R [17]. The depth-varying nature of the flow curvature suggests that a lateral shear stress could exist and play some role in the lateral balance [73].

The James River estuary study [61] showed that the mean, non-tidal vertical velocity was of the order of 10^{-5} m/sec, compared with a mean horizontal velocity of order 1 m/sec. It also determined that the level-pressure surface and the surface of net no-motion were both near mid-depth. The water surface and upper isopycnals (surfaces of constant density) were tilted towards the Bay proper, and the isopycnal surfaces near the bottom were tilted in the opposite direction.

Mean Conservation Equation for Salt and Other Conserved Properties

The local rate of change of salt (or other constituent) after neglecting molecular diffusion can be expressed as:

$$\begin{aligned} &\frac{\partial \bar{S}}{\partial t} + \bar{U}\frac{\partial \bar{S}}{\partial x} + \bar{V}\frac{\partial \bar{S}}{\partial y} + \bar{W}\frac{\partial \bar{S}}{\partial z} \\ &+ \frac{\partial}{\partial x}\overline{\tilde{U}\tilde{S}} + \frac{\partial}{\partial y}\overline{\tilde{V}\tilde{S}} + \frac{\partial}{\partial z}\overline{\tilde{W}\tilde{S}} \\ &= -\frac{\partial}{\partial x}\overline{us} - \frac{\partial}{\partial y}\overline{vs} - \frac{\partial}{\partial z}\overline{ws} \end{aligned} \tag{7}$$

where the instantaneous salinity S is decomposed into a non-tidal mean $\bar{S}$, a tidal fluctuation $\tilde{S}$ and a turbulent component s. Pritchard [59] assumed that the tidal fluctuation for the longitudinal velocity and salt were 90° out of phase and that the terms involving the transverse and vertical tidal oscillations were negligible. Then equation 7 reduces to:

$$\frac{\partial \bar{S}}{\partial t} + \bar{U}\frac{\partial \bar{S}}{\partial x} + \bar{W}\frac{\partial \bar{S}}{\partial z} = -\frac{\partial \overline{us}}{\partial x} - \frac{\partial \overline{vs}}{\partial y} - \frac{\partial \overline{ws}}{\partial z} \tag{8}$$

In most cases, the time rate of change of salt is small, so that the main balance in equation 8 is between the mean salt advection (left hand-side) and turbulent diffusion (right hand-side).

Equation 8 can be reduced further by integration in the transverse direction [7, 59]:

$$\frac{\partial \bar{S}}{\partial t} + \bar{U}\frac{\partial \bar{S}}{\partial x} + \bar{W}\frac{\partial \bar{S}}{\partial z} = -\frac{1}{b}\frac{\partial b\overline{us}}{\partial x} - \frac{1}{b}\frac{\partial b\overline{ws}}{\partial y} \tag{9}$$

where b is the breadth of the estuary (width at a given depth). Pritchard [59] was able to compute all the terms in equation 9 in the James River estuary and

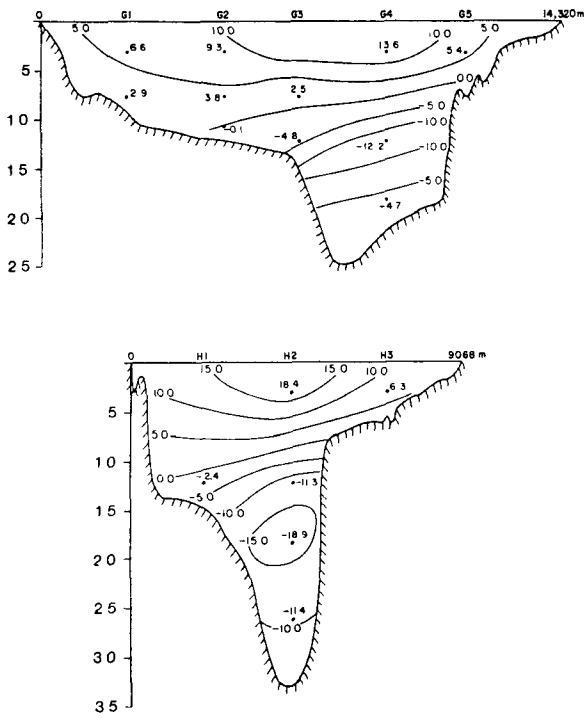

Figure 1. Longitudinal component of the non-tidal velocity averaged over 13 days (17-29 October 1977) showing a two-layer circulation (from Pritchard and Rives [65]). All velocities are in cm/sec. Top and bottom measurements were taken at 38° 29' N lat. and 38° 23' N lat., respectively.

showed that the salt balance was between the mean horizontal advection $\overline{U}\,\partial\overline{S}/\partial x$ and the vertical turbulent diffusion $(1/b)\partial(b\overline{ws})/\partial z$. The mean vertical advection $\overline{W}\,\partial\overline{S}/\partial z$ can be important near the surface of no-motion, where the mean horizontal velocity vanishes.

Observations of Gravitational, Two-layer Circulation

The early current measurements for examining the non-tidal circulation and its associated salt balance were made in the tributary rivers rather than the Bay proper. Pritchard [58] measured vertical profiles of horizontal currents and estimated the vertical velocity in the James River during the summer of 1950. These extensive measurements of salinity and current profiles were made across three sections during three five-day periods. The tidally averaged velocity profiles were consistent with a two-layer circulation and a diffusive vertical salt flux [59, 61].

Another study [65, 84] consisted of five moorings at 38° 29' N lat and three moorings at 38° 23' N lat, north of the mouth of the Patuxent River. All moorings, containing a total of 20 current meters, were deployed for about three weeks starting in mid-November 1977. Three additional moorings were deployed between these two sections. The tidally averaged records showed that maximum flood currents occurred within an hour of each other in the two cross-sections, in good agreement with the tide tables from NOAA. Daily averages of the non-tidal velocity showed substantial variability in current distribution and strength. Long-term averages (over 13 days) show a classical two-layer circulation with maximum longitudinal currents varying from -15 to +15 cm/sec and a depth of no motion around 8 meters (see Figure 1). The difference observed in flow rates between the two cross-sections by Vieira [84] implies that the vertical advection from the lower to the upper layer contributes significantly to the balance of equation 5. Vieira also reports large fluctuations in the laterally integrated subtidal flow, reaching values of 20,000 m^3/sec over a day, which appear to result from wind forcing.

Departures from the Two-layer Circulation

It is often assumed that the two-layer, gravitational (averaged over several tidal cycles) circulation observed by Pritchard [58] in the James River also exists in the Chesapeake Bay proper and the other tributaries. More recent current meter measurements [20] in the Potomac River showed two-layer circulation only 43% of the time. A more complex three-layer circulation occurred during the other part of the tidal cycle and persisted when the current measurements were averaged over a tidal cycle. The measurements, made with vertically profiling current meters and a CTD taking hourly samples, covered two five-day periods at two cross-sections.

High-resolution (1 m vertically) current measurements made in the upper Chesapeake Bay in the fall of 1986 with a ship-mounted Acoustic Doppler Current Profiler [42] showed a three-layer circulation during part of the tidal cycle (Figure 2). It is unclear whether a three-layer circulation would appear in an average over several tidal cycles since no long-term, high-resolution current measurements exist. As discussed in SHORT-PERIOD PROCESSES: TURBULENT MIXING, a good knowledge of the velocity shear profile is critical to the identification of turbulent mixing mechanisms.

Three-layer circulations have also been observed in other tributaries where the freshwater input is small compared with the tidal oscillations, e.g., the entrance of Baltimore Harbor [15] and the Patuxent River [66]. In this type of circulation, waters near the surface and the bottom move towards the head of the subestuary (harbor) and water at intermediate depths moves away from it, with important consequences on the transport of pollutants. The reasons for this type of circulation appear to involve enhanced mixing near the head of

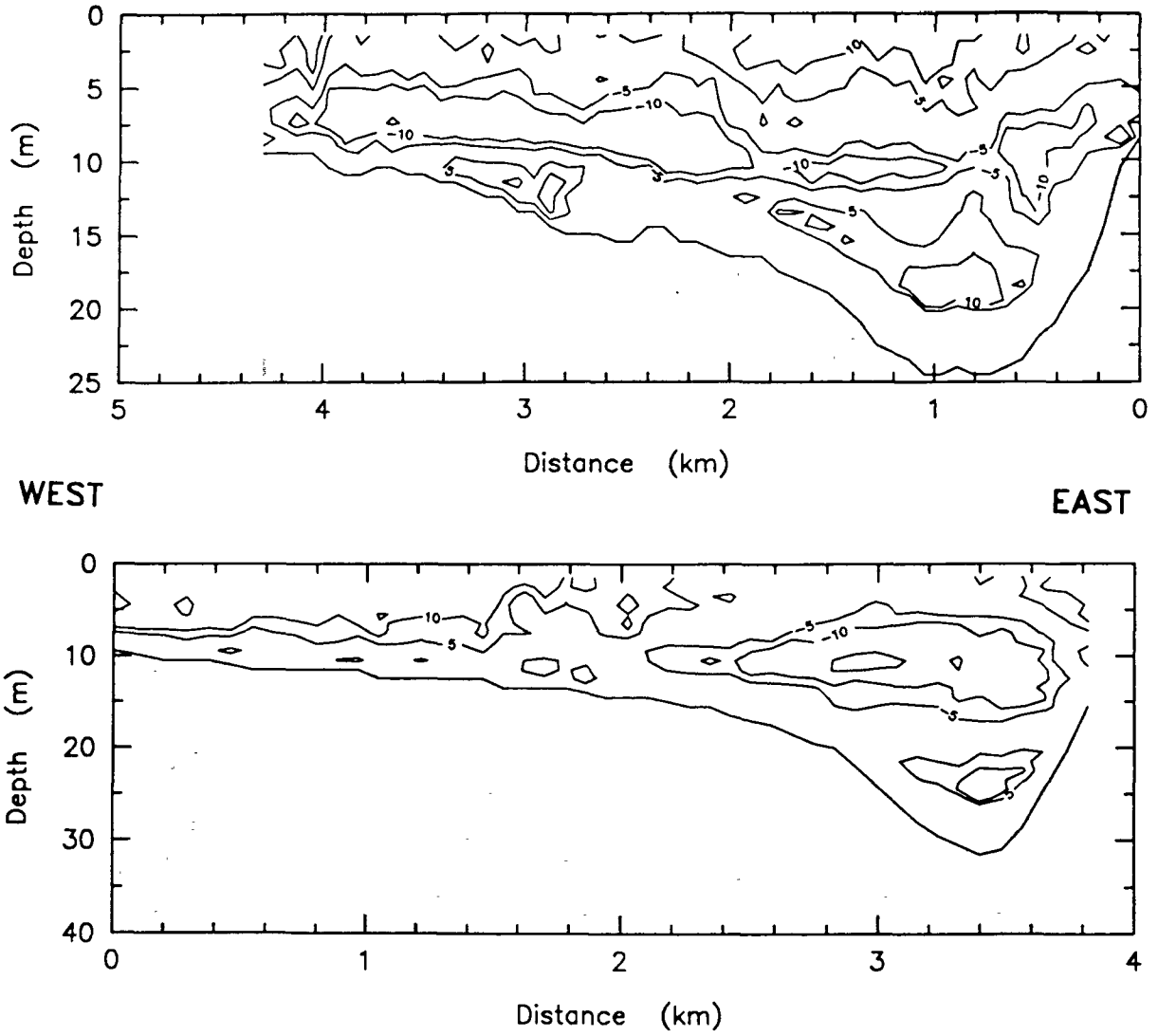

Figure 2. Evidence of three-layer circulation in the Chesapeake Bay: cross-sections of along-bay currents (from Itsweire and Osborn [42]). Measurements were taken in November 1986 with an Acoustic Doppler Current Profiler. Vertical resolution was 1 m, horizontal resolution 100 m. Negative velocities are northward (up-estuary) and positive velocities are southward (down-estuary). Top: cross-section at 38° 58' N lat.; end of flood tide. Bottom: cross-section at 38° 56' N lat.; end of ebb tide.

the harbor, with consequent reduction of the stratification there [5, 52]. Surface water becomes denser and deep water less dense than at corresponding depths in the Bay outside. The water column in the harbor tends to collapse and move outwards at an intermediate depth, drawing in Bay water at the top and bottom. These tributaries of the Chesapeake Bay have a very small freshwater flow compared to the tidal oscillations and cannot be classified as partially mixed estuaries.

Turbidity Maximum

Regions of maximum turbidity have been observed in the upper reaches of estuaries throughout the world. Schubel [68] showed that the turbidity maximum near the head of Chesapeake Bay is caused by the continual resuspension of bottom sediments in combination with the sediment trap produced by the non-tidal, gravitational circulation. Throughout the year, sediment is resuspended by tidal pumping (maximum near the head and mouth of the Bay) and wind waves (important near the head of the Bay where the mean depth is less than 5 m). In the bottom layer, Schubel [68] observed maximum concentrations (60-280 mg/l at depths of 8-9 m) of suspended sediments near maximum ebb and flood tides and minimum concentrations (20 mg/l) shortly after slack water. In contrast, the upper layer had a nearly constant, lower

concentration (14 mg/l) of suspended sediments. The sediment trap produced by the gravitational, two-layer circulation can be explained as follows: during intense tidal pumping, resuspended sediments are mixed into the upper layer. Then, as they are transported downstream (seaward) in the upper layer, sediments settle into the lower layer and are carried back upstream by the net upstream flow of the lower layer. The location of the turbidity maximum depends on the freshwater discharge from the Susquehanna River. Observations in the Tamar estuary [83] suggest than the turbidity maximum reaches an extremum during spring tides when tidal currents are the largest.

Development of Anoxic Basins

Anoxic basins have been observed for many years in the middle portion of the Chesapeake Bay [50]. These basins develop yearly from March to September. From April to September 1980, all the deep water (below 15 m) in the mid-portion of the Bay (between Annapolis and the mouth of the Potomac River) was completely anoxic. In 1984, meteorological conditions combined to produce catastrophic anoxia in the upper and middle Bay [72]. Although anoxia is usually limited to the deep central channel of the Bay, a shallow pycnocline (5 to 8 m) caused it to extend to the shallow reaches of the eastern shores. Officer et al. [50] attribute the development of the anoxia to a combination of benthic respiration and high summer stratification. The rate of change of dissolved oxygen concentration would be mainly a balance between the reoxygenation rate of the lower layer through advective and diffusive turbulent processes (source of oxygen) and the benthic respiration rate (sink of oxygen) due to the decay of organic material. Bacterial metabolism of organisms in the water column could also be a substantial sink of dissolved oxygen [79].

As stratification increases in the spring with high freshwater runoff, vertical mixing across the pycnocline is reduced, minimizing the reoxygenation rate of the lower layer. Concurrently, the benthic respiration rate increases in the spring due to the oxidation of organic detritus. Plankton blooms, which have a slow decay rate, have accumulated from the previous summer and fall. In September, large wind mixing events break the stratification [34], through processes not clearly understood. One (less likely) possibility is that enhanced turbulence in the upper layer associated with the wind event, combined with the reduced stratification, erodes into the anoxic region and enables the mixed layer to reach the bottom. Reoxygenation rates would then be larger than the benthic respiration rates and deep-water dissolved oxygen levels would return to normal values. More likely is the sudden instability described by Bell and Thompson [3]. The anoxic layer is essentially stagnant throughout the summer, with the estuarine circulation above it, the shear at the top of the anoxic layer being stabilized by the strong stratification there. During fall or early winter, the stratification is reduced and during a storm, particularly one moving up or down the Bay, the storm surge augments the shear until the system becomes unstable. The whole anoxic basin is flushed out and then ventilated by more normally oxygenated water.

Officer et al. [50] point out that other parameters, such as water exchanges between the mid-Bay and the upper and lower portions of the Bay, internal recycling of organic material on the bottom, variations in the freshwater runoff flow, and spring bloom of diatoms should also be included in the analysis. Finally, it should be pointed out that the physical processes governing gravitational circulation, density stratification, and vertical mixing cannot account for the long-term aggravation of the development of anoxia in the Chesapeake Bay. Rather, this long-term trend is correlated with increased yearly plankton production and nutrient inputs in the Bay [25]. Officer et al. [50] postulated that the increase in nutrients (particularly nitrogen and phosphorus) stimulates growth of algae, which ultimately die and decay, consuming large amounts of dissolved oxygen.

SHORT-TERM PROCESSES: SUBTIDAL CIRCULATION

To the simple schematic pattern of gravitational circulation, one must add the effects of topography, atmospheric forcing, and oceanic forcing. They produce an important subtidal circulation that can completely obscure the gravitational, two-layer circulation [20]. The effects of both longitudinal and transverse winds have to be considered.

