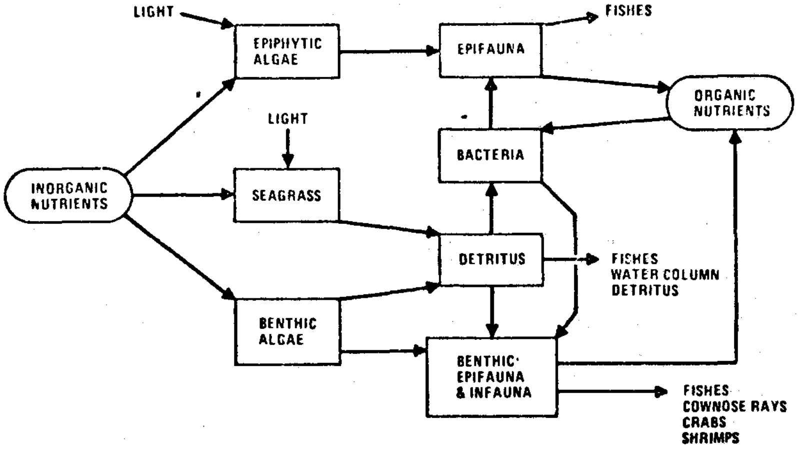
Biological Services Program

FWS/OBS-78/69
SEPTEMBER 1978

A CONCEPTUAL ECOLOGICAL MODEL FOR CHESAPEAKE BAY



Seagrass Community

Sponsored by the Chesapeake Bay Program
U.S. Environmental Protection Agency

Fish and Wildlife Service

U.S. Department of the Interior

The Biological Services Program was established within the U.S. Fish and Wildlife Service to supply scientific information and methodologies on key environmental issues that impact fish and wildlife resources and their supporting ecosystems. The mission of the program is as follows:

- To strengthen the Fish and Wildlife Service in its role as a primary source of information on national fish and wildlfe resources, particularly in respect to environmental impact assessment.
- To gather, analyze, and present information that will aid decisionmakers in the identification and resolution of problems associated with major changes in land and water use.
- To provide better ecological information and evaluation for Department of the Interior development programs, such as those relating to energy development.

Information developed by the Biological Services Program is intended for use in the planning and decisionmaking process to prevent or minimize the impact of development on fish and wildlife. Research activities and technical assistance services are based on anaysis of the issues, a determination of the decisionmakers involved and their information needs, and an evaluation of the state of the art to identify information gaps and determine priorities. This is a strategy that will ensure that the products produced and disseminated are timely and useful.

Projects have been initiated in the following areas: coal extraction and conversion; power plants; geothermal, mineral, and oil-shale development; water resource analysis, including stream alterations and western water allocation; coastal ecosystems and Outer Continental Shelf development; and systems inventory, including National Wetland Inventory, habitat classification and analysis, and information transfer.

The Biological Services Program consists of the Office of Biological Services in Washington, D.C., which is responsible for overall planning and management; National Teams, which provide the Program's central scientific and technical expertise and arrange for contracting biological services studies with states, universities, consulting firms, and others; Regional Staff, who provide a link to problems at the operating level; and staff at certain Fish and Wildlife Service research facilities, who conduct in-house research studies.

FWS/OBS–78/69
September 1978

A CONCEPTUAL ECOLOGICAL MODEL FOR CHESAPEAKE BAY

by

Katherine A. Green
11801 Rockville Pike, No. 802
Rockville, Maryland 20852

Order Number–SFWB 144807

Project Officer–David A. Flemer
Coastal Ecosystems Project
Office of Biological Services
Fish and Wildlife Service
Washington, D.C. 22022

This study was conducted in cooperation with the Chesapeake Bay Program, U.S. Environmental Protection Agency.

Performed for
Coastal Ecosystems Project
Office of Biological Services
Fish and Wildlife Service
U.S. Department of the Interior

DISCLAIMER

EXECUTIVE SUMMARY

A conceptual model for the Chesapeake Bay ecosystem (wetlands, tributaries, and bay proper) has been developed as an interrelated series of diagrams showing carbon and nutrient pathways. Information was based on an analysis of local literature and discussions with scientists who are studying the Bay. The ecological functions that produce the resources of commercial and recreational fisheries, habitat for migratory birds and other wildlife, waste disposal, and aesthetic water quality are indicated. Physical (light, turbidity, mixing, transport, sedimentation) and chemical (sediment-water interactions, presence of pollutants) aspects of the environment modify the rates of biological processes (primary production, nutrient regeneration, larval survival).

Marshes and other wetlands export carbon as detritus into the Bay system. They also trap nutrients, and release them gradually. Their natural buffering capacity can be, at times, exceeded by excessive nutrient loading from sewage or fertilizers.

Natural nutrients and detritus as well as pollutants such as trace metals, refined hydrocarbons, herbicides, and pesticides enter the Bay system through river flow and overland runoff.

