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Perspectives on The Chesapeake Bay: Recent Advances in Estuarine Sciences



PERSPECTIVES ON THE CHESAPEAKE BAY:

ADVANCES IN ESTUARINE SCIENCES

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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 impor-

tant 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 HydroQual, 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 pro-

cesses; (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 metallothionein 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 bio-monitoring. 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, management 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 of Chesapeake 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 and 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

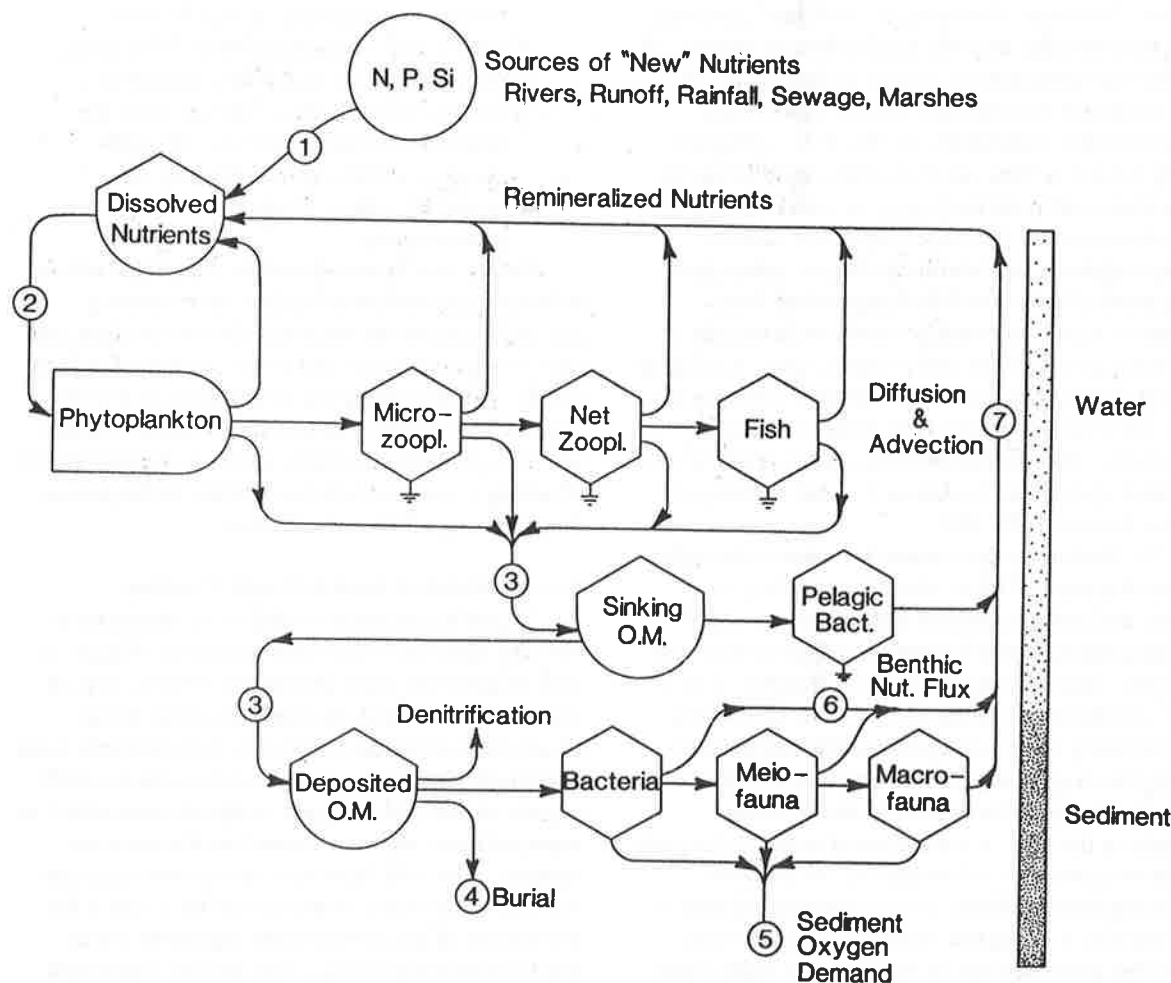


Figure 1. Conceptual model of nutrient element flows in plankton-based systems using Odum's energy flow symbols (modified from Nixon [85]). Pathways relevant to the coupling of benthic and pelagic systems are identified, with pertinent review papers, as follows: (1) inputs of nutrients from outside sources [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 constituents 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.

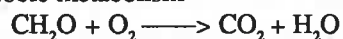
As illustrated in Figure 1, the cycling of materials between Bay waters and sediments begins with the formation of organic matter and its deposition on the

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.