Atmospheric and Oceanic Forcing: Baroclinic and Barotropic Modes

The two-month study (mid-July to mid-September 1974) of coastal sea level and surface winds of Wang and Elliot [88] showed a coupling of Bay and coastal sea levels consistent with driving via the coastal Ekman flux. A one-year study (October 1974 to September 1975) of subtidal sea level variations [85] showed the existence of a large barotropic fluctuation that dominates the estuarine circulation on time scales of several days. Wang [85] also found that on time scales of two to three days the barotropic fluctuations (i.e., those influencing the whole water

column) were driven by the local longitudinal wind (seiche oscillation), whereas on scales of three to five days they were driven by the local lateral wind. The local winds set up the horizontal velocity shears required to create the barotropic instability. In the three to five day time scale the transport was also found to be much larger than the river runoff.

Non-local forcing was important for time scales >10 days, and coupling of Bay and coastal sea levels was observed [85, 88]. A Wang and Elliot study [88] suggested that, at these large time scales, a coastal Ekman flux can cause a rapid rise of sea level. Winds blowing parallel to the coastline create an Ekman flux in the shelf waters, in turn causing sea level fluctuations that propagate up the Bay.

Later data on currents, sea level, and wind observations [86] in the upper Bay (38° 54' N lat.) and lower Bay (37° 31' N lat.) implied that, in the deeper upper mid-Bay, the response to wind forcing is mostly baroclinic (i.e., one in which the upper layer responds differently from the lower layer). Only the near-surface current in the upper layer was frictionally driven by the wind, resulting in large vertical velocity shears, a necessary condition for baroclinic instability.

More recent studies of subtidal circulation conducted in the upper Chesapeake Bay [35, 39] and the middle part of the Bay [84] also show the importance of external forcing on the non-tidal circulation in the Chesapeake Bay. Olson [51] used the volume transport and wind stress data of Grano [44] and Pritchard and Rives [65] to develop a two-layer model explaining the variability in the subtidal circulation in terms of a linear response to irregular, time-varying meteorological forcing. Olson's work [51], extending the model of Wang [85] and Vieira [84], showed that coastal sea level tends to dominate the low-frequency part of the transport spectrum, while wind stress tends to dominate the higher frequencies of the spectrum. Olson [51] also concluded that 90% of the transport variance at the mouth of the Bay is due to coastal sea level variations, in agreement with the Wang and Elliot [88] observations. In the upper Bay, the opposite is true: 90% of the transport fluctuations come from longitudinal wind stress and freshwater runoff from the tributaries as predicted by Vieira [84]. This conclusion agrees with that of Elliot et al. [21], whose three-month study of the circulation near the head of the Chesapeake Bay showed a baroclinic response at all time scales. In the mid-portion of the Bay, wind stress and sea level fluctuations contribute more evenly to the transport fluctuations, with the frequency marking the transition from sea level to wind stress dominance between 0.15 and 0.30 cycle/day (three- to six-day period).

Response to Tropical Storms and Cyclones

The response of the Chesapeake Bay to severe tropical storms and extratropical storms (cyclones) can be a combination of three phenomena: response to wind setup, sea level variations, or intense flooding of the tributaries.

In June 1972, tropical storm Agnes brought a very heavy rainfall, resulting in record flooding of the major tributaries [69]. In contrast there was little wind associated with Agnes when it reached the Chesapeake Bay, so that the intense freshwater runoff, primarily from the Susquehanna River, remained relatively unmixed as it moved down the surface of the Bay. Salinity levels as low as 4 parts per thousand were measured near the Chesapeake Bay Bridge [69], and significant depression of the normal salinity levels continued for six weeks.

In September 1975 the effects of another tropical storm (Eloise) on the circulation near the head of the Bay were observed by Elliot et al. [22]. Like Agnes, Eloise brought no severe winds to the Bay, so that the freshwater discharge from the Susquehanna River controlled the circulation and stratification for more than 10 days after the passage of the storm. Near the head of the Bay, the flow of the Susquehanna River determines the local stratification and the location of the salinity front between landward low-salinity, homogeneous water and seaward saltier, stratifed water. Therefore, large river discharges associated with tropical storm rainfalls reduce water salinity near the head of the Bay and move the salinity front seaward. Consequently, in the upper 50 km of the Bay, the two-layer gravitational circulation is replaced by a net seaward flow for several weeks.

Wang's observations [86] of the response of the Chesapeake Bay to wind forcing by extratropical storms have documented that large sea level fluctuations (0.5 and 1 m) are frequently produced, superimposed on the astronomical tides. The transports associated with these storm surges are, at maximum, much larger than the river runoff. The local seiching effect is reasonably well understood, but the coupling between the estuary and the coastal ocean beyond has only been partially explored.

Coastal Plume and Estuary-shelf Interaction

The dynamics of river and estuarine plumes discharging fresher water in the adjacent shelf waters have been studied intensively in New York Bight [9], the Connecticut River estuary [28-30] and the Chesapeake Bay [4, 6, 32, 33]. Observations of the Chesapeake Bay coastal plume [6] have shown that the fresher estuarine water takes a broad anticyclonic turn at the mouth of the bay and then forms a narrow,

high-velocity jet propagating southward along the coast. The plume spreading and the intensity of the jet are directly affected by the direction of the winds.

The water exchange between the Chesapeake Bay and the adjacent shelf is highly dependent on wind forcing and coastal sea levels [4, 32, 33]. Goodrich's data [32, 33] showed that the water exchange between the Bay and the ocean consists of a steady, seaward surface flow on which a larger, oscillatory, depth-independent, meteorologically driven flow is superimposed. Goodrich [33] also estimated that only 3% of the outflowing water was of mean estuarine salinity.

Wind-induced Destratification

Between early September and late February the mean stratification in the Chesapeake Bay reaches a minimum value for two reasons: surface cooling decreases the vertical temperature gradient (from September to January), and freshwater runoff remains small after reaching a minimum in August, so that the vertical salinity gradient can be reduced by vertical diffusion. A reduced stratification means a lower available potential energy of the system, so that a lower amount of kinetic energy is required in order to break the stratification and convert more potential energy into kinetic energy and viscous dissipation. Goodrich et al. [34] showed that large-scale destratification in the fall resulted from strong wind mixing events. During the fall of 1981, complete vertical mixing of the water column occurred after the wind induced a strong top-to-bottom velocity shear, i.e, the value of the Bulk Richardson <1. These results suggest that the flow might be dynamically unstable during those periods (Richardson number <0.25).

Spring-neap Overturn

Complete vertical mixing of small, partially mixed estuaries can also occur after strong spring tides. Haas [38] observed that the York and Rappahannock Rivers (both partially mixed tributaries of the lower Chesapeake Bay) oscillated during late summer between states of vertically stratified density profiles and homogeneous density profiles. The vertical velocity shear induced by the high spring tides was probably large enough for the flow to become unstable. Haas [38] and Hayward et al. [40] observed that complete vertical mixing of the water column was achieved four days after the high tides. The velocity shear produced by the following weaker tidal oscillations was insufficient to sustain vertical turbulent mixing, and the water column completely restratified within a week. This spring-neap overturn has been observed only in late summer when the right combination of large-amplitude spring tides and low river runoff is achieved. It is likely that this type of vertical mixing is confined to the tributaries rivers rather than the Bay proper. Goodrich [31] showed that spring-neap overturn is significant in the lower Bay, but is not the dominant mechanism for vertical mixing of the water column.

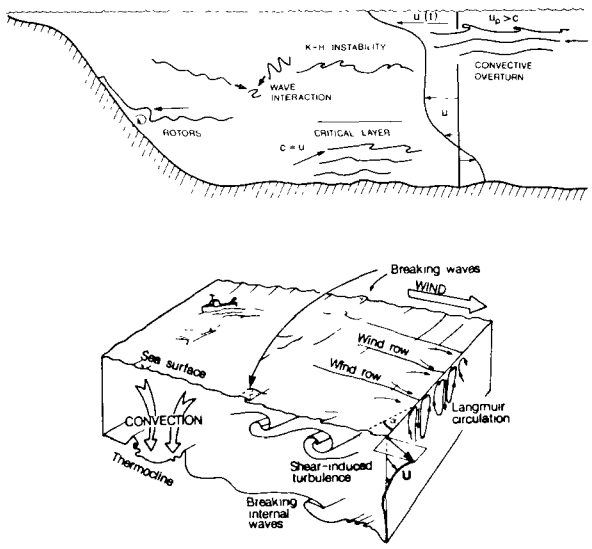

Figure 3. Mixing processes in the upper ocean (from Thorpe [75, 76]).

SHORT-PERIOD PROCESSES: TURBULENT MIXING

Much less is known about mixing processes in partially stratified estuaries than about those in the open ocean and laboratory flows. At best, past estuarine studies have suggested potential mechanisms that could produce vertical mixing in the Chesapeake Bay. It is therefore necessary to briefly review the fundamental results on small-scale mixing in oceanic and laboratory flows before examining the problem of turbulent mixing in the Chesapeake Bay and other partially mixed estuaries.

Small-scale Mixing Processes in the Ocean and Laboratory Flows

In their reviews on small-scale turbulent processes in stably stratified flows, Turner [78], Browand and Hopfinger [11], Gregg [36], and Thorpe [76] have presented complete summaries of the various mechanisms producing vertical mixing in the open ocean and laboratory flows. Only those processes most likely to occur in the Chesapeake Bay and its tributaries are reviewed in this section. Depictions of oceanic mixing mechanisms compiled from Thorpe [74-75] are presented in Figure 3.

Turner [78] pointed out the importance of identifying the sources of energy for turbulent mixing in order to classify mixing processes. Turbulence can have its source in kinetic energy (tides, mean shear, surface and internal waves) or potential energy (unstable density profile leading to intrusions and convection). Turbulence can also be thought of as being internally generated (internal wave breaking, Kelvin-Helmholtz and Holmboe instabilities) or externally generated (energy input at the boundaries due to wind stress and topography).

Turbulent kinetic and potential energies equations. It is convenient to introduce the equations for the evolution of the fluctuating kinetic and potential energies to illustrate the differences between the various instability mechanisms. Depending on the turbulence generating mechanism considered, the balance in these equations will be between different terms. The instantaneous velocity and scalar (temperature, salinity etc.) can be decomposed into a mean field (over an averaging period of 5 to 15 minutes) and a fluctuating field (with no mean value over the averaging period). This Reynolds decomposition is similar to the decomposition used in MEAN EQUATIONS OF MOTION and MEAN CONSERVATION EQUATION FOR SALT AND OTHER CONSERVED PROPERTIES with two exceptions: the tidal oscillations are not specified (instead they are assumed constant over the averaging period); and the averaging period is much shorter than a tidal period. The coordinates system is identical to the one used in MEAN CONSERVATION EQUATION FOR SALT AND OTHER CONSERVED PROPERTIES (the mean flow is along the x-axis).

Following Phillips [56] and Turner [77], who assumed that the fluctuating field is horizontally homogeneous, one can approximate the turbulent kinetic energy equation as:

$$\frac{\partial}{\partial t}(\tfrac{1}{2}\overline{q^2}) + U\frac{\partial(\tfrac{1}{2}\overline{q^2})}{\partial x} = -\frac{\partial}{\partial z}\left[\frac{\overline{wp}}{\bar{\rho}} + \tfrac{1}{2}\overline{wq^2}\right] - \overline{uw}\frac{\partial U}{\partial z} - \frac{g}{\bar{\rho}}\overline{\rho w} - \epsilon \qquad (10)$$

where $q^2 \equiv u^2+v^2+w^2$ is the total fluctuating kinetic energy, p is the fluctuating pressure and ε the dissipation of q^2. Eq. (10) is a good approximation for the upper ocean. The physical meaning of the various terms in equation 10 is as follows.

$\frac{\partial}{\partial t}(\tfrac{1}{2}\overline{q^2})$ Temporal evolution of the turbulent kinetic energy, usually considered to be small.

$U\frac{\partial(\tfrac{1}{2}\overline{q^2})}{\partial x}$ Horizontal advection of the turbulent kinetic energy by the mean flow. It could be important in tidal estuaries.

$\frac{\partial}{\partial z}\left[\frac{\overline{wp}}{\bar{\rho}}\right]$ Redistribution of the turbulent kinetic energy by the pressure field. Initially, the energy is put into the longitudinal component u, but is redistributed among all three components by the pressure. If the redistribution is slow, the turbulence will be anisotropic (e.g., in stably stratified flows, the vertical component $\overline{w^2}$ is smaller than the horizontal components due to the loss to buoyancy effects). The relative importance of this term compared with other terms in the right-hand side is not known, as pressure-velocity correlations have never been measured in water.

$\frac{\partial}{\partial z}\left[\tfrac{1}{2}\overline{wq^2}\right]$ Redistribution of the turbulent kinetic energy by the fluctuating field. It includes turbulent diffusion (spreading of turbulent energy by breaking internal waves).

$\overline{uw}\frac{\partial \bar{U}}{\partial z}$ Production of turbulent kinetic energy from the mean shear (usually a source term). Small-scale eddies in the presence of a mean shear extract energy from the large scales of the flow. This term is the primary source of energy in internal wave breaking, Kelvin-Helmholtz and Holmboe instabilities, forced convection, and mixing along a solid boundary.

$\frac{g}{\bar{\rho}}\overline{\rho w}$ Buoyancy flux, could be a source (free convection, restratification) or sink of kinetic energy (any shear-induced mechanism). Turbulent mixing in a stably stratified fluid converts kinetic energy into potential energy, raising the center of gravity of the system (positive buoyancy flux). This term is usually small compared with the shear production and the dissipation rate. On the other hand, an unstably stratified flow (produced by daytime evaporation and nighttime surface cooling) will convert potential energy into kinetic energy (negative buoyancy flux). Buoyancy flux can then be the dominant source of energy.

ε Dissipation rate of turbulent kinetic energy into heat due to viscous effects.

This term is the main sink of turbulent kinetic energy.

Similarly, the equation for the evolution of scalar ($C=\overline{C}+c$) variance in a mean vertical gradient can be expressed as:

$$\frac{\partial \overline{c^2}}{\partial t} + U\frac{\partial \overline{c^2}}{\partial x} = -\frac{\partial}{\partial z}\left[\overline{wc^2} - \kappa_C \frac{\partial \overline{c^2}}{\partial z}\right] - 2\overline{wc}\frac{\partial \overline{C}}{\partial z} - \chi_c \qquad (11)$$

The terms in equation 11 can be interpreted as follows:

$\frac{\partial \overline{c^2}}{\partial t}$ Time rate of change of scalar variance.

$U\frac{\partial \overline{c^2}}{\partial x}$ Horizontal advection of scalar variance by the mean flow.

$\frac{\partial \overline{wc^2}}{\partial z}$ Redistribution of scalar variance by the turbulent field (includes turbulent diffusion).

$\kappa_C \frac{\partial^2}{\partial z^2}\overline{c^2}$ Divergence of scalar variance transport through molecular diffusion (usually neglected)

$2\overline{wc}\frac{\partial \overline{C}}{\partial z}$ Rates of production of scalar variance from the mean scalar gradient. This term is the dominant source of scalar variance due to vertical turbulent mixing. It is mostly balanced by the rate of destruction of scalar variance.

χ_c Rate of destruction of scalar variance, always positive.

Fundamental parameters in turbulent stratified shear flows. Several parameters defined from the mean velocity and scalar field are useful for characterizing the state of stratified flows and predicting whether turbulent mixing is likely. They are defined as follows:

$N=\left[-\frac{g}{\overline{\rho}}\frac{\partial \overline{\rho}}{\partial z}\right]^{\frac{1}{2}}$ The Brunt-Väisäla or buoyancy frequency, which is the highest frequency at which internal waves can exist.

$Ri = N^2/S^2$ The Richardson number, which is a measure of the dynamical stability of the flow. A sufficient condition for stability is $Ri > 0.25$. In hydraulics, the Froude number $Fr=Ri^{-1/2}$ is usually used. These two numbers are the most important parameters in stratified shear flows. When there is no mean shear (or no measurements of it) a Bulk or overall Richardson number can be defined as $Ri = (g\Delta\rho d/\overline{\rho})u^2$ where u and d are representative turbulent velocity and length scales and $\Delta\rho/\overline{\rho}$ the fractional density change over d.

$R_f = \frac{g\overline{\rho w}}{\overline{\rho}\overline{uw}S}$ The Flux Richardson number, which is a measure of the mixing efficiency. It represents the fraction of kinetic energy (extracted from the mean shear) going into mixing the fluid (buoyancy flux).