In the Bay and tributaries, primary producers are phytoplankton, seagrasses, and benthic algae. Plankton dynamics facilitate nutrient regeneration, as do sediment chemistry and benthic organisms. Plankton, benthos, and marsh organisms provide food for fin- and shellfishes of commercial importance.

A detailed ecosystem model combining the wetlands, plankton, seagrasses, other benthos, and fish trophic dynamics submodels shows the importance of material transfer and interactions between subsystems. In hierarchical research designs, there is a tendency to focus on interactions within subsystems. Exchanges between subsystems should also be studied. Quantitative data and estimates of flows on a Bay-wide, annual basis are needed.

In relating observed changes in the system, such as the decline of submerged aquatic vegetation or reduction in oyster spatfall, to water quality, the ecosystem context is useful in indicating possible causal mechanics and pathways. Potential indicators of water quality and ecosystem health are distribution and abundance of seagrasses, chlorophyll a, dissolved oxygen, water transparency, blue crab abundance, larval setting, and concentrations of pollutants in the tissues of commercial fin- and shellfishes, plankton, and forage fishes.

To provide information on the relative importance of various biological processes for water-quality maintenance, and the relative magnitude of different pollutant impacts on the Bay, quantitative estimates of the flows in the conceptual models should be made.

PREFACE

The Chesapeake Bay Program of the U.S. Environmental Protection Agency (EPA) has as a principal objective the development of a Chesapeake Bay Water Quality Management Plan. A major problem for the U.S. Fish and Wildlife Service (FWS) and other agencies that are responsible for the living resources in the Bay has been the significant decline in the submerged aquatic vegetation (SAV). It is hypothesized that the reduction in abundance and distribution of SAV is the result of changes in water quality.

Through an interagency agreement, FWS and EPA are cooperating to develop information concerning the ecology and value of SAV in the Chesapeake Bay. To serve as a base of reference, A Conceptual Ecological Model for Chesapeake Bay was devised to indicate the major components of the ecosystem and to illustrate their interrelationships. Funding to support this report was provided by Region 3, Chesapeake Bay Program, EPA, through the coordinating efforts of the Office of Biological Services, FWS.

Any suggestions or questions regarding this publication should be directed to:

Information Transfer Specialist
National Coastal Ecosystems Team
U.S. Fish and Wildlife Service
National Space Technology Laboratories
NSTL Station, Miss. 39529

This report should be cited as follows:

Green, K. A. 1978. A conceptual ecological model for Chesapeake Bay. U.S. Fish and Wildlife Service, Biological Services Program. FWS/OBS–78/69. 22 pp.

ACKNOWLEDGMENTS

I wish to thank R. Ulanowicz, D. Heinle, R. Morgan, W. Boynton, M. Kemp, C. Stevenson, and L. E. Cronin from the Center for Environmental and Estuarine Studies, University of Maryland; L. Bongers, T. Polgar, A. Lippson, and L. Moran from Martin-Marietta; J. Taft and L. Brush from the Chesapeake Bay Institute, Johns Hopkins University; D. Flemer from the Office of Biological Services; D. Correll, Chesapeake Bay Center, Smithsonian Institution; R. Wetzel, K. Webb, R. Orth, D. Boesch, M. Lynch, R. Harris, D. Haven, J. Merriner, and D. Markle from the Virginia Institute of Marine Science. All have generously provided information and ideas for the development of this conceptual model of the Chesapeake Bay. Insights are attributable to them; errors are my own.

A CONCEPTUAL ECOLOGICAL MODEL FOR CHESAPEAKE BAY

Katherine A. Green[1]

INTRODUCTION

PURPOSE

The main objective of this project was the development of a conceptual model of the Chesapeake Bay ecosystem. The model indicates carbon and nutrient pathways in the Bay.

The Chesapeake Bay and adjacent wetlands provide habitat for migratory birds and other wildlife, maintain an aesthetically pleasing environment, and support recreational and commercial fisheries. Resources are affected by biological interactions and the physical and chemical processes of Bay waters, as well as by water quality and the impacts of human activities.

For planning research to support management decisions on renewable resources, Chesapeake Bay should be viewed as an estuarine ecosystem. Such a broad perspective is practical using a conceptual model to indicate interrelationships among resources and habitats. Within the ecosystem context, key processes and potential indicator species can be identified.

A conceptual model, as an explicit statement of the functioning of Bay ecosystem, will provide a biologically realistic context for considering the ramifications of changes in water quality.

The information used to develop the conceptual model comes mainly from discussions with scientists currently doing research on the Bay. (Questions asked in interviews are listed in appendix A). Some references are given, but the author's principal role was synthetic, that is, combining ideas and information from various sources into a conceptualization of the ecosystem gestalt. Previous models of the Bay ecosystem have been implicit mental concepts. This report presents a concrete ecosystem concept to facilitate the objective examination of assumptions.

The project represents only 8 weeks of work for interviews and writing. The model is general and simplified for any given area of research. Its utility lies in its holistic perspective, placing the relationships among systems components into the ecosystem context.

This model, while necesarily limited in scope, is a starting point for an ecosystem perspective on the Bay, and should serve as a basis for discussion on systems structure and relationships.