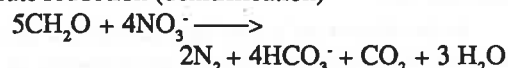
The material deposited at the surface of estuarine sediments comprises a complex mixture of organic matter and inorganic minerals. Although inorganic phases are unquestionably involved in early sediment

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



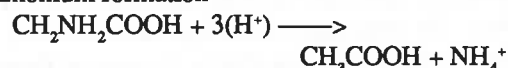
Nitrate reduction (denitrification)



Sulfate reduction



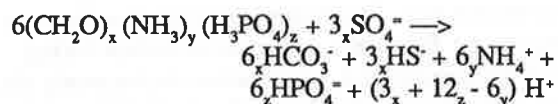
Ammonium formation



Methanogenesis



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]:



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 originally 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 ^7Be 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 (^7Be , ^{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:

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

where J is the flux of constituent i in $\text{mols m}^{-2} \text{time}^{-1}$, V is the volume of water contained in the chamber (liters), C_o and C_i 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 ground-water 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 approaches 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 $\text{m}^{-2} \text{y}^{-1}$ 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 ($160 \times 10^6 \text{ kg/year}$) and phosphorus ($30.3 \times 10^6 \text{ kg/year}$) entering the bay [129] by the area of Bay bottom (about $11 \times 10^9 \text{ m}^2$, 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 ($3010 \times 10^6 \text{ kg m}^{-2}$ [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 $1.70 \pm 0.32 \text{ kg m}^{-2}$ (mean \pm 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 $3\text{-}5 \text{ g m}^{-2}$ 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 $1 \text{ g C m}^{-2} \text{ daily}$. 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		No. stations or areas	No. obs. per year	Method	Fluxes reported							Other	Sponsor	
		From	To				O ₂	NH ₄	N ₄ N	NO ₃	DON	DIP	DOP			Si
MAINSTEM BAY																
A	Bricker & Troup [18]	Aug 1972		12	NG	PW									Various anions and cations Cl ⁻ , S ²⁻ , Fe ³⁺ , Mg ⁺⁺	AEC
B	Matisoff et al. [77]	Jun 1971	Sep 1973	2	13	PW		X				X		X		AEC
C	Matisoff et al. [77]	Apr 1974		4												
D	Boynton et al. [14]	Jun 1977	May 1978	5	4	BC	X								Total community metabolism	MdDNR
E	Smullen et al. [129]	NG		5-8	3	PW		X								EPA
F	D'Elia et al. [34]	Aug 1980	May 1981	4	2	BC									Sediment C, N, P Surf. sediment C, N, P	EPA, MdSGC
G	Boynton & Kemp [11]	Jul 1980	May 1981	5	2	BC	X		X			X		X		EPA, MdDNR
H	Boynton et al. [12]	Jul 1984	May 1986	4	4	BC	X	X	X	X		X		X		
WESTERN SHORE TRIBUTARIES																
Pauxent River Estuary																
H	Boynton et al. [13]	May 1978	Jun 1979	2	6	BC	X	X	X		X	X		X	Water column studies Analysis of data reported in H	MdPPSP
I	Boynton et al. [16]	May 1978	Jun 1979	2	6	BC	X	X	X		X	X		X		MdPPSP
J	Boynton et al. [15]	Jul 1978	Aug 1978	3	2	BC	X								Effect of water circulation Sediment traps	None
K	Boynton et al. [17]	Jul 1979	May 1980	4	6	BC	X	X	X	X	X	X		X		MdDNR-PPSP
E	D'Elia et al. [34]	Aug 1980	May 1981	1	2	BC									See E Further analysis of data in K	MdDNR-PPSP
L	Kemp & Boynton [67]	May 1978	May 1980	5	6	BC		X						X		MdSGC
M	Yamada & D'Elia [138]	Late Summer		1	NG	LC								X		
N	J. Boynton [9]	June NG	Sept NG	3	1	BC	X	X		X	X	X		X	Sed. and pore water profiles See G	
G	Boynton et al. [12]	Jul 1984	May 1986	2	4	BC	X	X	X	X	X	X		X		
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 Compared BC, PW methods	USGS, NSF
P	Callender & Hammond [22]	Aug 1979		12	1	BC, PW	X	X	X	X	X	X		X		USGS, NSF
Q	Cerco [25]	Jul 1984	Oct 1984	1	NG	LC	X	X	X	X		X			Effect of temp. and O ₂ on fluxes Effect of pH on DIP flux	NSF
R	Seitzinger [119]	Sep 1985	Dec 1985	8	1	LC	X	X	X	X	X	X		X		EPA, MWCOCG
G	Boynton et al. [12]	Jul 1984	May 1986	2	4	BC	X	X	X	X	X	X		X	Continuing study Effect of temp., DO on fluxes	MdOEP
S	Cerco [24]	Nov 1986				LC	X	X	X	X						NSF
T	Cerco [27]	Jul 1984	Oct 1984	1	weekly	LC	X	X	X	X	X	X				
York River Estuary																
U	Phoel et al. [106]	NG		3	1	BC	X	X	X						Sandy shoal site, <2 m deep	NG
V	Rizzo [112]	Mar 1983	Dec 1983			BC	X	X	X	X	X	X				
James and Appomattox Estuary																
W	Cerco [25]	Jul 1983	Oct 1984	23	2	BC	X	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	See G	NSF
G	Boynton et al. [12]	Jul 1984	May 1986	2	4	BC	X	X	X	X	X	X		X		
Pocomoke Sound																
E	D'Elia et al. [34]	Aug 1980	May 1981	1	2	BC								X	See E	
F	Boynton & Kemp [111]	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 impacts 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