$Ra = \frac{g\Delta\rho d^3}{\overline{\rho}\kappa\nu}$ The Rayleigh number. $\Delta\rho/\overline{\rho}$ is the destabilizing density fraction over the vertical distance d and κ is the thermal diffusivity. This number is important when convection is the dominant turbulent mechanism. Temperature and salinity Rayleigh numbers can be defined specially when convection is driven by surface cooling and evaporation, respectively.

$\mathrm{Re} = \frac{ud}{\nu}$ The turbulent Reynolds number where u is a turbulent velocity scale and d a turbulent length as defined previously. It is a measure of the strength of the turbulence.

$R_\rho = \frac{\alpha\Delta T}{\beta\Delta S}$ The density ratio, which is a measure of the contribution of temperature and salinity to density across an interface. This ratio is the most important parameter for doubly-diffusive processes (not likely to occur in the Bay). In the Chesapeake Bay, salt contributes mostly to the density gradient, yielding a density ratio $|R_\rho|<<1$. The temperature contribution to the density gradient can be either positive (up to 20% in the summer) or negative (-10% in the fall).

Vertical mixing in the upper ocean boundary layer. In the upper ocean most of the energy-producing vertical mixing is introduced externally through the air-sea interface. Surface stress, surface waves, and internal waves are thought to be responsible for

creating most of the turbulence. Laboratory and oceanic observations lead to the following conclusions: The temperature and salinity (and hence density) profiles in the surface layer are well mixed. The mean velocity is nearly constant with depth, implying a rapid flux of momentum through the layer. The depth of the mixed layer is limited by buoyancy and the turbulent fluxes at the bottom of the mixed layer depend on the deepening rate of the layer. The influence of surface waves on the small-scale processes in the mixed layer is not well understood. The best-known phenomenon created by the interaction of surface waves and the wind-driven current is Langmuir circulation [74] shown in Figure 3. Langmuir circulation could be a very important mechanism for transfering gases to the upper ocean. Finally, convection due to nighttime cooling can induce motion through the depth of the mixed layer and contribute to the entrainment across the thermocline. Recent measurements of turbulent dissipation rates at the equator [46] show a strong diurnal cycle due to surface cooling.

Mixing in the ocean interior and in stratified shear flows. Turbulence in the thermocline [36, 74] results from internal wave breaking and interactions, shear instabilities (small, short-lived turbulent puffs), and near inertial shear (creating persistent mixing patches extending several meters vertically). In all cases, turbulent mixing is created and maintained by extracting energy from the local mean shear. The strength and duration of mixing events appear to be highly correlated with the mean shear distribution [41].

Figure 3 shows the role played by internal waves in generating turbulent mixing. Internal waves can break or interact with each other or solid boundaries to form critical layers. The most important role played by internal waves is probably more indirect: propagating waves can increase the shear at interfaces, thereby reducing the Richardson number and leading to instabilities such as Kelvin-Helmholtz and Holmboe instabilities. Lee waves generated over topography can break and produce rotors (see Figure 3).

Bottom and boundary mixing. As mentioned in the previous section, internal wave interaction with a sloping boundary or reflection off the bottom can create mixing in the ocean interior. The most important mechanism for generating turbulence near the bottom is flow (generated by large-scale and gravity currents) around topography. These currents create mixed layers that are advected into the ocean interior. Bottom mixing itself is localized in the bottom boundary layer, whose thickness is limited by buoyancy effects. In the deep ocean, it is not clear whether the boundary layer is more likely to be well-mixed or stratified. In shallow water, mixing driven by the bottom produces turbulence that can extend to the surface. This weak stratification is governed by the balance between the kinetic energy put in by the bottom-generated turbulence and the potential energy input due to solar heating.

Small-scale Mixing Processes in Partially Mixed Estuaries

In his review of estuarine circulations, Pritchard [63] speculated that the dominant mixing agent of moderately stratified estuaries is turbulence caused by tidal action (bottom, surface, and boundary mixing) rather than the velocity shear at the interface between the two layers (dynamical instabilities). Turbulent eddies mix the salty water upward and the fresh water downward. In addition to the salt flux, there is a momentum flux with turbulent shear stresses extending through the water column. These conclusions come from indirect inferences, since turbulent mixing processes have not been directly measured. The enhanced mixing (compared with highly stratified estuaries) produces a horizontal axial pressure gradient in both layers.

Some early turbulence measurements made in the Patuxent River [70, 89] with a three-component Doppler shift meter showed that the turbulence was very anisotropic (the vertical turbulent velocity was much smaller than the horizontal turbulent velocities). That work was never pursued in the Bay proper with modern instrumentation.

Time dependence of mixing events in tidal estuaries. Nearly all studies of mixing processes in estuaries (partially mixed, salt-wedge or homogeneous estuaries) have implied that turbulence is very patchy in time and space. Mixing events across the pycnocline (density interface) seem to occur for short periods (several minutes) during part of the tidal cycle (ebb tide).

Partch and Smith [54] noted that turbulent mixing in the Duwamish River (a shallow, salt-wedge estuary) was highly time-dependent. They observed that the kinetic energy and the vertical salt flux are maximum when the tidal currents are the largest (maximum ebb). Their most exciting finding was the high intermittency of turbulent mixing. Nearly half of the vertical salt flux occurred in 16% of the tidal cycle. Partch and Smith [54] also identified the dominant mixing mechanism in the Duwamish River as an internal hydraulic jump generated by the tidal flow over bottom topography. In that case, entrainment driven by the turbulent bottom boundary layer and Kelvin-Helmholtz shear instabilities were less important.

Bottom mixing and topographical effects. In well-mixed and weakly stratified estuaries, most of the turbulence is produced near the boundaries, and especially the bottom. Large velocity shears and turbulent shear stresses are created in the bottom boundary layer by tidal action. Three-dimensional variations in the topography, curvature effects, and the time-dependent nature of the tidal forcing will affect the magnitude and spatial and temporal distribution of near-bottom velocities and turbulent stresses, and hence vertical mixing. Stratification due to suspended sediments can also affect the turbulent stress near the bottom [37].

In partially mixed estuaries the situation is even more complex because the gravitational circulation is superimposed on the tidal oscillations, and because the bottom boundary layer and the pycnocline may interact to add buoyancy effects. Erosion of the pycnocline by entrainment from the bottom boundary layer can be an important factor in the ventilation of the anoxic bottom water during the summer [43]. This erosion of the pycnocline observed in Lake Erie [43] could be significant in the shallow reaches of the Bay and needs to be investigated.

Shear instability and internal wave breaking. Brandt et al. [10], using thermistor chains and an acoustic echo sounder, observed both trains of monochromatic internal waves and random internal wave fields in upper Chesapeake Bay. Some of these internal waves eventually break, producing turbulence around the pycnocline. The generating mechanism for the internal waves is thought to be similar to the internal hydraulics associated with tidal flows in Knight Inlet [24]. In Knight Inlet, during ebb tide, the flow separates behind the sill, setting up a mode 1 lee wave above the sill. Then, at slack water, the lee wave moves over the sill, leaving a train of internal waves propagating up-inlet at a speed of 0.5 m/sec [23]. Gargett et al. [27] observed that the small-scale structures shown on the acoustic images of the echo sounder were indicative of turbulence. Since there are important differences in depth, width, and stratification between Knight Inlet and the Bay Bridge area of Chesapeake Bay, smaller amplitude waves, and hence less turbulent mixing, are expected in the Chesapeake Bay. The thermistor chain observations of Brandt et al. [10] are encouraging enough to justify pursuit of their study with actual turbulence measurements from a towed body, which would be the best suited instrument for shallow water turbulence measurements.

New et al. [49] observed intense mixing periods in the Tees River estuary. The intense mixing periods were thought to be produced at high water by a series of bridges, with mixing subsequently advected downstream by internal waves traveling downstream during ebb tide. As a result the surface layer increased in thickness and salinity, and the center of mass of the water column was raised. New et al. [49] also observed some internal waves breaking into billows over topography. In the Chesapeake Bay, similar intense mixing events could be generated by the pilings of the Bay Bridge and could play a significant role in the exchange of nutrients and plankton between the upper shallow Bay and the deeper mid-Bay.

Boundary mixing and lateral dispersion. Tyler's current meter study [79] was done in conjunction with dye tracing of a 22-meter subsurface chlorophyll maximum of a red-tide dinoflagellate near the Bay Bridge. Three strings of current meters were moored at 38° 58' N lat. south of the Bay Bridge, and three strings were moored north of the bridge at 39° 2' N lat. Each string had three or four meters (depending on the water depth), and current data were recorded from 1 May to 12 May, 1980. Again the 12-day average of the non-tidal velocity showed the two-layer circulation pattern predicted by Pritchard [59, 61] with maximum velocities of 10-16 cm/sec. In addition to the longitudinal non-tidal currents, the isotach contours of the cross-channel currents at 38° 58' N lat. averaged over the 12-day period showed a mean convergence at the interface of the two layers. Phillips et al. [57] showed in the laboratory that a similar flow pattern results from boundary mixing along a sloping wall and produces a third layer in the middle. Their experiment suggested that, in a tidal estuary like the Chesapeake Bay, a mean lateral circulation develops with an intrusion from the boundary layer into the pycnocline. This lateral convergence in the pycnocline is compensated for by a divergence in the homogeneous layers below and above the pycnocline. The Phillips et al. conclusions are supported by Tyler's observations [80] of weak lateral dispersion and some vertical spreading of a Rhodamine dye patch injected in the lower part of the pycnocline below the Bay Bridge.

Estuarine and plume fronts. Small-scale fronts occurring along the shallow side of the Bay and near the mouth of the tributaries on time scales of a tidal period can be important factors in vertical and lateral mixing of the water column and the development of an unsteady lateral circulation. Bowman and Iverson [9] described the physical mechanism leading to frontogenesis for both estuarine and river plume fronts.

Estuarine fronts can extend several kilometers along the side of the estuary [9, 44] and have a lifetime on the order of a tidal period. In the Chesapeake Bay, estuarine fronts are most likely to occur along

the eastern side of the Bay where the pycnocline is tilted upward and the river runoff is smaller than on the western side. There, tidal bottom mixing can homogenize the shoaling water when the tidal currents are large, causing the pycnocline to break the surface and creating a front [2]. Beardsley and Boicourt [2] attributed the occurrence of lateral fronts in the lower Chesapeake Bay to a combination of factors: an increase of the gravitational circulation (in geostrophic balance), the addition of fresh water from the western side and the widening of the bay south of the Patuxent River. Aerial photography [44] of several estuarine fronts inside Delaware Bay showed strong convergence velocities (~10-20 cm/sec) associated with the fronts. This unsteady lateral circulation is very efficient at accumulating organic and toxic material. Seliger et al. [71] observed increased phytoplankton production in interfrontal regions of the Chester River. Garvine [29] suggested that both vertical and lateral mixing could be important components of lateral fronts.

Plume fronts often form where the freshwater runoff from the tributaries discharges into the estuary [9]. Plume fronts have also been observed inside the tributaries, at flood tide [13]. These plume fronts are similar to the larger estuarine plume discharging on the continental shelf [28, 30] described in COASTAL PLUME AND ESTUARY-SHELF INTERACTION. Byrne et al. [13] showed that a plume front is a persistent feature of the flow at Hampton Roads in the lower James River, which plays an important role in retaining oyster larvae within the James River estuary. Although the driving mechanism for a plume front (buoyancy spreading) is different from that of the lateral estuarine front (tidally generated bottom mixing), the two types of front appear to have similar properties (cross-front convergence and intense vertical and lateral mixing).

Lateral seiche. Dyer [18] and New and Dyer [48] showed that lateral first- and second-order surface seiches interacting with the longitudinal currents and topography could generate lateral internal waves several times during the tidal cycles. Their observations were made in Southampton Water, a partially mixed estuary, 10 km long, 2.5 km wide, and less than 13 m deep. Dyer [18] proposed that these lateral internal waves would move the pycnocline closer to the high-shear bottom layer when resonant conditions were satisfied. Near the bottom, the velocity is stronger and the local Richardson number (a measure of the flow dynamical stability) could fall below the critical value necessary to produce turbulence. Although lateral seiching has been frequently observed in the Chesapeake Bay, it is not clear whether it could generate large enough velocity shears to produce turbulent mixing.

SUMMARY

Our present knowledge of the physical processes that control circulation and mixing in the Chesapeake Bay is very incomplete. The external energy sources driving the circulation (tides, wind forcing, solar heating, freshwater discharge, and oceanic coupling) have been identified, but their effects on the circulation are only qualitatively known. In contrast, fundamental questions remain about turbulent mixing processes in the Bay: what are the generating mechanisms, where and when do mixing events occur, and how do they affect biological productivity.

Gravitational, tidal and sub-tidal circulations combine to set the local currents, stratification, and vertical shear. The vertical shear is important in creating and sustaining mixing events. It gives a qualitative measure of the kinetic energy available for vertical mixing. In turn, vertical mixing is an important process in partially mixed estuaries. It determines the vertical distribution of salinity, temperature, dissolved oxygen and nutrients, but it has not been localized or quantified in time and space. Studies by Partch and Smith [54] and Brandt et al. [10] have underlined the highly time-dependent nature of mixing events in partially mixed and salt-wedge estuaries, although much more remains to be done to uncover the long-term effects of the various transient events.

The mean estuarine circulation consists of a two- or three-layer flow, but the vertical and horizontal resolutions of past current meter moorings have been insufficient for a definite conclusion. High-resolution (1 m vertically and 100 m horizontally) current profiling in the mid-Chesapeake Bay with an Acoustic Doppler Current Profiler revealed a three-layer circulation during part of the tidal cycle. This study emphasizes how poorly the shape of the current profile is known in the Bay and how it varies during a tidal cycle. We need to accurately determine the shape of the current profile (two, three, or more layers) and the relationship between the shear and the density profiles to quantify the dynamical stability of the flow. Once the dynamical stability of the flow is known, it will be possible to estimate when and where mixing will occur. As can be seen in the data of Goodrich et al. [34], the existence of a strong vertical shear is a necessary condition for complete vertical mixing.

Past studies were based on the premise that the two-layer non-tidal circulation observed in the smaller

tributaries also applied to the Bay proper. The scale difference between the Bay and its tributaries contributes to making the circulation of the tributaries simpler than the Bay's. Since the tributaries are narrow, very little transverse variation in the flow is possible except near river bends where curvature effects are important, and wind forcing tends to be simpler. Also, the effects of the earth's rotation are small, as the internal Rossby radius of deformation (a measure of the width required for propagating long period internal waves in a channel) is larger, at 100 km, than the width of most tributaries (4 to 7 km, depending on the stratification). In the Bay proper, Kelvin waves can freely propagate and a longitudinal Ekman transport can be set up. Although few direct observations have been made [13], large-scale eddies generated by the fresh water inflow, topography and coastline variations are likely to exist. These eddies could play an important role in the horizontal turbulent mixing and dispersion of water properties and momentum.

PROSPECTS FOR FUTURE RESEARCH IN THE CHESAPEAKE BAY

Future research on the oceanography of the Chesapeake Bay should emphasize identifying and assessing the relative importance of all the physical processes driving the circulation and turbulent mixing. Such knowledge is a minimum requirement for the development of three-dimensional numerical models of the circulation of the Chesapeake Bay with a predictive ability. Two complementary sets of observations using new technologies developed for open ocean research should be conducted.

Long-term Monitoring

First, surface features such as eddies, fronts, and plumes should be observed synoptically with remote-sensing (satellite and aircraft) and land-based (CODAR) instrumentation. Satellite instrumentation can now measure surface wind, ocean surface topography, sea surface temperature, and chlorophyll concentration on 1-km scales. These observations should be complemented with higher-resolution (10 m scales) and more accurate aircraft measurements, as well as surface current measurements using a CODAR system such as the one deployed in Delaware Bay [1, 55]. A similar system could be deployed in the Chesapeake Bay and combined with the remote sensing observations of the surface temperature and phytoplankton concentration to define the general circulation of the Chesapeake Bay and validate the numerical models. Ultimately, the surface observations should be complemented with high-resolution in-situ vertical measurements from ships and moorings.

Second, long-term stations with high vertical resolution comprising upward-looking acoustic Doppler profilers (currents), CTD, dissolved oxygen and microstructure (kinetic and potential energy dissipation) mooring should be used to quantify the seasonal and meteorologically induced changes in the vertical distribution of properties, examine the development and erosion of the pycnocline, and estimate the intermittency of mixing events. These stations should be located in the Bay proper along the deep channel, and should be complemented with meteorological land-based stations. The long-term observations should also be used to calculate budgets for mass, heat, salt, momentum, and energy.

Studies of Specific Processes: A Multidisciplinary Approach

First, the development of anoxia and its consequences on the environment should be studied. Detailed field studies aimed at capturing the formation, break-up, and ventilation of anoxic regions should clarify the processes involved and the precise conditions necessary for break-up. Measurements must be frequent and of high resolution, particularly in the vertical dimension, if they are to catch the transient but important mixing events. These measurements should be combined with measurements of bacterial and benthic oxygen consumption measurements in order to model the oxygen budget.

Second, relationships between physical processes and larval recruitment at the mouth of the Bay should be clarified. This type of study should be aimed at determining the variations in recruitment of larvae (e.g., blue crab, croaker, and menhaden) from the ocean into the Bay due to natural physical processes (gravitational, tidal, and meteorologically induced flows) at the mouth of the Bay. Acoustic sensors with multiple frequencies may be useful for measuring larval concentration. These measurements should be conducted during or shortly after wind events (Goodrich, pers. comm., 1987).

Third, the influence of wind-induced mixing on primary productivity should be studied. Wind-induced mixing events produce temporary breakdowns of the pycnocline resulting in discrete bursts of nutrient input to the surface. This intermittent change in environmental conditions affects plankton productivity, and therefore affects the whole ecosystem.

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Genetics and the Conservation of Estuarine Species

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INTRODUCTION

The physical and chemical structure of an estuary presents organisms with a mosaic of habitats to which they must adapt. The two most obvious features of this environment are the saline and thermal gradients produced by the interaction of fresh water from rivers, land runoff, and rain with water of oceanic salinity. As discussed elsewhere in this volume, the interaction of these two water masses, coupled with physical features such as topography, wind forcing, and tides, produces a complex and variable environment. This environmental mosaic presents many challenges to species that depend upon estuaries during all or part of their life cycles. A species may respond with a single, broadly adapted form, or it may subdivide into many local populations, each adapted to a narrow range of environmental conditions. Understanding which of these adaptive responses has occurred in a particular species is critical for both conservation and management.

Evidence of adaptive response by a species can be derived from studies of morphology, physiology, demography, ecology, or genetics. In general, such studies compare the characteristics of two or more groups of individuals separated in time or space and seek to infer similarity or difference. These studies take on added significance when the characteristics used have a known pattern of origin and transmission, as is the case with genes. Differences of morphology or physiology can be misleading because they may represent transient responses to the environment by individuals that are genetically alike. Conversely, because not all genes have morphological effects, individuals that appear to be identical may be genetically unlike. Studies of genetic composition will look past surface similarities and differences to the permanent characteristics of an individual. Any differences in genetic characteristics must represent differences in parental background, and such differences arise only from mutation followed by differentiation, either through drift or through natural selection.

Except for a small number of domesticated species where pedigrees are well known, data on genetic relationships come from analyses of nuclear genes or their protein products. The total genetic variation obtained from these data can then be divided into variation within populations and variation between populations [35]. At the extremes, a species may form a single unit which contains much variation, uniformly distributed, or it may form many quite different units, each one uniform within itself. This range of possibilities is referred to as genetic structure. Where along the continuum of possibilities a species falls depends in part on the patchiness of the environment and in part on the biological characteristics of the species—its dispersal capabilities, its

reproductive schedule, and its typical population size. Because the genes with all their variants represent the permanent heritage of a species, efforts to preserve or protect an organism must rest on an understanding of its genetics.

GENETICS AND CONSERVATION

Conservationists and resource managers must make a fundamental decision on the intensity of intervention for any species that is either threatened or in need of management for greater productivity. While in real instances their strategy will often be mixed, the choice is among four levels of increasing intervention: (1) to protect existing natural populations through control of harvesting; (2) to enhance reproduction and survival through the creation of suitable habitat; (3) to supplement natural recruitment with captive-bred and released individuals; or (4) to attempt full domestication so that natural populations are not harvested at all. An understanding of the genetic structure of the species is essential at this stage. No matter what a program's goal may be, the manager must know whether the species involved has many highly differentiated populations or whether it is genetically similar throughout its range. A high degree of differentiation implies isolated gene pools and genetic adaptation to highly localized conditions. Interference with such a system risks destroying that adaptation, with irreversible loss of genetic potential. When a species has a more uniform distribution of genetic variation, managers and conservationists can act more freely.

If the manager's choice is protection or enhancement, the effort must extend over a much wider area, must be tailored to each site and must include detailed monitoring of many local populations when the species is highly differentiated [35]. When the choice includes captive propagation, the manager must be aware of the genetic background of animals chosen as breeding stock and must consider what genetic impact captive-bred animals may have on natural populations in the areas where they are released. When a species is highly differentiated, release of genetically incompatible animals may in itself cause disruption or extinction of the native population. Even when the species involved is genetically uniform throughout its range, release of hatchery-bred individuals should be done cautiously. The manager must guard against the unintended genetic drift and loss of useful variation that can occur when a small number of parents produces all the animals released [1, 21, 35]. Another problem against which the hatchery manager must guard is inadvertent selection in favor of traits that enhance survival in the hatchery but are deleterious in nature. A system of genetic monitoring can detect such changes before they become a serious problem.

On occasion, the manager may wish to produce animals different from those in wild populations and here captive breeding offers a special opportunity. If the situation warrants, managers may attempt to influence the genetic composition of a natural population through the release of genetically improved individuals. Such a situation may arise when a newly introduced disease threatens unprepared natural populations, as has happened with the disease MSX infecting oysters in the Chesapeake. If full domestication is the choice, then careful selection of broodstock from the wild followed by selection of genetically improved animals will be the normal course. For this review, we focus on genetic information useful to managers and conservationists as they decide on measures to protect the living resources of the Chesapeake Bay. In particular, we assess the evidence on genetic subdivision and local adaptation for selected species.

METHODS OF GENETIC ASSESSMENT

The most direct method of genetic assessment is analysis of the breeding results of controlled matings. In some cultured species, genetic relationships among individuals can be calculated directly from pedigrees that trace the parentage of individuals back to a few wild-caught ancestors. Such data are available for catfish, salmonids, and a few other freshwater species. For invertebrates, similar records are kept on certain hatchery-bred stocks. These stocks are mass-mated, however, with both identities and numbers of parents known only approximately, so that analysis is complex. The pedigree method also has the substantial disadvantage that the species must be breedable in captivity. Molecular techniques developed over the past few years avoid this problem and allow one to infer actual genotypes to individuals for which no breeding data are available.

The molecular method longest in use is gel (either starch or acrylamide) electrophoresis of enzymes and other proteins. It is based on the well-verified principle that genes are DNA sequences which directly encode protein sequences. If a change in DNA sequence produces a change in a protein, it often also changes the electric charge or the shape of that protein. Electrophoresis separates proteins according to their movements in an electric field, the rate of which depends on a combination of molecular charge and size. The investigator then employs a specific stain to identify a particular enzyme known to be the

product of a single gene. Each mobility variant is believed (and sometimes verified) to represent a different allelic form of the gene produced by a mutation. The method is indirect and cannot detect all variants, but electrophoretic surveys have the advantage that many individuals can be examined for a large number of genes relatively quickly, often without killing the organism. Most judgments about genetic structure, genetic relatedness, and speciation are based on these data.

Sometimes, useful genetic information can be developed from karyotyping, that is, the microscopic examination of chromosome numbers, sizes, and shapes. This technique has been very fruitful with mammals. Fish, however, are remarkably uniform in their chromosome numbers, and the techniques that work so well in mammals have not proved transferable to these animals. Menzel [28] has pioneered the application of the technique to bivalves, but again the transfer of a technique developed for mammals has been too difficult to permit general use.

In the newest and most direct molecular method, the DNA sequence of a gene is determined directly for each individual. Comparison among individuals and populations, however, requires that the gene be recloned and resequenced separately for each individual. Because this technique is extremely laborious, an approximation of it using restriction enzymes and mitochondrial DNA, rather than nuclear DNA, is growing in popularity [3]. Mitochondrial DNA (mtDNA) is a small, circular DNA molecule that codes for only a few genes and is found in the mitochondria within the cells of all eukaryotic organisms. It can be purified separately from the nuclear DNA that encodes most of a cell's genes. After isolation, the mtDNA is treated with restriction endonuclease enzymes that cut the DNA only where a specific sequence is present. The resulting fragments are separated by gel electrophoresis (much as in the enzyme technique) and their lengths estimated from their mobilities. If mutation causes a new site to appear, a smaller fragment will be found; and if a mutation causes a restriction site to disappear, a new and larger fragment will be seen. The method permits one to construct maps of these sites and compare them among individuals. Unlike nuclear genes, which follow the rules of Mendelian inheritance, these mtDNA variants are maternally transmitted. Only the mitochondria present in the egg appear in the progeny, while the mitochondria present in the sperm are lost. This fact makes mtDNA particularly useful for the assessment of geographic limits of lineages, of colonization patterns, and of contribution by individual lineages to recruitment in a given year. Protein electrophoresis is the more useful technique in determining the genetic structure and genetic identity of a species.

Seldom have all of these techniques been used in the study of a single organism. Data from enzyme electrophoresis are available for many species in diverse phyla, while mtDNA data exist primarily for vertebrates. Studies based on chromosomal analysis or pedigrees are very rare. For this review, we focus our attention on a few well-studied organisms that are also of biological, recreational, or economic importance to the Chesapeake Bay. We have selected the mummichog *(Fundulus heteroclitus)*, the striped bass *(Morone saxatilis)*, and the white perch *(Morone americana)*, from the fishes, because these species represent sedentary, anadromous, and semi-anadromous life histories, respectively, and because their biology and genetics are better known than those of most species. Some fish species not considered here have been the subjects of interesting studies that specialists will wish to consult: the American eel [4, 41], menhaden [19], sea trout [34], Atlantic croaker [40], and blue fish [40]. From the bivalve mollusks, we have chosen to review the blue mussel *(Mytilus edulis)*, the hard clam *(Mercenaria mercenaria)*, and the oyster *(Crassostrea virginica)*, for much the same reasons as the fish were selected. Because of its great importance in the bay, we have included the blue crab *(Callinectes sapidus)*, although virtually nothing is known of its genetics. We have excluded estuarine plants entirely because so few data exist for them. For extensive references to work with terrestrial plants and animals, the reader may consult Schonewald-Cox et al. [35].

FINDINGS FOR FINFISH

Fundulus

Studies of the mummichog *(F. heteroclitus)* provide and excellent example of what can be accomplished when the techniques of molecular genetics are combined with those of physiology and ecology to explain the distribution, abundance, and evolutionary history of an organism. For a comprehensive review of this effort, readers should consult Powers et al. [31]. Several investigators have demonstrated that different electrophoretic variants of a gene can affect traits important to the survival of an individual. A series of studies on *Fundulus* have shown that respiratory stress triggers hatching [16] and that the enzyme lactate dehydrogenase, form B (LDH-B) influences the oxygen carrying capacity of the blood. Finally, DiMichele et al. [17] demonstrated that embryos with different genetic forms of LDH-B

differed in their hatching times. Investigation of other genes with electrophoretic variants shows that some of these variants also have a very significant effect on developmental time [32]. All of these studies and many more on a variety of organisms suggest that electrophoretic variants of enzymes represent heritable variation traits important to evolutionary fitness. Thus, populations can diverge genetically in the process of microevolution to produce locally adapted races.

Evolutionary biologists believe that microevolution proceeds either by random change (drift) or by directional change (selection) in the frequencies of these variants and of other genes [18, 35]. If this belief is correct, then examining the pattern of gene frequencies throughout the range of a species will show whether that organism forms locally adapted races. Sometimes, such information will also provide clues about the evolutionary forces that are acting and the amount of genetic exchange between areas [18]. Powers et al. [31] summarized investigations of the geographical distribution of variants for 16 genes in *F. heteroclitus* along the eastern coast of North America. These investigators found a clear differentiation into northern and southern populations, with a sharp cline in gene frequencies around 41° N lat. This pattern repeats itself within the Chesapeake Bay, where fish from the fresh headwaters of the rivers show the "northern" suite of variants, while fish near the mouths of the rivers and the entrance to the bay show the "southern" set.

Such a pattern has two possible explanations. A series of clines might each be maintained by active selection and represent adaptation to salinity and/or temperature gradients. Conversely, *F. heteroclitus* might form just two broadly adapted subgroups. In that case, the northern types within the bay would represent refugees trapped after the last glaciation as water temperatures rose and organisms that were adapted to low temperatures retreated north. Studies of mtDNA sequences are well suited to distinguish between these possibilities. Gonzalez-Villasenor and Powers [31 and unpublished] have examined mtDNA frequencies in four samples of *Fundulus* and found a clear distinction between fish on each side of the line at 41° N lat. Fish from specific localities above and below this line could be interrelated through a series of single DNA alterations. Powers estimated that the two groups differed by a minimum of nine changes in their mtDNA. The length of these series and the extent of the differences indicate that these two groups have been separated for at least several thousand years. This conclusion clearly supports the refuge interpretation of the electrophoretic data.

Because more information is available for *Fundulus* than for other species of fish, the mummichog can serve as a model for other, less well understood, systems. Genetic and biochemical evidence of the sort outlined above provides guidance to anyone interested in managing or protecting this species or species with similar life history strategies. *F. heteroclitus* does not migrate extensively either before or during sexual maturity, yet a large proportion of the genetic variation in this fish exists within populations rather than between them. Recognition of just two long-standing subgroups in this fish, and the association of those groups with adaptations to northerly or southerly environments, indicates that species like this one can be managed over broad areas rather than river by river.

Striped Bass

Unlike *Fundulus heteroclitus*, the striped bass *(Morone saxatilis)* has a typical anadromous life history. The fish spawn in the low-salinity tributaries to the Chesapeake Bay and then enter the oceanic environment to grow and mature. Early efforts to identify distinct subpopulations of *M. saxatilis* focused entirely on morphological differences (such as fin ray numbers and body proportions) among fish taken from various rivers [36]. More recent studies employing electrophoresis of serum transferrin and other proteins as well as morphometric traits have produced conflicting results. Using these techniques, Morgan et al. [29] distinguished four assemblages of bass from the Choptank, Nanticoke, Elk, and the Patuxent-Potomac rivers. However, Sidell et al. [37] were unable to replicate these results using the same techniques. Berggren and Leiberman [5] were able to discriminate fish from the major regions of the Atlantic coast—Chesapeake Bay, Hudson River, and Albemarle Sound—but they could not replicate the earlier genetic distinctions among Chesapeake Bay stocks. In part, the lack of agreement in these studies is due to the limited amount of genetic variation shown by *M. saxatilis*. In a typical species of fish, 30% of the genes will be variable. In striped bass, only 3 of 56 genes tested (5%) had more than one variant [38]. Very few species of any organism show such low levels of genetic variation.

Because of the conflicting findings based on morphology and nuclear genes, Chapman and Powers [14] initiated a study of mtDNA variation in striped bass from the Chesapeake Bay and from Dan River, NC. They found that *M. saxatilis* from these areas consists of 14 distinct matriarchal lines whose frequencies differ significantly both between the Chesapeake and North Carolina sites and among four

major regions of the Chesapeake. On the basis of mtDNA sequence differences, these investigators recognized four major subpopulations in the Bay — Worton Point, Choptank, Patuxent-Potomac, and Rappahannock. Their data also support a separation between fish from the Patuxent and Potomac areas, whereas previous studies could not find significant differences. Overall, the work on striped bass shows a species that can be subdivided but that has limited genetic variation and is not strikingly different from place to place.

A more important finding in Chapman and Powers's study concerns recruitment and the source of each year class. Table 1 summarizes the data for the 1982 cohort of striped bass sampled over a three-year period [14]. These fish contained a new mtDNA sequence that had not been detected among the adult females that presumably produced the cohort. This sequence, designated "C," was found in 25% of the males from the 1982 cohort taken on the spawning grounds in 1984, 53% of the 1982 females taken near Hart-Miller Island in February of 1985, and 50% of the 1982 males taken on the spawning grounds in 1986. Furthermore, male mtDNA sequences differed significantly in frequencies among the spawning areas in the 1984 sample but not in the 1986 sample. These data present two challenges to our understanding of population dynamics in this fish—to understand the origin of the new sequence and to explain the marked change in its frequency over time.