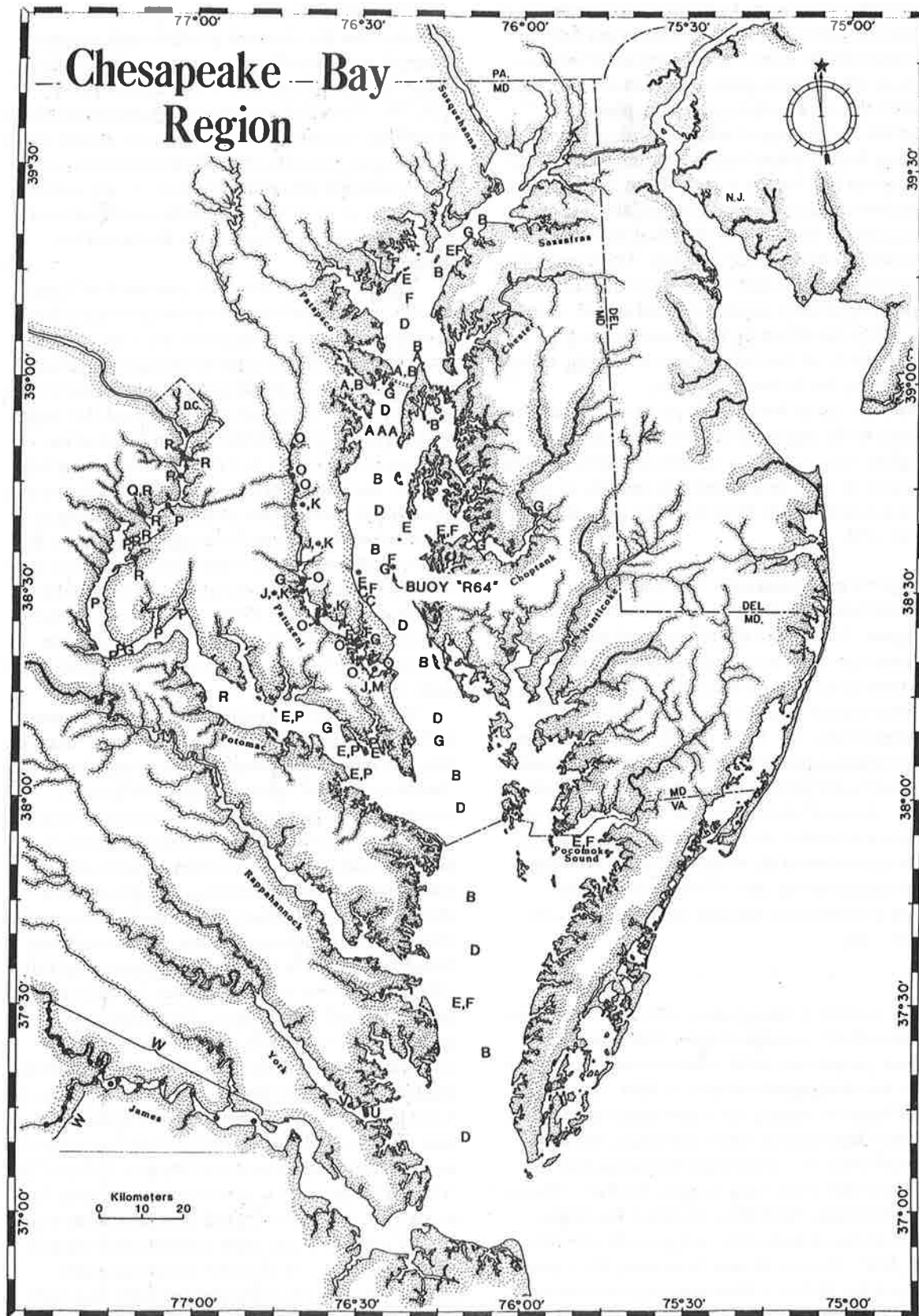


Figure 2. Map of the Chesapeake Bay showing locations of sediment-flux studies (letters) and sediment trap deployments (asterisks). Letters correspond to studies listed in Table 1.