The large increase in type C frequencies between 1984 and 1985 may be caused by migration into the Maryland portion of the Chesapeake Bay from localities where this type is more common. Data from distant areas are simply not available, but the life history of *M. saxatilis* [36] suggests that this explanation is correct. Striped bass do not migrate extensively from their natal rivers during the first two years of life. After this sedentary period, fish move into the deeper portions of the Bay, where the histories of males and females diverge. During their third and fourth years, females migrate offshore, and most do not return until age five or six when they spawn for the first time. Males reach sexual maturity at age two. Because they do not migrate extensively at this age, their mtDNA frequencies in a given spawning area reflect the contribution of matriarchal lineages within that area two years earlier. Males do migrate extensively within Chesapeake Bay between the ages of two and five years, after which they begin oceanic migrations. Thus, mtDNA frequencies in males that are two years old may differ among spawning grounds due to the influence of matriarchal ancestry, but extensive mixing after this age obliterates these differences among aggregations of males. If this hypothesis is true, a survey of females from the 1982 cohort during their first spawning run in 1987 should reveal differences among spawning aggregations around the bay. The samples necessary to examine this hypothesis have been collected, but the mtDNA data are not yet available.

Table 1. Numbers observed for each mtDNA genotype in adult females during 1984 and in the 1982 cohort of fish during a three-year period [14].

Fish tested			mtDNA genotype				
Cohort	Collected	Sex	A	B	C	D/E	F
Adult	1984	F	7	24	0	2	1
1982	1984	M	11	43	18	0	0
1982	1984	F	4	16	23	2	2
1982	1986	M	2	21	34	4	8

The life history strategy of *Morone saxatilis* produces a complex demographic structure. Whether genetic mixing is sufficient to prevent-long term differentiation is not yet clear, but the appearance of a new mtDNA sequence in young fish that was not detected in spawning females suggests that an additional factor is acting. Clearly the C sequence must have been present in breeding females, because it is far too frequent in the 1982 cohort to be a new mutation. It is plausible that the C form was sufficiently rare to be overlooked in the survey by Chapman and Powers but that females of this type contributed a disproportionately large number of progeny to the 1982 cohort.

The hypothesis that a large percentage of a year class are the progeny of a small proportion of available females may, in conjunction with population declines over the past 15 years, explain the disparity between the findings of Morgan et al. [29] and those of later investigators [5, 37]. The hypothesis may also explain the remarkable lack of protein variation in *M. saxatilis*. Both a declining census and an unequal contribution to recruitment will reduce the "effective" size of the population and increase the rate of genetic drift (i.e., random changes in gene frequencies and loss of variant forms) to produce a classic "genetic bottleneck." Morgan and his group collected their data primarily in 1967, before the decline in numbers of striped bass began, whereas Grove's and Sidell's work coincided with rapidly falling numbers. It is quite possible that the conclusions of each study were correct at the time but that the genetics of the species changed between one study and the next. Morgan

(pers. comm.) has noted the complete elimination of infrequent transferrin types from the Potomac River bass over the past 15 years. If the conclusion that *M. saxatilis* has experienced a severe genetic bottleneck can be substantiated, it will have profound implications for the protection and management of this species. Ongoing studies of mtDNA frequency distributions should provide an answer. If this study substantiates the hypothesis that loss of variation is a recent event, conserving what variation does remain must be a very important aim of all captive breeding programs.

White Perch

Studies of the white perch (*Morone americana*) are important in their own right and also because they provide a comparison to the closely related striped bass. Conclusions for each species are more robust in the context of conclusions for the other. *M. americana* is abundant and widely distributed along the eastern coast of the United States. It has a semi-anadromous life history. Like the fully anadromous striped bass, it migrates from the low-salinity mouths of rivers into fresh headwaters to spawn, but, unlike *M. saxatilis*, it does not migrate into the high-salinity waters of the main bay and ocean. In a tagging study of *M. americana*, Manseuti [27] found that Patuxent River animals rarely migrated to adjacent areas and concluded that this population should be managed as a single stock. Woolcott [1961], using meristic and morphometric characters, found evidence that supported Manseuti's conclusion and extended it to include most riverine populations in the Chesapeake Bay.

In the early larval stages, *Morone americana* is extremely difficult to distinguish from *Morone saxatilis* and studies of larval recruitment in these species are difficult. This problem led Morgan [29] and Sidell et al. [37] to develop electrophoretic methods for distinguishing larvae of the two fish in mixed collections. Morgan used general protein staining of soluble muscle proteins separated on polyacrylamide gels, while Sidell's group employed enzyme-specific staining and starch gel electrophoresis. Each method has its advantages and both provide unambiguous and relatively rapid species identification. However, neither study was intended to assess the overall amount of genetic variation present in *M. americana* or the genetic structure of this species.

Studies in progress by Mulligan and Chapman [30] and by Bowen [6] on mtDNA sequences provide some information on the genetic background of white perch in the Chesapeake. Mulligan and Chapman have found evidence that *M. americana* forms only three distinct groups within the bay: (1) a southern assemblage inhabiting the James and York rivers, (2) a Potomac population, and (3) a large upper-Bay assemblage encompassing all western shore tributaries from the Patuxent north and all eastern shore tributaries north of the Nanticoke. Bowen's work suggests that the white perch in the Rappahannock also form a group distinct from all others. These mtDNA data on genetic divergence, together with the observation that *M. americana* prefers water of low salinity (<10 ppt), suggest that water of high salinity at the mouths of the southern tributaries is an important barrier to movement in this fish. This hypothesis should be confirmed and the genetic structure of this species determined by a survey of electrophoretic variants of nuclear genes.

FINDINGS FOR INVERTEBRATES

Blue Mussel

Just as *Fundulus heteroclitus* is among the most thoroughly studied of the fishes, the ecological and evolutionary genetics of the blue mussel (*Mytilus edulis*) are among the best studied of any mollusk. Much of our understanding of allozyme genetics in natural populations of bivalves comes from the work of Koehn's laboratory with this mussel (for a comprehensive review see [26]). Several studies have demonstrated that individuals with different electrophoretic variants of enzymes (hence of genes) have different tolerances for environmental factors. Evidence is also strong that survival and vigor increase with increasing heterozygosity (possession of two different variants for a given gene). These findings imply that if *Mytilus* forms distinctive local races, that fact will be reflected in distinctive local frequencies for electrophoretic variants. These studies also suggest that inbred, highly homozygous animals will be less fit than outbred individuals with large amounts of genetic variation.

Virtually all of the data on geographic variation in *M. edulis* comes from studies of electrophoretic variants of enzymes, and a clear pattern has emerged from these studies [26]. Gene frequencies are relatively uniform over large areas, with an occasional abrupt change in frequency over a short distance. The evidence is clear that these sharp clines are maintained by natural selection acting on post-larval stages through increased mortality of less favored variants [25]. Thus *Mytilus* does show adaptation to environmental conditions. The geographic scope of these adaptations is a broad one, however, and one does not see highly differentiated local races with very re-

stricted ranges. The adaptations themselves are not extreme either. The same set of variants is present at both ends of a cline with only the relative frequencies of the individual types changed. Each cline is opposed by the mixing of pelagic larvae of all types from both ends, and this mixing is in most cases sufficient to prevent the formation of distinctive local races.

The same pattern occurs in European waters where a second species, *Mytilus galloprovencalis,* is also present. The two mussels can be distinquished by their electrophoretic variants, but neither shows a high degree of differentiation. The first study of mtDNA sequences in these animals confirms the findings of earlier studies [39]. Much less is known about other genera of bivalves, but whenever a species has a planktonic larval form, isolated local races seem not to form.

Hard Clams

Like the blue mussel, the hard clam *(Mercenaria mercenaria)* shows very little differentiation in the frequencies of electrophoretic variants along the Atlantic coast of Virginia [2]. Unlike *Mytilus, Mercenaria* shows no significant changes in frequencies even across an extreme gradient in salinity. Because hard clams do not tolerate low salinities, they inhabit only the lowest portion of the Chesapeake Bay up to the mouth of the James River at a salinity of about 17 ppt. In the James River region, a polluted area at the limit of its salinity tolerance, these clams maintain gene frequencies like those along the ocean shore [7]. Data on mtDNA variation in *M. mercenaria* are now being gathered but are not expected to contradict the conclusion that these clams do not form genetic strains adapted to very localized conditions.

The State of Virginia supports a long-standing program of mariculture for hard clams, which includes efforts to produce genetically improved strains with increased growth rates. Although stocks that have been maintained by hatchery culture for several generations do show some effects of genetic drift, these effects are very minor and do not include either the substantial increases in homozygosity to be expected from inbreeding or a marked departure from the gene frequencies of wild populations [1]. Experience with these hatchery stocks demonstrates that there are no genetic barriers either to domestication or to release of hatchery individuals into natural populations.

Oysters

Abundant data are available for American oysters of the genus *Crassostrea* [23] with the commercially important species *C. virginica* [9] and the Pacific species *C. gigas* [10, 11] particularly well studied. Buroker [8] has made an extensive study of electrophoretic variants in *C. virginica* from 10 oyster bars throughout the main body of the Chesapeake. He found statistically significant differences in gene frequencies that permitted him to separate Bay populations into four assemblages, much as perch and striped bass can be divided. He recognized (1) an upper Bay assemblage of Broad Creek, Patuxent River, and Herring Bay oyster bars, (2) a mid-Bay region including Swan Point, Wicomico River and the Potomac Rivers, (3) a lower Bay group covering the Tred-Avon River, Pocomoke Sound, and the Rappahannock River, and (4) near the mouth of the Bay, the James River as a distinct site. The differences among the groups are subtle changes of frequency, not unique variants in each assemblage, and the genetic distances calculated by Buroker show very little differentiation. Buroker particularly noted that the differences in frequencies do not correlate with any obvious environmental variable such as salinity, water depth, or temperature. He concluded that these assemblages result from different mortality patterns among variants in different areas causing divergence in gene frequencies that are prevented from becoming distinctive local races by larval mixing each year. Such a process is much like the one demonstrated in *Mytilus edulis.*

Buroker's data apply to the main body of Chesapeake Bay. Rose [33] has determined gene frequencies in samples of oysters taken in transects from the mouths to the low-salinity limits of three Chesapeake tributaries—the Potomac, Rappahannock, and James rivers. Rose reasoned that if oysters did form local races in response to environmental conditions, this fact would be most obvious moving from the main bay to the low-salinity limit of the species. As Buroker had, Rose found significant differences in gene frequencies, but these differences were slight and followed no obvious pattern. No river had the distinctive set of frequencies that one would expect if the population within it were isolated. Neither did the observed differences in frequency correlate with distance from the mouth of the river, as one would expect if salinity were an important selective agent. Together, Rose's and Buroker's work clearly demonstrate that oysters do not form distinct races within the Bay.

Because oysters are extensively cultivated, they offer special opportunities for selective breeding as well as special problems in preventing loss of genetic variation in captivity. Both Pacific and Atlantic populations have suffered serious losses from disease

in natural populations, and oysters have been the object of intense selective breeding efforts on both coasts. In the State of Washington, Hershberger and his group [24] have worked to develop stocks of *C. gigas* resistant to summer die-off. They report considerable improvement after only a few generations of selection. Both these workers and Gosling [21] have determined that hatchery breeding and selection have not resulted in a substantial loss of genetic variability. This encouraging finding suggests that artificial selection can produce improved stocks that still maintain most of the species's natural genetic variation.

The most important disease of *C. virginica* along the Atlantic coast and in Chesapeake Bay is infection with MSX, (the protozoan *Haplosporidium nelsoni*). This disease can cause mortalities of more than 50% in a population, and an animal once infected does not recover. A team based at Rutgers [20] has bred for resistance to MSX for six successive generations of oysters from Delaware Bay. Their stocks are slower to develop infection even with severe challenge, and mortality in infected stock is later than in unselected lines. These stocks have not been tested for loss of genetic variation, but the results with *C. gigas* suggest that such loss will not occur. The hatchery at the Virginia Institute of Marine Science has combined use of wild broodstock with efforts to breed resistant oysters [12 and pers. comm.]. The oysters are released as newly set individuals in an effort to supplement natural recruitment. This operation spawns healthy animals taken from natural populations in an area that has experienced very high levels of infestation and mortality in the past. These oysters should represent survivors of intense natural selection while still representing native genotypes.

Blue Crab

Although the blue crab (*Callinectes sapidus*) has great economic and cultural importance in the Chesapeake Bay, very little genetic information is available for this species. What is known suggests that this species may be genetically similar over a wide range. In the only study available, Cole [15] compared crabs taken from the Choptank and Patuxent rivers within the Bay and crabs taken from Chincoteague Bay along the Atlantic coast of Virginia. While the straight-line distance between these sites is small, the dispersal path for marine organisms is enormous, going as it does from oceanic salinities to brackish ones and involving more than 100 miles of coastline. Cole found that although some differences in allele frequencies were statistically significant, the two samples were similar in overall genetic content. He attributed this fact to extensive mixing of larvae flushed into the mid-Atlantic Bight before reentering the Chesapeake. His findings are encouraging, but they require substantial amplification before any management decisions can be made. Cole's sample sizes were extremely small (only 24 crabs from each site), and he reported that the resolution for many of the enzymes was poor. Because these crabs are not at present bred in captivity, questions of hatchery impact are irrelevant. However, much more needs to be known about genetic variation in natural populations before any conclusions are made about natural subdivisions.

CONCLUSIONS AND RECOMMENDATIONS

All of the species reviewed here show a similarity in what is known of their genetic structures. Each shows a moderate amount of differentiation suggesting that populations in the upper, middle and lower reaches of the Bay develop slightly different adaptations. However, none of the species shows evidence of forming highly localized races adapted to fine gradations in the environment. From a manager's point of view, these findings mean that biological resources in the bay can be treated as a single unit if necessary, but that best practice is to recognize broad subdivisions. Although the genetic data give no special insight into what forces are endangering species in the bay, the results do show clearly that no damage is likely from reliance on captive breeding to supplement recruitment. Managers should continue to give strong support to the operation of hatcheries and to research on hatchery techniques for all important species.

For fish, future research should obviously focus on the endangered striped bass. This species shows clear evidence that its dramatic decline in population size has caused loss of genetic varitation. Hatchery operators should therefore take great care to have as many parents as possible contribute their genes to any fish bred for release into the wild. Genetic monitoring to ensure that inbreeding does not increase is very desirable. In conjunction with hatchery efforts, a study should go forward immediately to confirm or disprove the mtDNA evidence that a small proportion of adult fish contributes disproportionately to recruitment. Techniques exist to slow the rate of inbreeding in the smallest of populations [35], but these methods should not be applied until it is known whether great differences in fecundity exist between genetic variants.

Although this review has concentrated on large, economically and esthetically important species such

as the striped bass, no one should forget that plants and many individually insignificant animal species form the ecological foundations of the Chesapeake Bay. No amount of effort will sustain healthy populations of bass if that foundation is destroyed. For this reason, some research effort must go to obscure species rather than all effort being concentrated on only a few organisms. The program to protect the Bay would benefit from study of important forage species such as herring, anchovies, and menhaden.

Among invertebrates, the release of hatchery-bred animals to supplement natural recruitment is essential for oysters. The present research on remote setting of oyster larvae [12] should continue to be given a very high priority in combination with the development of disease-resistant broodstock. The efforts to breed MSX-resistant animals should be supplemented with efforts to develop resistance to another diseases and pollutants. The greatest assistance to existing programs of genetic selection for disease resistance would come from the development of a standardized assessment of larval performance and infection/resistance to MSX and other agents. Once such an assay exists, it should be used in a vigorous selective breeding program. Continued support should be given to programs that investigate the mechanisms of infection and mortality in oysters. The facts that oysters do not form highly differentiated populations and that they are routinely cultivated in hatcheries without loss of genetic variation offer a great opportunity to produce and release genetically improved animals without fear of damaging natural populations.

The need for basic research in population genetics is obviously greatest in blue crabs. While research on oysters has progressed into the area of practical applications, work on the genetics of crabs has been almost nonexistent. A survey of basic genetic variability, fitness differentials, and geographic differentiation should begin immediately so that data are available before management decisions are necessary. This information will be important when, as seems inevitable, new decisions about restriction of harvesting and protection of breeding stocks must be made. The most productive research would be an initial study of electrophoretic variation to discover whether locally adapted populations do exist. Such a study could examine a far larger number of individuals in a relatively short time than could a DNA-based survey, and Cole's work shows that such studies are possible. Any pattern of differentiation that the electrophoretic study reveals can then serve as a guide to the most promising areas of investigation for later DNA work.

Genetics can make a real contribution to the management and conservation of living resources in Chesapeake Bay. Because decisions are already being made that affect the genetic structure and perhaps future evolution of species in the bay, an informed understanding of these issues is essential. No amount of genetic manipulation will compensate, however, for lethal degradation of the environment. Therefore the most important task is simply to make the bay a cleaner, healthier habitat for all estuarine organisms.