(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

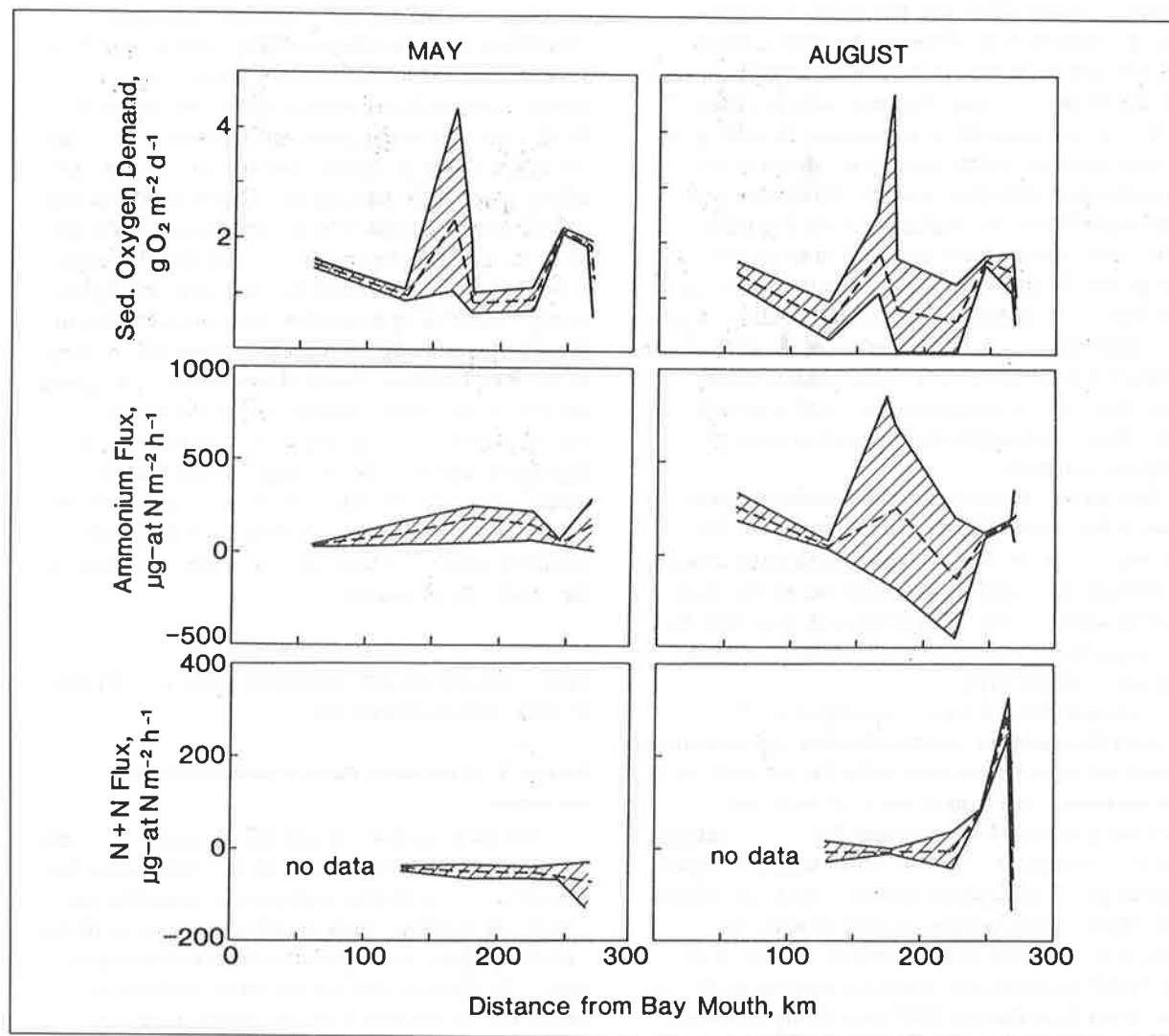
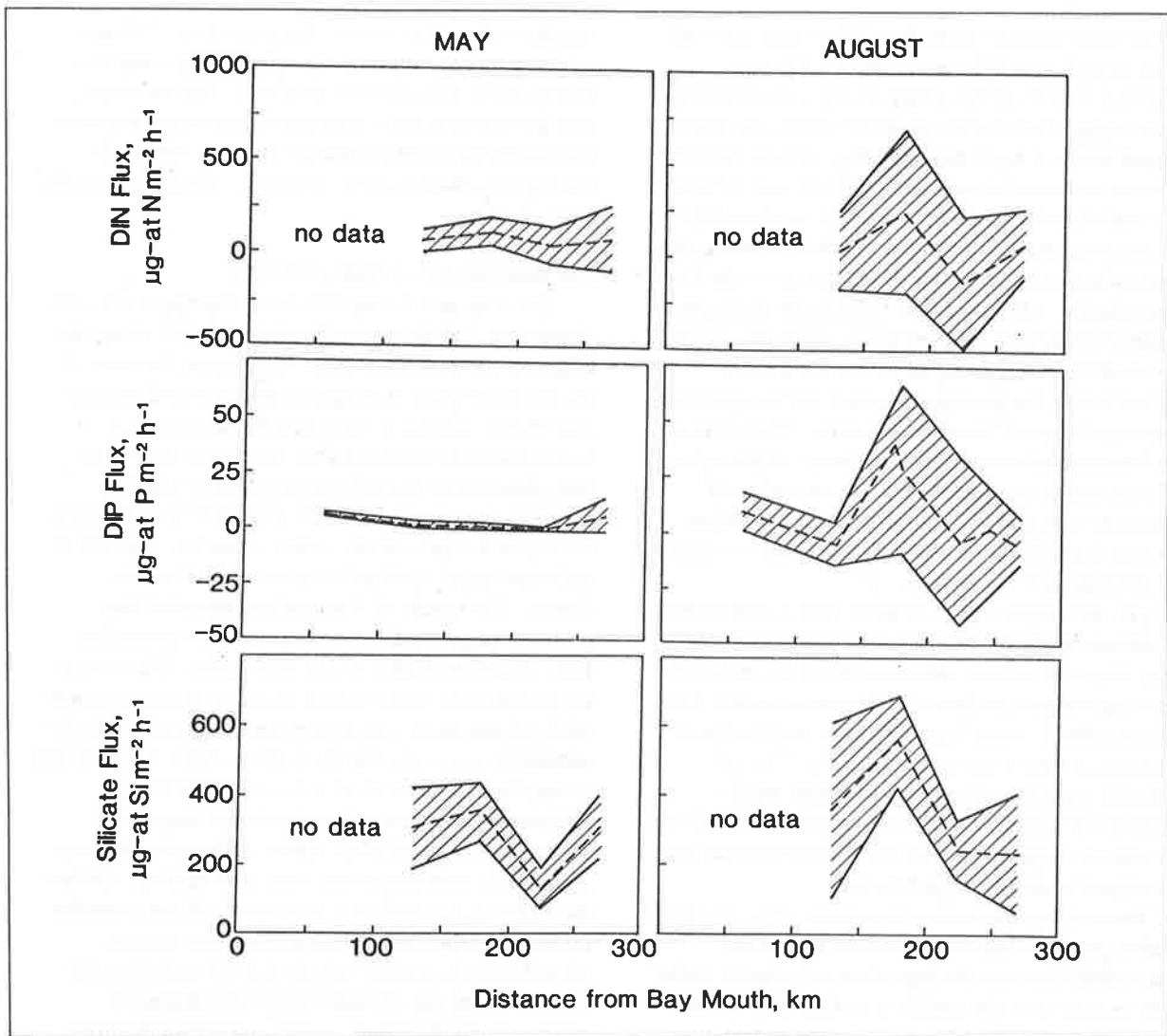