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Chemical and Physical Processes Influencing Bioavailability of Toxics in Estuaries

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INTRODUCTION

The transport, availability, and impact of toxic substances in the Chesapeake Bay are matters of major concern to those charged with the management of the Bay. The human attraction to the coastline surrounding the Bay ensures that population and industrial growth will continue, and with it the loading of toxic substances. It is imperative, therefore, that we as a regional society address the potential toxic effect of anthropogenic inputs to the Chesapeake Bay. A number of factors, however, control the transport and impact of such substances. This chapter addresses several such factors, primarily the chemical and physical controls of pollutant availability.

Among the many factors altering the bioavailability of toxic substances, we may generally consider two major groupings. In the first group are processes that change the availability of the contaminant without altering the total amount present. This group of factors includes organic and inorganic complexation, ionic strength, pH, redox reactions, and competition with similar compounds. In the second group are processes that do alter the concentration of the contaminant within the system. Factors in this group include sources and sinks, such as adsorption, flocculation, sedimentation, and remobilization.

We also include a separate section discussing the direct and indirect effects that organisms have on the bioavailability of these compounds, even though individually these effects could be legitimately be considered as belonging to the first or second group of factors.

General Mechanisms of Uptake

It is useful to consider groupings of compounds that have similar patterns of availability to organisms. A focus of recent research has been the effect of chemical form, or speciation, of trace elements on their availability to aquatic biota. Generalizations concerning bioavailability are available for three groups of contaminants: cationic trace elements, anionic trace elements, and organic compounds (Figure 1).

For cationic elements, free ion activity appears to be the major factor determining bioavailability [4, 5, 36, 61, 96, 125, 150, 152, 153, 181]. The hypothesis that the free ion activity represents the sole (or most important) biologically available form can be derived from a thermodynamic model in which the ion is complexed by the active site of the enzyme where it interacts or where it passes across the cell membrane. Other chemical forms, however, may be available. For example, an uncharged complex may provide a second route of access to the cell. For grass shrimp (*Palaemonetes pugio*) [37] and several species of phytoplankton [132, 133], it appears that the calculated activity of the uncharged species $AgCl^0$ better explains the availability and toxicity of silver than does the calculated free silver ion activity.

For anionic trace elements (e.g., chromate, molybdate, selenate, arsenate, and germanate), bioavailability is most often controlled by competition for uptake with a similar nutrient ion of greater abundance (i.e., sulfate, phosphate, or silicate). For those elements whose availability varies inversely with sulfate (e.g., chromate [119, 120], selenate [136, 170], molybdate [26, 28]), salinity plays a dominant role in their bioavailability. Arsenate behaves as a phosphate analog [18, 115, 126], and germanate as a silicate analog [9], so the availability of these elements varies according to the concentrations of their

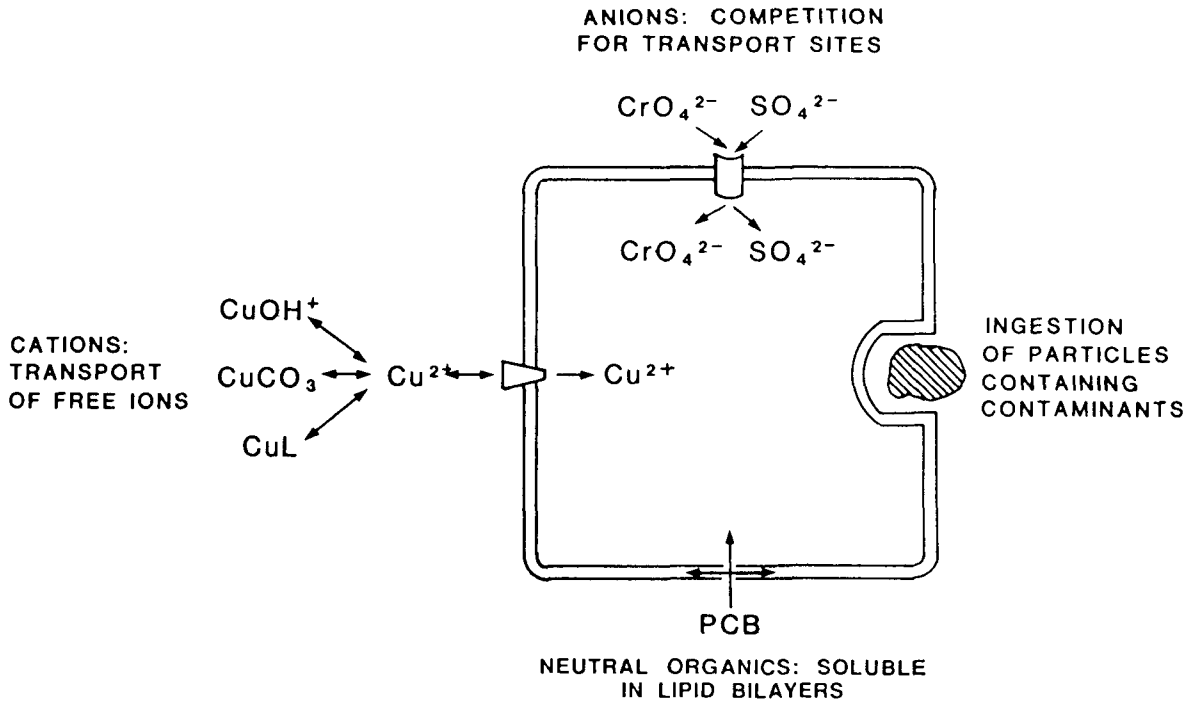

Figure 1. Dominant routes of uptake for three important contaminant classes.

analogs, which in turn are highly dependent on biological activity.

Many of the toxic organics are neutral xenobiotic compounds, and accumulation is presumed to occur via passive diffusion through semipermeable lipid bilayer membranes, such as epidermis, gills, gut wall, or in the case of microorganisms, cell membranes [117]. Therefore, the most available form for such compounds is often the un-ionized form. Ionized forms, as with trace elements, must rely on active transport sites, for which evolution has not provided many models. For neutral molecules, the lipid solubility of compounds is commonly measured in terms of their octanol/water partition coefficient (P_{ow}). This coefficient correlates well with bioaccumulation for a wide variety of organics, including polyaromatic hydrocarbons (PAH's), polychlorinated biphenyls (PCB's), and neutral pesticides [24, 55, 97, 108, 145, 163].

CHEMICAL FACTORS

In the Chesapeake Bay, salinity varies from fresh water at the river heads to 30 parts per thousand (ppt) at the entrance of the Bay; many other chemical parameters show similar gradients or local variations due to biological activity. Therefore, salinity and changes in other chemical parameters are major factors in the availability of many substances to organisms.

Ionic Strength

In concentrated salt solutions, the activity of an ion is reduced because of the interaction of its charge with other nearby ions. In general, the individual ion activity coefficient ranges from 1.1 for uncharged species to approximately 0.1 for triply charged species in full-strength seawater [148]. In practice, changes in bioavailability due to ionic strength alone must be considered in conjunction with changes due to inorganic and organic complexation. Powerful computers have made these calculations routine; several computer programs exist to calculate speciation (see [102] for a review of several such programs).

Inorganic Complexation

A number of ions are present in seawater in almost constant ratio to one another. Although these ions (sodium, magnesium, potassium, calcium, strontium, chloride, sulfate, bromide, and borate) and carbonate, bicarbonate, hydrogen, and hydroxide ions (which are not conservative, but rather vary somewhat with pH and biological activity), are not particularly strong complex formers, their concentrations in seawater are high enough that the most predominant chemical species of most trace elements and many other inorganic ions are ion pairs or other complexes with these ions. Other ions are of biological origin (e.g., sulfide) and have wide variation independent of salinity. They may be important, however, in deter-

mining the chemical speciation of inorganic pollutants under some circumstances.

Complexation of the various inorganic pollutants differs greatly. For example, the inorganic speciation of copper is dominated by complexation by hydroxide and carbonate species; it is only slightly complexed by the very abundant chloride ion [149]. However, silver and cadmium have comparatively high binding constants for chloride, and their inorganic speciation is dominated by chloride complexes [37, 76, 133]. The binding of various ions is a highly interdependent process since they compete for common ligands; however, the majority of the important equilibrium constants are well enough known that computer models can readily estimate the activity of most ions from their measured concentrations.

Organic Complexation

In addition to the inorganic ligands present in aquatic systems, organisms produce, through excretion, leakage, or decay, a variety of organic compounds that may also complex and reduce the free ion activity of trace elements. Levels of dissolved organic compounds (DOC) range from 0.1 mg/l in unpolluted fresh water to 1-2 mg/l in seawater to >10 mg/l in highly productive or polluted water. Concentrations in the Chesapeake Bay range from 1.9 to 13 mg/l [98, 99, 128, 142, 181]. The composition of the organic matter varies depending on the source, but it contains many functional groups with metal complexing capabilities. Unlike the situation with inorganic complexing ions, natural organics contain a large number of compounds of varying complexing strengths [34, 38]. Therefore, except for a few studies on specific chelators found to be excreted by algae, or released into the environment by human activity, the studies of complexation by natural DOC are largely empirical. Many biological and analytical methods of measuring the organic fractions of metals (or alternatively the metal-complexing capacity) have been devised [e.g., 86, 99], some of which are specific for certain types of complexes (e.g., polar vs. non-polar organics). It is extremely difficult to compare one method with another, and one site with another.

Only a few metals (iron, copper, zinc, and mercury, which have the greatest affinity for ligands) are complexed significantly by natural DOC. Some species of algae can secrete special iron-chelating compounds (siderophores), which solubilize iron and facilitate uptake [157]. The types of algae that exhibit this behavior include dinoflagellates [157], cyanophytes [83], and diatoms [158], which are common in the Chesapeake Bay, but the extent of production of these compounds in the Bay and their importance to the system as a whole is unknown. Copper is also organically complexed to a large extent (50-98%) [56, 92, 151, 187] by a variety of dissolved organic compounds, some of which are relatively labile and some of which are kinetically inert. In fresh water, where the source of DOC is highly variable, there is little correlation between DOC and copper complexation capacity between different sites; however, in marine and estuarine waters, including the Chesapeake Bay, where the DOC is largely of autochthonous origin and is more homogeneous on spatial and temporal scales, there is a significant correlation between DOC concentration and copper complexation capacity [99, 160].

Lipid-soluble copper complexes have been demonstrated to have exceptionally high bioavailability and toxicity [8, 19, 40]. The organic compounds used in these studies were synthetic, however, and the existence of similar compounds in the environment is unconfirmed. This mechanism could be important in the event of combined trace element and organic pollution.

The uptake of toxic organics can also be modified by the presence of natural dissolved organic compounds. The uptake of DDT by *Daphnia magna* from water is reduced by association of the DDT with dissolved humic material (S. Friant, pers. comm.). Presumably, the DDT-humic complex is more soluble and less lipophilic than DDT alone, so the uptake of DDT is controlled by the remaining unbound DDT.

pH

Many of the inorganic compounds important in the complexation of some toxic metals (e.g., carbonate, phosphate, and sulfate), as well as many of the pollutants, have equilibria dependent on pH within the pH range of aquatic systems [184]. Control of the relative abundance of such species through these equilibria is perhaps the most direct way in which pH determines the bioavailability of pollutants. In addition, the active site of most organic complexing agents are pH-sensitive groups (e.g., carboxylic acids, amines, and sulfhydral residues), so that pH has a strong influence on the extent to which organics complex toxic trace elements [86]. Finally, the active sites of enzymes and trace element uptake sites contain the same variety of pH-sensitive groups, and the activity of these systems varies with pH as well. In the case of enzyme systems, most have an optimal configuration over a narrow range of pH [137]. Thus, the effect of pH on the availability of a given compound to a particular organism in a specific site depends on a variety of effects, some of which (e.g., the effect of pH on inorganic complexation) are rather

straightforward to predict, while others (the effect of pH on organic complexation and on uptake) are rather difficult.

The input of acidic precipitation to the Chesapeake Bay watershed may be an important process. Rainfall with a pH as low as 3.8 has been measured within Maryland; within small streams such rainfall causes a pH reduction of up to 1.1 pH unit within four hours [6, 7]. Such events may lead to the mobilization of metals, or changes in the uptake of metals by organisms, but the duration of such events is limited, and their importance to the ecosystem is still being investigated.

pH can also play an important role in the bioavailability of ionizable toxic organic compounds. The uptake and toxicity of pentachlorophenol to goldfish (and probably most organisms), for example, is determined by pH, because of the equilibrium between hydrogen ion, pentachlorophenol, and the pentachlorophenolate ion [79]. Atrazine, an herbicide of interest in the Chesapeake Bay, is a slightly basic compound, so its solubility and bioavailability are also dependent on pH [177].

Redox Reactions and Equilibria

Several of the toxic trace elements participate in redox reactions that alter their biological availability. Most of the important redox reactions of trace elements are relatively slow compared to inorganic and organic complexation reactions. Most of the important redox couples are directly or indirectly the result of the activity of organisms, for without the constant formation of reduced compounds and oxygen by autotrophs from external energy, the world would eventually reach redox equilibrium.

In the sediments and bottom waters of the Chesapeake Bay, a strong oxygen demand is fueled by organic carbon from the highly productive surface waters. This demand produces anoxic, sulfide-rich interstitial water and seasonally anoxic bottom waters in the deep channel of the Bay. In such waters a variety of metals (arsenic, chromium, iron, manganese, and selenium) can be reduced to forms different from the commonly oxidized form. Arsenic, for example, is most stable in oxidized waters as the arsenate ion. However, in anoxic bottom and interstitial waters, arsenate is largely reduced to arsenite [111, 122, 129]. Arsenite in the sediments and bottom waters can diffuse or be mixed up into the surface waters, where it slowly oxidizes back to arsenate. Arsenate is primarily available and toxic to phytoplankton, which have a requirement for phosphate, while arsenite is more toxic to fauna [94, 109]. Selenium, which has selenate and selenite as the major oxidized and reduced species, probably undergoes a similar cycle, although selenite is apparently more stable under oxidizing conditions than arsenite [31]. Selenite is generally the more biologically active of the two forms of selenium, satisfying trace requirements at lower concentrations [116]. Anoxic waters also reduce the highly toxic (but relatively unavailable) chromate ion to chromite, which is much less toxic.

Indirect evidence suggests that sulfide is present in oxidized seawater and in the Chesapeake Bay at concentrations of 10^{-10} to 10^{-11} M (G. Cutter, pers. comm.) [35], enough to have significant effects on the speciation of trace metals such as silver and mercury. However, standard analytical techniques are not sensitive enough to measure sulfide at those concentrations. Moreover, in the Chesapeake Bay, where there is occasional anoxia and a constant source of sulfide diffusing from the sediments, concentrations are likely to be more variable.

Another source of reduced metal ions is photoreduction. The interaction of light or ultraviolet radiation on DOC or on metal organic complexes has been shown to directly reduce certain metal ions and to produce redox-active compounds such as peroxide or superoxide that can reduce metals. It has been shown that peroxide concentrations in the Patuxent River undergo a diurnal cycle, with concentrations increasing in the daylight hours and decreasing at night [77]. Peroxide, in turn, has been shown to reduce chlorine from industrial sources to chloride [63], reduce some copper(II) to copper(I) [93], and reduce and solubilize manganese dioxide to manganous ion [154]. DOC and light can reduce ferric iron to ferrous iron [67, 166]. Chromate is reduced photochemically in the presence of high DOC levels [121] (G. Helz and R. Kieber, personal communication), but it is unknown whether the photoreduction proceeds through peroxide or a similar intermediate. The importance of photoreduction in modifying the biological and chemical behavior of pollutants is not yet clear; however, since photochemical reactions are favored by the presence of high DOC and abundant light, shallow, organic-rich estuarine systems such as the Chesapeake Bay are likely to be sites where it is most important.