Figure 3 (above and next page). Seasonal and spatial patterns of oxygen and inorganic nutrient fluxes in the mainstem Chesapeake Bay. The mean and standard deviations of data [10, 12, 14, Boynton et al., unpublished data] for the months of May (left series of panels) and August (right series) are shown 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 $O_2 \text{ flux} = e^{0.0991+2.118}$. 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 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 ($\text{O}_2 \text{ flux} = 0.11 [\text{O}_2] + 0.44, r=0.54$) 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 O₂ 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 requirements 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 assembled 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

[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, respire at a mean rate of $2.7 \times 10^{-5} \text{ nl O}_2 \mu\text{m}^{-3} \text{ h}^{-1}$ [29], a community of nanoplankton present at $5 \times 10^6 \text{ cells/l}$ [47, 241] would consume $0.1 \text{ ml O}_2 \text{ l}^{-1} \text{ d}^{-1}$. 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 phytoplankton, 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 butterfly and harvestfish on *Chrysaora* and ctenophores, although not quantified in the Chesapeake Bay, may be significant there and elsewhere [124, 150]. Predation by the tentaculate ctenophore *Beroë* 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 $12 \times 10^3 \text{ m}^{-3}$. The average concentration of ctenophores during their blooms is 10-100/m³ [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 (2x10³ nanoplankton ml⁻¹) suggest potential removal of 10⁷ 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 model-

ing 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 eutrophication 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, eutrophication 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:

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

where the $(\bar{})$ represents a time average over one or more tidal periods. $(\tilde{U}, \tilde{V}, \tilde{W})$ 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:

$$\begin{aligned} \frac{\partial \bar{U}}{\partial t} + \bar{U} \frac{\partial \bar{U}}{\partial x} + \bar{W} \frac{\partial \bar{U}}{\partial z} + \frac{\partial}{\partial x} \bar{U} \tilde{U} + \frac{\partial}{\partial z} \bar{U} \tilde{W} = \\ -\alpha \frac{\partial \bar{p}}{\partial x} - \frac{\partial}{\partial x} \bar{u} \tilde{u} - \frac{\partial}{\partial y} \bar{u} \tilde{v} - \frac{\partial}{\partial z} \bar{u} \tilde{w} \end{aligned} \quad (2)$$

and

$$0 = -\alpha \frac{\partial \bar{p}}{\partial y} - f \bar{U} - \frac{\partial}{\partial x} \bar{u} \tilde{v} - \frac{\partial}{\partial y} \bar{v} \tilde{v} - \frac{\partial}{\partial z} \bar{v} \tilde{w} \quad (3)$$

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 \bar{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:

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

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 $\partial(uw)/\partial z$ and $\partial(vw)/\partial z$. 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:

$$\bar{U} \frac{\partial \bar{U}}{\partial x} + \bar{W} \frac{\partial \bar{U}}{\partial z} + \tilde{U} \frac{\partial \tilde{U}}{\partial x} = -\alpha \frac{\partial p}{\partial x} - \frac{\partial}{\partial z} \bar{u}w \quad (5)$$

and

$$f\bar{U} = -\alpha \frac{\partial p}{\partial y} - \frac{\partial}{\partial z} \bar{v}w \quad (6)$$

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 $\partial u w / \partial z$ but that the non-linear tidal term $\tilde{U} \partial \tilde{U} / \partial x$ 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:

$$\begin{aligned}\frac{\partial \bar{S}}{\partial t} + \bar{U} \frac{\partial \bar{S}}{\partial x} + \bar{V} \frac{\partial \bar{S}}{\partial y} + \bar{W} \frac{\partial \bar{S}}{\partial z} \\ + \frac{\partial}{\partial x} \bar{U} \tilde{S} + \frac{\partial}{\partial y} \bar{V} \tilde{S} + \frac{\partial}{\partial z} \bar{W} \tilde{S} \\ = -\frac{\partial}{\partial x} \bar{u} \tilde{s} - \frac{\partial}{\partial y} \bar{v} \tilde{s} - \frac{\partial}{\partial z} \bar{w} \tilde{s}\end{aligned}\quad (7)$$

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:

$$\frac{\partial \bar{S}}{\partial t} + \bar{U} \frac{\partial \bar{S}}{\partial x} + \bar{W} \frac{\partial \bar{S}}{\partial z} = -\frac{\partial \bar{u} \tilde{s}}{\partial x} - \frac{\partial \bar{v} \tilde{s}}{\partial y} - \frac{\partial \bar{w} \tilde{s}}{\partial z} \quad (8)$$

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]:

$$\frac{\partial \bar{S}}{\partial t} + \bar{U} \frac{\partial \bar{S}}{\partial x} + \bar{W} \frac{\partial \bar{S}}{\partial z} = -\frac{1}{b} \frac{\partial b \bar{u} \tilde{s}}{\partial x} - \frac{1}{b} \frac{\partial b \bar{w} \tilde{s}}{\partial z} \quad (9)$$