Organo-metallic Compounds

Several metals (antimony, arsenic, lead, mercury, selenium, and tin) are present in the Chesapeake Bay partly as covalently bound compounds (e.g., methylarsonic and dimethylarsinic acids [129,130], alkyl lead, methylmercury [185], organic selenium [156], methyl and butyltin compounds [47, 52, 53, 54, 169]). In

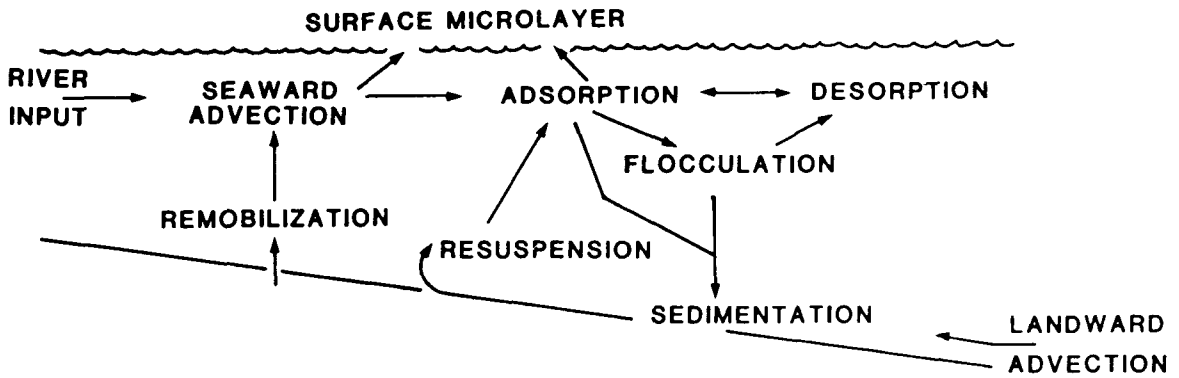

Figure 2. Processes affecting transport and availability in the Chesapeake Bay.

some cases (methylarsenic compounds, methyl mercury, organic selenium, and methyltins), these compounds are formed in the environment from inorganic metal by the local biota. In others (alkyl lead and butyltins) the compound is primarily anthropogenic, and the biota ultimately act to degrade the compound [106]. Metals can also be methylated by exchange reactions with other methylated compounds [13, 20, 85].

There are few direct comparisons of the bioavailability of alkyl compounds and their inorganic precursors, but in general it appears that their transport is enhanced by their greater lipid solubility. For example, in a study of the uptake of inorganic and methylmercury by the diatom, *Skeletonema costatum,* and the copepod, *Acartia clausi,* exposure to methylmercury resulted in much greater uptake of total mercury than exposure to inorganic mercury [43]. Certainly, toxicity is enhanced [23]. Methylated tin species are more toxic than inorganic forms, and di- and tri-substituted alkyls are more toxic than mono-substituted ones (J.J. Cooney, pers. comm.). For inorganic and organo-tin compounds, there is a general correlation between the P_{ow}, an index of the lipophilicity of the compound, and the toxicity to phytoplankton [174] and animals [186]. In Chesapeake Bay sediments, concentrations of tin are high enough to affect the microbial community, inhibiting sensitive species and probably selecting for resistant species and those able to methylate tin [53, 54].

As an example of how chemical factors combine to affect the bioavailability of contaminants in the Chesapeake Bay, consider the following. A strong negative correlation has been observed between salinity and the copper uptake and accumulation in natural Patuxent River oysters. This observation fits the expectation of increased copper availability at low salinity due to low ionic strength and less inorganic complexation [176, 181]. A similar negative correlation between salinity and copper in oysters has been noted Bay-wide [72]. Further research, however, using nitrilotriacetic acid-copper buffer systems, has shown a greater effect due to salinity than could be explained on the basis of free ion activity alone, which might be explained by competition for uptake with calcium or magnesium.

CONTAMINANT SOURCES AND PROCESSES AFFECTING DISTRIBUTION

In addition to the above-discussed factors which alter the bioavailability of toxic substances, there are also factors that control the total concentration to which organisms are exposed, factors that relate to the sources, sinks, and cycling of toxics in the Chesapeake Bay. These are discussed below and are diagrammed in Figure 2.

Sources

There are several sources of toxic substances to the Chesapeake Bay (Table 1). One of the most important is runoff of fresh water from the land. Industry, agriculture, and municipal effluents each contribute a significant load of compounds. Many toxic substances are present in the air as suspended particles (e.g., copper, zinc, and PAH) or as vapors (e.g., mercury, lead, selenium, arsenic, and volatile organics), and can be deposited by rain or through dry fall. Sampling aeolian deposition, however, is a difficult exercise, as it is extremely variable in time and space. Aeolian flux of some metals has been estimated for the Chesapeake Bay (Table 1) and the nearby Delaware Bay [25], and while the loadings are not large compared to runoff, they are significant. Aeolian inputs may be a particularly significant source to the surface microlayer (see below) where a variety of toxics are concentrated, and to areas remote from industry or other concentrated sources.

Table 1. Estimated sources of toxic trace elements, in metric tons per year, entering the Chesapeake Bay. Taken from Bieri et al. [17].

Source	Cd	Cr	Cu	Ni	P	Zn	Fe	Mn
Major tributaries	75	551	517	402	307	1444	199683	19000
Industry	178	200	190	ND	155	167	2006	ND
Municipal wastewater	6	200	99	ND	68	284	625	ND
Urban runoff	7	10	9	20	111	63	977	22
Shore erosion	1	83	29	ND	28	3	57200	ND
Wet fall	3	ND	28	25	34	825	87	15

ND=not determined.

Distribution

The Chesapeake Bay and similar estuaries are extremely dynamic systems, moving and changing constantly in response to winds, tides, and runoff, so it is difficult to discuss the distribution of a given toxic compound in the water except on a statistical basis. Nevertheless, some general trends in contaminant distributions can be discussed. Compounds whose source is in fresh water are inversely correlated with salinity, i.e., mean concentrations decrease from the head of the Bay to the ocean, and from tributaries to the main Bay. This pattern has been observed for metals such as cadmium, copper, and lead [78]. Conversely, for contaminants whose concentrations in seawater are normally higher than those in fresh water, a reverse trend is observed, with bottom water and more saline waters having higher concentrations [78, 129]. Elements that are reduced and solubilized in sediments (e.g., iron, manganese, arsenic, and zinc) also tend to be more concentrated in deep waters of the Bay [22, 78, 129, 159].

The phenomenon of seasonal anoxia in the Chesapeake Bay is undoubtedly a dominant factor in the spatial and temporal distributions of redox-reactive elements such as arsenic, chromium, iron, manganese, and selenium. Unfortunately, virtually no published studies on this aspect of the anoxia are available yet. This should be an active area of research in the near future.

Surface Films

Contaminants can concentrate in two different areas within water bodies: the sediment and the surface microlayer. The surface microlayer is the upper 50 μm to 1-mm surface film that lies between the water and the atmosphere. Many natural organic compounds and contaminants concentrate there, due to their hydrophobic nature [11, 57, 58]. This film also contains a variety of particles, including a unique fauna and flora [58]. In addition, the presence of natural organics ensures the presence of trace contaminants that normally bind to organic complexing agents [44].

An interesting question for research is whether the high concentrations of contaminants found in the surface microlayer pose a particular threat to any part of the ecosystem. The higher concentrations in the microlayer are offset to some extent because the processes that cause the concentration there also inhibit uptake by organisms.

Recent studies in the Chesapeake Bay have found high concentrations of many pollutants, including metals, alkanes, and aromatic hydrocarbons in the surface microlayer [12, 50, 52, 59]. Atrazine was found to concentrate by a factor of up to 110 in the surface microlayer of the Chesapeake Bay [177, 178]. When seagrass microcosms received additions of atrazine dissolved in water, associated with particles, or as a component of surface film, differences in toxicity were not observed [29].

Because of the high concentrations and the potential for direct uptake by biota, this layer may represent an efficient and important transfer mechanism for pollutants. This process might be particularly important for periodically emergent organisms, such as sedentary animals in the tidal zone or emergent vegetation or neuston, including commercially important fish eggs. Certainly, concentration in the microlayer reduces to some extent the exposure of organisms that do not come into that boundary, and may expose the contaminant to a higher rate of removal through photooxidation or adsorption. For example, substantial photooxidation of benzanthracine and similar compounds has been observed in surface waters [81].

Adsorption

Adsorption of inorganic pollutants to a particle is analogous to complexation as discussed in the previous section, and is subject to most of the same controls, including the effects of pH, ionic strength, and competing ions. Adsorption reactions may be the important controlling factors for the distribution of many toxic trace metals in estuaries, including copper, lead, and zinc [60]. These reactions are partly reversible, so that the material can be desorbed from solids by lowering the concentration of the pollutant in solution, or by changing the chemical system to favor the release (a change in pH, or an increase in competing ions, for example).

Adsorption of organic compounds to suspended particulates is a function of the hydrophobic interactions much like the binding of organics to cells [87], so that nonliving particles compete with living cells for these substances as well. In a study of the fate and effects of the herbicide atrazine in microcosms with Chesapeake Bay vegetation, 78% of the atrazine applied became associated with either suspended particulates or sediments [29]. A number of herbicides have been shown to bind strongly to colloids in the Chesapeake Bay [88, 89]. Preferential binding to such small particles will greatly affect the transport and eventual fate of such compounds, allowing longer residence times within the water column.

Flocculation

Suspended solids and colloids carrying adsorbed trace elements or organics can aggregate to form larger particles, which become more susceptible to the processes of sedimentation and filtration. An important component of the suspended solids in most river systems is clay particles. In fresh water, the aggregation of clay particles is quite slow, whereas in seawater, clay particles aggregate readily [148]. Flocculation can lead to segregation and concentration of trace metals. In studies of metal interactions with Chesapeake Bay flocs, most metals were concentrated in the smaller size fractions [45, 46].

In a typical estuarine circulation, particles are carried into the estuary by the river; as the water moves downstream and becomes more saline, the particles agglomerate, and eventually settle to the bottom water. The bottom water, carrying more saline water toward the river, returns the particulates upstream, where the lower salinity tends to disaggregate them. They may then reenter the surface water through mixing and begin the cycle again. In this way, a zone called the turbidity maximum is formed. The high concentration of suspended solids in this area may be both an important barrier to the movement of toxic compounds through the estuary and a primary reservoir of the same compounds. Because of the high concentrations of toxics in this zone, it is likely to be a primary site for any effects of the toxicant.

Sedimentation

The ultimate repository of most particles is the sediment. In particular, the sediments of the turbidity maximum zone downstream of a major source are often a major repository of toxic trace elements and organic compounds. For example, high concentrations of kepone (a halogenated pesticide released into the James River in the 1960's and 1970's) have been incorporated into the sediment in the James River turbidity maximum zone, and buried under as much as 50 cm of cleaner, more recent sediment [62, 69].

Within the Chesapeake Bay, Officer et al. [103] and Helz et al. [65] determined that most of the particulates and associated toxics entering from the Susquehanna River are deposited at the head of the Bay.

In an estuary a variety of solids may be important in adsorption, flocculation, and sedimentation, including clay particles, iron and manganese oxides, sulfide minerals, organic films, and plant debris. Since adsorption is a surface phenomenon, finer solids have a greater adsorptive capacity than coarser solids of the same type. Unlike complexation, adsorption removes the pollutant from solution, and if the solid leaves the water column, the pollutant is also removed, and may become completely unavailable to organisms in the water column. This process is no doubt largely responsible for the high concentration of toxics found in the sediments near sources of pollution [16, 32, 33, 49, 70, 71, 90, 107, 110, 112, 143, 164, 165, 173, 175]. For example, the concentrations of arsenic, copper, manganese, nickel, lead, tin, and zinc in Chesapeake Bay sediments decline seaward from maxima at the Baltimore Harbor, Susquehanna River, and Elizabeth River [62, 100], and a similar distribution is seen with PAH's and PCB's [62, 70, 175].

Sedimentation and resuspension by storm events may be a major factor in the sedimentation patterns of a shallow estuary such as the Chesapeake Bay. It has been estimated that 80% of the sedimentation between 1966 and 1976 occurred during two storm events and that approximately 50% of yearly sedimentation occurs during a short period in spring [103]. The importance of such episodic events in controlling contaminant availability is not well documented, however, probably because of sampling difficulties.

Remobilization

Incorporation into sediments and subsequent burial does not forever remove toxics from possible uptake by organisms. Many organisms reside in the sediments and are thus exposed to the toxic material. Toxic substances may be present in the pore waters of sediment in higher concentration than in the water column. For example, in experimental microcosms the concentration of atrazine in pore waters was fourfold higher than surface water concentrations [29]. Because the benthic biota can be the majority of the biomass in such a system, the net effect of incorporation of atrazine into the sediments might actually be a net increase in its availability to organisms.

Other toxics, normally less available to organisms in an oxidized state, can be reduced in anoxic sediments and their bioavailability enhanced. For example, arsenic present in water as arsenate can be adsorbed onto surface sediments. When buried in reducing sediments, the arsenic is reduced to arsenite, which is present in much higher concentration in the interstitial waters than in the water column. In the Patuxent River, the arsenite concentration in the pore waters is up to 50 times higher than the arsenate concentration in the surface waters [122]. Other metals coprecipitated with iron and manganese oxyhydroxides, such as copper, zinc, and lead, can be remobilized in pore waters, particularly in the northern Chesapeake Bay, where low sulfate concentrations result in less sulfide formation under reducing conditions [22, 159]. Cadmium also may be remobilized from Chesapeake Bay sediments [64].

Toxic compounds in sediment pore waters can also be returned to the water column by diffusion, resuspension of the sediments, or activities of benthic organisms. Detectable fluxes of arsenic from contaminated Chesapeake Bay sediments have been measured, with a variety of chemical forms (arsenate, arsenite, and methyl arsenic) detected [122]. Burrowing organisms (*Nereis succinea*) at levels approximating natural abundances caused an enhancement of the fluxes by a factor of five over molecular diffusion; this biological enhancement was slightly less than the enhancement caused by daily resuspension of 8 cm of sediment, and more than the enhancement caused by resuspension of the top 2 cm.

BIOLOGICAL PROCESSES

Many inorganic compounds are capable of participating in the oxidative and reductive reactions that comprise cellular metabolism. Some elements are required in small quantities but toxic in larger quantities. Both inorganic and organic substances can be incorporated by the organism after uptake, and partitioned according to their chemical structure. Incorporation of a toxic compound markedly affects the compound's transport through the Chesapeake Bay, depending on the organism, its life cycle, behavior, mobility, and persistence. Materials associated with phytoplankton and pelagic microorganisms behave in a manner somewhat similar to particulates, as discussed in the previous section. Toxic compounds may pass to successively higher trophic levels through predator/prey relationships.

Active participation of toxic substances in biological processes can lead to chemical transformation of the compound into a form quite different from the original. If these transformed chemical species have biological affinities or chemical stabilities that differ from the original compound, this transformation can alter the compound's reactivity and perhaps its transport through the estuary. In addition, biological uptake and transformation may enhance or alleviate its toxicity to other organisms, increasing or minimizing the potential for harm.

In addition to direct uptake and modification of toxic substances, biological activities can substantially modify the chemical environment surrounding them, thus altering the bioavailability of some contaminants. For example, algal photosynthesis, particularly during bloom conditions, can significantly alter the pH and the oxygen concentration of the water column. Microbial activities within sediments and in stratified water columns cause anoxia, altering redox conditions. A number of organisms are capable of excreting large quantities of organic compounds that can complex toxic substances, altering their toxicity and transport. The production of feces in higher trophic levels leads to the aggregation and sedimentation of particles and associated toxics. Finally, the movement of infaunal organisms affects the cycling of contaminants between estuarine sediments and the overlying water column.

All of the above processes, both those associated with direct uptake and modification of toxic substances and those associated with biologically induced changes in the environment, are discussed in more detail below.

Uptake and Incorporation

The ability of marine organisms to accumulate contaminants has been well documented; the literature is replete with studies of pollutant levels in organisms from the Chesapeake Bay [1, 2, 16, 17, 32, 33, 39, 51, 66, 70, 74, 75, 82, 95, 113, 114, 123, 141, 146, 147, 161, 162, 175, 180]. Less well known, and currently

under study, is the role of various processes that affect contaminant availability and uptake. Organisms have the ability to extract contaminants dissolved in the water column, adsorbed on suspended particles and detritus, and contained within their food. Uptake occurs either by adsorption of the contaminant onto cell surfaces or by absorption across body surfaces such as gills and guts, or through a combination of both.

For those organisms (primarily animals) that live in a medium containing a dissolved toxic compound, contact sediment with high concentrations of the toxic substances, and ingest other organisms that have already incorporated the toxic substance, the logical query is which source contributes most to the uptake of the toxic. The answer, of course, varies for different organisms and pollutants; in general, however, water appears to be the most important source of most toxics to the greatest number of organisms. Much of the metal present in food is not passed across the gut wall. More lipophilic materials such as alkyl compounds are generally more readily incorporated from food, but they are also more readily taken up from water [43]. The solubility of the most lipophilic compounds ($\log P_{ow} \geq 8$) is such that water is a poor source, and food becomes more important. Generally speaking, uptake of contaminants from food is more important for larger animals, for which surface absorption is less important. Animals have been shown to take up large amounts of metals from contaminated sediments, but it is usually not clear whether the materials have been ingested or absorbed directly from interstitial water.

The uptake of silver by oysters from Chesapeake Bay is solely from silver dissolved in water. Uptake from either algal food or sediment is insignificant in comparison [131, 134]. Copper uptake by the same organism is more complex. Uptake of dissolved copper occurs readily, largely controlled by the availability of the free copper ion [182]. Copper is also taken up from food, although to a lesser extent [181]. It appears that colloidal organo-cupric complexes are also available [183].

Through the predator/prey relationship, the potential exists for pollutants to be passed up the food chain from autotrophs to herbivores to carnivores. In past years, such food chain transfer was thought to lead to increased body burdens at each step in the chain, resulting in top carnivores with extremely high concentrations of toxic substances, toxic responses within the population, and even potential toxicity to human consumers. Recent work has shown, however, that most contaminants do not get magnified as they are passed up the food chain [179]. Available studies from the Chesapeake Bay support this claim; accumulation of kepone from the contaminated James River showed no evidence of biomagnification, but rather an increase in body burden proportional to the individual's residence time in the vicinity of the spill [15, 73], with little evidence of uptake from food [14]. In a study of the passage of kepone through a simple plankton-mysid-fish food chain, spot (*Leiostomus xanthurus*) obtained only 0.2% via food [10]. Grass shrimp (*Palaemonetes pugio*) fed cadmium-"loaded" brine shrimp (*Artemia salina*) obtained only 1.2% of the cadmium that they would obtain from the water used to load the brine shrimp [101]. Biomagnification through food appears to be a significant factor for very few compounds; DDT [84] and methylmercury [42] appear to be notable exceptions. Again, biomagnification correlates with very high lipophilicity and low biodegradability.

The incorporation of a contaminant can drastically alter its transport and impact within the Chesapeake Bay. In general, because organisms try to maintain position within a specific environment, incorporation within tissues will lead to the contaminant remaining within the estuary. For example, silver has a high affinity for particle surfaces and is rapidly taken up and incorporated by phytoplankton as well as by suspended sediments. As these different particles move down the estuary, the silver is desorbed from the suspended particles and remains in a dissolved state, complexed with chloride. Silver associated with phytoplankton, however, does not desorb, thereby remaining in the Chesapeake Bay and probably recycling [132, 133]. Many organisms within the estuary are sedentary; contaminants incorporated by these species will accumulate within the population's growth zone. Uptake and incorporation of toxics by migratory organisms such as pelagic fish presumably will result in transport of Chesapeake Bay toxics into other ecosystems. By the same process, toxic substances can be transported into the Chesapeake Bay region. On the whole, however, an overwhelming percentage (97%) of the carbon produced within the Bay remains within the Bay [144, 155]; very little is exported. Also, only a small percentage of the total biomass of the Chesapeake Bay system is composed of migratory species; thus any transfer via this mechanism is likely to be minor. For example, it has been estimated that less than 0.01% of the arsenic contained within the coastal shelf off Georgia was exported from the system by biological uptake and subsequent migration [127].

Many marine animals detoxify trace metals by binding the metals to metal-binding proteins. These proteins have a high affinity for such metals as silver,

cadmium, copper, mercury, and zinc. A cadmium- and copper-binding protein has been isolated from American oysters (*Crassostrea virginica*) [41]. The ratio of cadmium to copper bound to this protein varied considerably through the year, with higher copper binding noted during the summer spawning period. An inducible protein binding cadmium, copper, and zinc has also been found in three Chesapeake Bay fish: striped bass (*Morone saxatilis*), white perch (*Morone americana*) and channel catfish (*Ictalurus punctatus*) [3]. Similar proteins appear widespread, also occurring in cyanobacteria [105] and algae [48]. These proteins not only reduce the toxic impact of the metal on the individual organism, but also sequester the metal from the environment and reduce the chance that another organism will encounter the same metal. In addition, prior exposure to sublethal levels of one metal can enhance an organism's ability to withstand another toxic metal through the induction of metal-binding proteins that are broadly specific [124].

Transformation of Chemical Form and Modification of Toxicity

Another important aspect of biological uptake is the transformation of chemical form of a contaminant. Aside from the concentration and sequestering of toxic substances, organisms have the capability to alter the chemical form or partitioning of many inorganic elements and organic compounds. Such shifts alter biological reactivity and toxicity of these compounds and can alter their rate of transport through the estuary as well as their eventual fate. Potential metal/phytoplankton transformations are illustrated in Figure 3. For example, biological uptake of arsenic leads to the production of reduced and methylated arsenic compounds, some of which are more toxic to higher trophic levels than was the original arsenic compound [94, 109, 127, 129]. Within the Chesapeake Bay, large fractions (up to 80%) of the arsenic may be present in these reduced or methylated forms [129]. The production of such compounds also increases the rate of transport of arsenic through the coastal zone by altering its biological and geochemical reactivity [130].

Zoller et al. [185] measured elevated levels of inorganic and organic mercury species around the Chalk Point Steam Electric Station on the Patuxent River, and concluded that inorganic mercury released by the plant was being biologically transformed.

A number of microorganisms, particularly those in anoxic sediments, are capable of methylating trace metals. Within the Chesapeake Bay, a slow, stepwise methylation of tin occurs in sediments [47]. Other

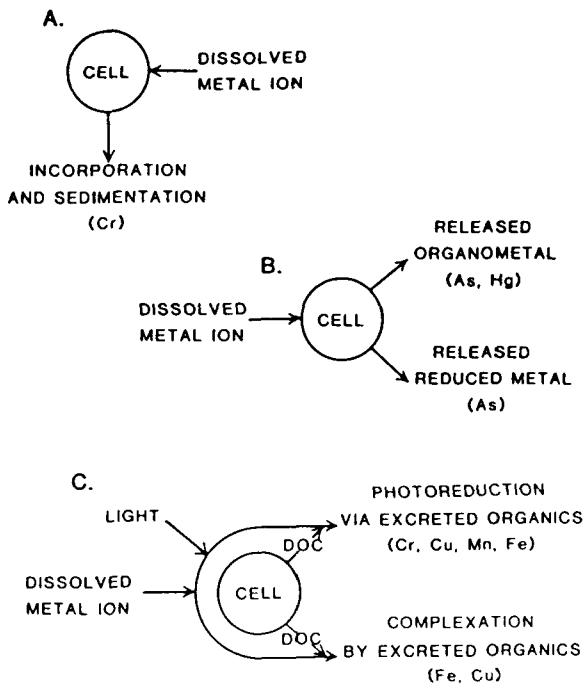

Figure 3. Possible interactions of dissolved metal ions with phytoplankton, including changes in partitioning (A), direct transformation of chemical speciation (B), and indirect facilitation of complexation and photoreduction (C).

metals, such as mercury, lead, and arsenic, have been shown to undergo methylation in similar aquatic systems or in experimental enclosures (C.C. Gilmour, pers. comm.) [23, 122, 172]; although not reported for the Chesapeake Bay, these reactions presumably are occurring.

Degradation

Degradation of toxic compounds by biota is an equally important process. A number of organisms have been shown to possess enzyme systems capable of degrading trace organics, leading to their transformation and presumably their detoxification. Such reactions are more complex than those discussed above for inorganic compounds, as the initial organic parent compounds are metabolized through several steps into a variety of metabolites with varying solubility, reactivity, and toxicity. Often degradation is not complete. Four different petroleum products showed very different rates of degradation when presented to microorganisms and sediments from polluted Baltimore Harbor [168]. None of the oils was degraded completely; thus, the overall process is quite uneven.

There is evidence that prior exposure to the same pollutant selects for a microbial community better

able to degrade new contaminants. Such selection may, however, simply increase the rate at which a substance is degraded, and not affect ultimate fate. In a comparison of microorganisms from Baltimore Harbor and the eastern Bay, Colwell and Walker [27] found that although rates of degradation were much more rapid in Baltimore Harbor sediments, similar compounds were degraded eventually by the microbial community from the eastern Bay.

Rates of degradation, as with most other microbial processes, vary greatly. In general, temperature, nutrient concentrations, and prior exposure appear to be the most important factors limiting degradation [27, 106]. The presence of toxic substances within the organic fraction can also be important; for example, the preferential partitioning of metals such as mercury in the oil component of sediments [135] can retard degradation because of the toxicity of mercury to the microbial community [167]. Some organic compounds may be degraded through co-metabolic processes. Phenanthrene is both degraded directly and co-metabolized in the presence of a variety of carbon sources in Chesapeake Bay sediments, and microorganisms capable of such degradation are present in elevated numbers in sediments polluted with hydrocarbons [28, 80, 140].

Herbicides associated with Chesapeake Bay sediments were found to degrade at rates 2-30 times the reported rates in soils and lake sediments, suggesting that estuarine sediments have an increased capacity for degradation of synthetic organics [89].

In general, although transformation of organic and inorganic substances plays an important role in contaminant transport and impact, the processes are not well understood. Further studies are warranted to fully understand the role of biological transformation in the transport and reactivity of toxic substances. Alterations of contaminant geochemistry by biota are extremely important to the estuarine ecosystem as a whole, and must be considered when impact predictions and management assessments are made. Too often, such biogeochemical concerns are ignored.

Modification of the Environment

In addition to direct uptake and modification of contaminants, the activity of biota can substantially modify the chemistry of the surrounding environment. Algal photosynthesis results in the removal of inorganic carbon from the water column and a resulting increase in pH; during bloom events, such increases can be substantial. In the freshwater section of the Potomac River during 1984, a persistent bloom of *Microcystis* sp. caused substantial variability in pH and maximum pHs of >10 [138]. Such a large shift in pH will greatly affect the geochemistry of many trace substances, as discussed in Chemical Factors. In this instance, the persistently high pH in the water column increased the mobility of phosphorus in the sediments and led to increased flux of phosphorus across the sediment/water interface, maintaining the high levels of algal growth and the high pH. Although not measured, presumably other pollutant fluxes were affected as well.

Large pH shifts are found not just within the freshwater portions of the Chesapeake Bay; large algal blooms can significantly affect pH even in areas of moderate salinity. A persistent bloom of *Katodinium rotundatum* in the mesohaline portion of the Patuxent River during January-March 1987 drove the surface pH of the river to above 9 on a daily basis, and caused a maximum pH of >9.5, approximately 1.5 pH units higher than normal (J.G. Sanders and S.J. Cibik, unpublished data).

Another effect of biota is the variability in dissolved oxygen concentrations. As a consequence of nutrient enrichment, high algal productivity and increased respiration rates drive large swings in the diurnal oxygen cycle, with higher oxygen concentrations during the day and lower concentrations during the night. In the Patuxent River, the daily swing in oxygen concentration increased during the late 1960's from approximately 3 mg/l to 7 mg/l [30]. Similar trends have been shown for the entire estuarine portion of the Patuxent River [91]. In stratified water columns, high levels of respiration can deplete oxygen concentrations. In the mainstem of the Chesapeake Bay and some of the tributaries, water column stratification during summer and high respiration rates lead to depletion of oxygen in the bottom waters, often for long periods [104, 139]. Oxygen depletion and resulting sulfide formation causes large changes in the mobility and complexation of some compounds, particularly metals that form insoluble hydroxide or sulfide complexes (see Chemical Factors).

Autotrophs have been shown to excrete DOC during normal growth. Under conditions of high cell densities, such excretions can become quite significant. For example, concentrations of DOC commonly vary from 1.9 to 6.0 mg/l in the Patuxent River [99, 128, 142, 181]. During dense algal blooms, however, concentrations are much higher (K.G. Sellner, unpublished data). These very high concentrations of dissolved organics have the potential to alter speciation of both inorganic and organic pollutants. The effects of these enhanced organic compounds should be a focus of further research.

Organisms within the water column and on the bottom produce aggregated fecal pellets containing

unassimilated organic matter and inadvertently ingested sediment particles. Fecal pellets provide perhaps the most efficient mechanism for transfer of both inorganic and organic pollutants from the water column to the sediments, because they are produced at a high rate, sink relatively rapidly, contain high concentrations of contaminants, and break down slowly (see review [42]). For example, studies of zinc have indicated that rapid recycling between the sediment and water column takes place in the northern Chesapeake Bay. This cycle has been attributed to uptake by phytoplankton, ingestion by zooplankton, and rapid return to the sediments in fecal pellets [22]. In addition to providing a rapid mechanism for transport, fecal pellets presumably alter the availability of the pollutants as discussed in CONTAMINANT SOURCES AND PROCESSES AFFECTING DISTRIBUTION. Little work within the Chesapeake Bay, however, has focused upon this problem.

Benthic infauna may change the distributions of contaminants in sediments in a variety of ways, including mechanical disturbance (mixing, pelletization, and sorting), chemical changes (increased oxygen penetration or organic enrichment), increased microbial activity, the effects of ingestion on sediment constituents, increased surface area, and the uptake of metals by the organisms themselves [118]. Burrowing activities of *Nereis succinea* in contaminated sediments, for example, increased the flux of arsenic by a factor of five [122]. This enhancement corresponded to an approximately equal change in the surface area of the sediment due to worm burrows.

SUMMARY AND RESEARCH DIRECTIONS

In this chapter, we have attempted to outline the various chemical and physical factors that affect contaminant input, distribution, and availability, and to discuss our current knowledge of these factors within the Chesapeake Bay. Ideally, we would like to be able to summarize our discussion with a general ranking of the various factors and their relative importance to the movement of toxic substances. Unfortunately, such a summary is not possible. There are many different compounds, each with a different reactivity and behavior. Factors that control one compound or group of compounds may well be unimportant for another. All of the processes discussed here are important for some contaminant, but no one process is a major factor for all contaminants. The best that we are able to provide here is a general survey of different kinds of compounds and the processes that are important in determining their distribution and rate of transport.

In contrast, the general pathways of biological uptake for most compounds can be summarized, as in Figure 1. Most contaminants can be placed in one of the three groups illustrated. Again, however, the relative importance of these various pathways in the natural system is not fully understood for many compounds; we must continue to support investigations into the mechanisms of contaminant uptake. In addition, we must remember that the number of contaminants for which information is available is quite limited. Thus, the application of our current knowledge, gained through laboratory studies, to the Chesapeake Bay could lead to serious errors in estimation of impact. For example, we cannot directly measure the free ion concentration of most cationic elements, and therefore we cannot predict rates or amounts of uptake, nor can we predict the potential availability of all sediment-bound organics from data available at present.

Organisms play an important role in the bioavailability of toxic compounds, both through direct modification of the chemical structure of the toxic compound, and through modification of the surrounding environment (pH, oxygen changes). Unfortunately, except for a relatively few compounds, we do not know the extent of such modifications.

The overall conclusion must be that the complexity of the interactions between physical, chemical, and biological factors is extreme. This complexity hampers our ability to fully understand (and more important, predict) pollutant transport, availability, uptake, and impact.

Past efforts, to a large extent, have focused upon determining the concentration of contaminants within the various compartments of the system. Although this research has value, we must move toward careful study of the processes themselves. It is only through the latter research that effective management of resources and protection from contamination can be achieved. We have identified a number of areas in which further research is needed. In no particular order, they are presented below.

(1) We need to determine how partitioning of a contaminant affects its toxicity, for a number of important model compounds. For example, is organic complexation a detoxification mechanism for many inorganic elements? What about organic compounds? Which contaminants are still available and toxic when associated with particulates? How important is the concentration of contaminants in the surface microlayer?

(2) We need to better understand the role of biota in the transfer of pollutants within the system, including transport across the sediment/water interface,

the importance of fecal pellet production, and the fate of contaminants associated with the biota themselves. An interesting question is what happens to tissue-associated toxics when an organism dies. Also, does the sequestering of pollutants by proteins protect predators when they consume prey containing these compounds?

(3) We must determine the importance of seasonal anoxia on the transport and availability of important contaminants. Does anoxia in general increase or decrease contaminant availability? Do anoxic sediments differ greatly from oxidized sediments in their ability to act as a pollutant reservoir?

(4) We do not understand the extent to which sediments control the movement and availability of contaminants. Sediments act as a sink for many substances; they can also retain toxics in the estuary and prolong the exposure. An integrated, wide-scale study of the flux of carbon and toxic substances across the sediment/water interface, and the processes that control this flux, is necessary.

(5) We need to collect better (and more) information on the role of communities in the transport and transformation of contaminants. Too much of our information is based on laboratory experiments with single species of organisms under controlled conditions. We need more realistic experimentation using more sophisticated methods, with microcosms, or using other approaches. It is data of this sort that will be most amenable to the modeling efforts that must eventually form the basis of predictive capabilities.

(6) Finally, we need to continue descriptive studies of the sources of toxic compounds entering the Chesapeake Bay, their location within the system, and their availability to important organisms. This type of research will always be useful. In particular, we need information on the sources and reservoirs of key organic compounds.

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