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

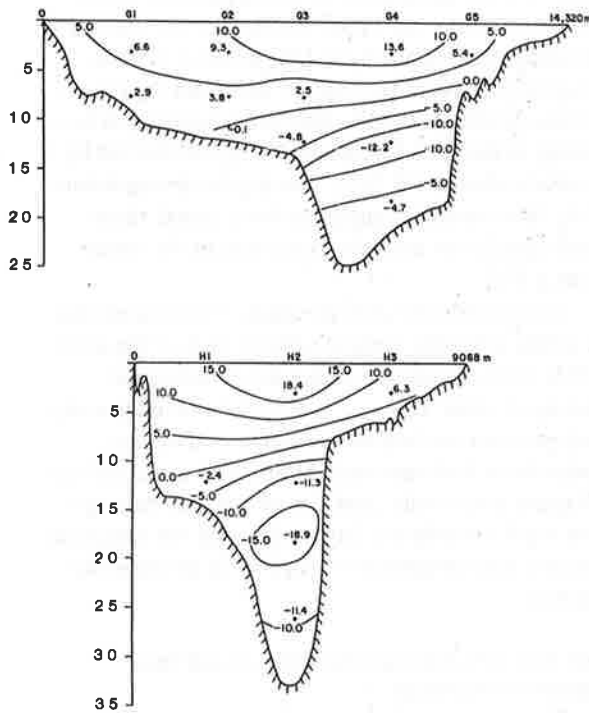


Figure 1. Longitudinal component of the non-tidal velocity averaged over 13 days (17-29 October 1977) showing a two-layer circulation (from Pritchard and Rives [65]). All velocities are in cm/sec. Top and bottom measurements were taken at 38° 29' N lat. and 38° 23' N lat., respectively.

showed that the salt balance was between the mean horizontal advection $\bar{U} \partial \bar{S} / \partial x$ and the vertical turbulent diffusion $(1/b) \partial (b \bar{w} \bar{S}) / \partial z$. The mean vertical advection $\bar{W} \partial \bar{S} / \partial z$ 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 m³/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

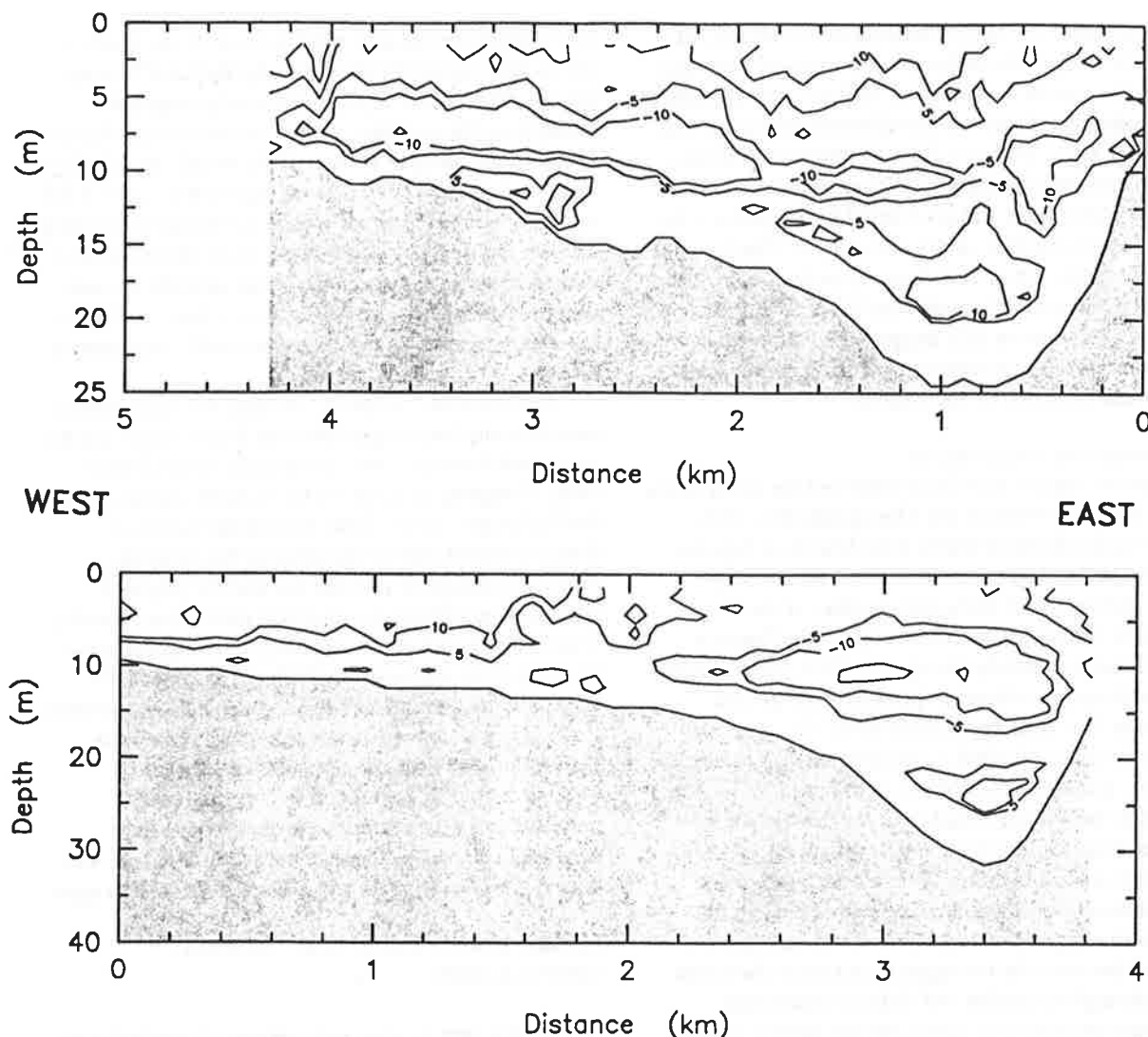


Figure 2. Evidence of three-layer circulation in the Chesapeake Bay: cross-sections of along-bay currents (from Itsweire and Osborn [42]). Measurements were taken in November 1986 with an Acoustic Doppler Current Profiler. Vertical resolution was 1 m, horizontal resolution 100 m. Negative velocities 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 that 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 ($38^{\circ} 54' N$ lat.) and lower Bay ($37^{\circ} 31' N$ 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, stratified 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 seiche 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

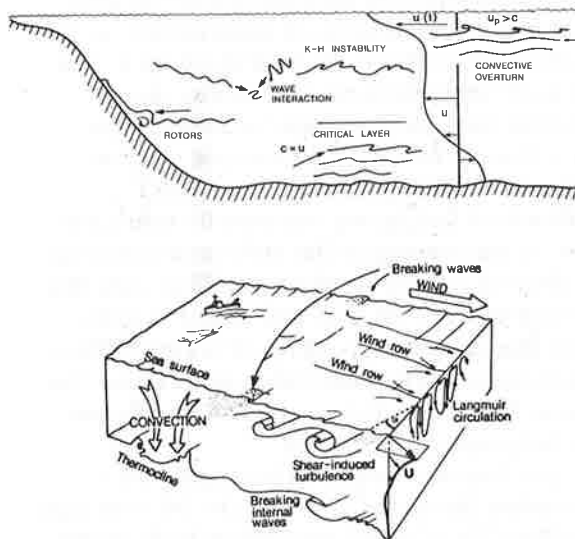


Figure 3. Mixing processes in the upper ocean (from Thorpe [75, 76]).

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.

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:

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

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.

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

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

$$\frac{\partial}{\partial z}\left[\frac{\overline{wp}}{\rho}\right]$$

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 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.

$$\frac{\partial}{\partial z}\left[\frac{1}{2}\overline{wq^2}\right]$$

Redistribution of the turbulent kinetic energy by the fluctuating field. It includes turbulent diffusion (spreading of turbulent energy by breaking internal waves).

$$\overline{uw}\frac{\partial U}{\partial z}$$

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.

$$\frac{g}{\rho}\overline{\rho w}$$

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.

$$\epsilon$$

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 ($C = \bar{C} + c$) variance in a mean vertical gradient can be expressed as:

$$\frac{\partial \bar{c}^2}{\partial t} + U \frac{\partial \bar{c}^2}{\partial x} = - \frac{\partial}{\partial z} \left[\bar{w} \bar{c}^2 - \kappa_c \frac{\partial \bar{c}^2}{\partial z} \right] - 2 \bar{w} \bar{c} \frac{\partial \bar{C}}{\partial z} - \chi c \quad (11)$$

The terms in equation 11 can be interpreted as follows:

$\frac{\partial \bar{c}^2}{\partial t}$	Time rate of change of scalar variance.
$U \frac{\partial \bar{c}^2}{\partial x}$	Horizontal advection of scalar variance by the mean flow.
$\frac{\partial \bar{w} \bar{c}^2}{\partial z}$	Redistribution of scalar variance by the turbulent field (includes turbulent diffusion).
$\kappa_c \frac{\partial^2 \bar{c}^2}{\partial z^2}$	Divergence of scalar variance transport through molecular diffusion (usually neglected)
$2 \bar{w} \bar{c} \frac{\partial \bar{C}}{\partial z}$	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.
χc	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:

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

$$Ri = N^2 / S^2 \quad \text{The Richardson number, which is a measure of the dynamical stability of the flow. A sufficient condition for stability is } Ri > 0.25. \text{ In hydraulics, the Froude number } Fr = Ri^{-1/2} \text{ is usu-}$$

ally 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 $Ri = (g \Delta \rho d / \bar{\rho}) u^2$ where u and d are representative turbulent velocity and length scales and $\Delta \rho / \bar{\rho}$ the fractional density change over d .

$$R_f = \frac{g \bar{\rho} \bar{w}}{\rho \bar{u} \bar{w} S}$$

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).

$$Ra = \frac{g \Delta \rho d^3}{\bar{\rho} \kappa \nu}$$

The Rayleigh number. $\Delta \rho / \bar{\rho}$ 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.

$$Re = \frac{u d}{\nu}$$

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 transferring 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 down-

stream 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 seicheing 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 break-downs 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