The conceptual model is structured as a set of box-and-arrow diagrams. Boxes represent system components; arrows represent flows between components or compartments. Components represented are carbon (C), nitrogen (N), and phosphorus (P), but the same basic structure could be used for energy units.

PHILOSOPHY

An ecosystem is a system open in at least one property, and in which at least one entity is living (Dale 1970). Ecosystem behavior is regulated by feedback loops, time lags, and external physical factors (King and Paulik 1967). More generally, an ecosystem consists of organisms including plants, herbivores, carnivores, and decomposers, with associated abiotic resources used by those organisms, all located within a definable geographic area and interrelated through a food web. It is an open system, with radiant energy entering from, and matter and energy lost to, the surrounding environment. Energy is dissipated within an ecosystem, but nutrients are recycled (Green 1975).

A model should simplify the real system, while preserving essential features (Levins 1966). Ecological theory looks upon ecosystems as hierarchical systems that can be subdivided for analysis, with

---

[1] 11801 Rockville Pike, No. 802, Rockville, Md. 20852.

complexity derived from successional addition of organizational states (King and Paulik 1967). But an ecosystem is more than a collection of subsystems. Present modeling research is focusing on the linkages among systems components. The coupling structure has been demonstrated to be important to overall system behavior (Walsh 1975, Lane and Levins 1977).

Throughout this report it is assumed that the Chesapeake Bay, adjacent wetlands, and tributaries comprise a single ecosystem. Subsystems can be identified and studied, but a holistic perspective is necessary to understand the responses of the Bay system to changes in water quality.

CONCEPTUAL MODEL OF THE BAY SYSTEM

OVERVIEW

The Chesapeake Bay system as defined here includes the Wetlands, the Bay proper, and its tributaries. It can be considered a single system from an ecological point of view. Few species are found throughout the system; their distributions vary with salinity, depth, and time of year. But the web of species interactions does span the whole system, and includes opportunistic feeding, the movement of fish from one end of the Bay to the other, and the large-scale impacts of human activities.

The Bay system can be viewed as a mechanism for turning oak leaves into bluefish, or as an enormous nutrient-cycling system, or as a menhaden-blue crab community, or as a nursery ground for Bay and Atlantic fisheries. Each of these perspectives is appropriate for some purpose, and all share the concept of the entire Bay as a single system.

Exchanges of material and energy between the Bay system and its air, land, and water environments are indicated in figure 1. Sunlight is the major energy input, but winds and tides also add energy to the system. Water enters the system from groundwater, rainfall, land runoff, and tides, but the biggest input is river flow. Water is lost through tides, evaporation, and flow into the Atlantic Ocean. Natural nutrients and detritus enter the system from river flow and land runoff. Pollutants are introduced from rivers, runoff, pleasure boats and ship traffic, and sewage and industrial effluents. Chemical nutrients can be lost to the deep sediments or exported to Atlantic waters. Organic carbon exchanges occur through migration of birds and other wildlife, movements of adult and larval fishes between the Bay and the Atlantic, and removal by commercial and recreational fishing. Possibly the biggest single carbon loss from the living components of the system is the CO_2 loss through respiration. The gasses CO_2, O_2, and N_2 are exchanged with the atmosphere.

Losses of carbon and nutrients through respiration, to the sediments, and by export to the Atlantic will not be indicated on more detailed ecosystems diagrams, to keep them as simple as possible. However, such losses should be taken into consideration in any carbon or nutrient budgets based on the conceptual diagrams.

Driving the Bay system are inputs of light, nutrients, and carbon (a measure of organic matter derived from photosynthesis). Carbon sources vary throughout the system. Detritus of external origin is the main source in the upper reaches of the estuary and tributaries. Marsh plants and "seagrasses" (used here loosely as a term for submerged aquatic vegetation) fix carbon in some shallow areas; most of it enters the system as detritus. In the deeper parts of the estuary, carbon is fixed in situ by phytoplankton, as well as being transported from shallower areas. A large part of the carbon fixed in the system goes through detrital pathways and supports an abundant shallow benthic community that turns over rapidly. Nutrients from drainage are absorbed in the marshes and the shallows, and are recycled there and in deeper waters by the activities of microplankton and microbenthos.

Zooplankton in the Bay are eaten by ctenophores, Atlantic menhaden *(Brevoortia patronus)*, and other fishes, and have abundant algal food sources on which to graze. Plankton support menhaden and other forage fishes, which in turn support commercial and recreational fisheries as well as unexploited fish groups. Most of the fishes are transient, spending only part of their life cycle or part of the year in the Bay system. Atlantic continental-shelf fisheries are partially supported by the Bay. The benthic communities support a large population of blue crabs *(Callinectes sapidus)*, which are effective predators as well as scavengers. Oysters and clams, also commercially important, derive most of their nutrition from water-column sources.

This broad overview of the biology of the Bay system (fig. 2) provides a framework for more detailed discussions of its ecological dynamics.

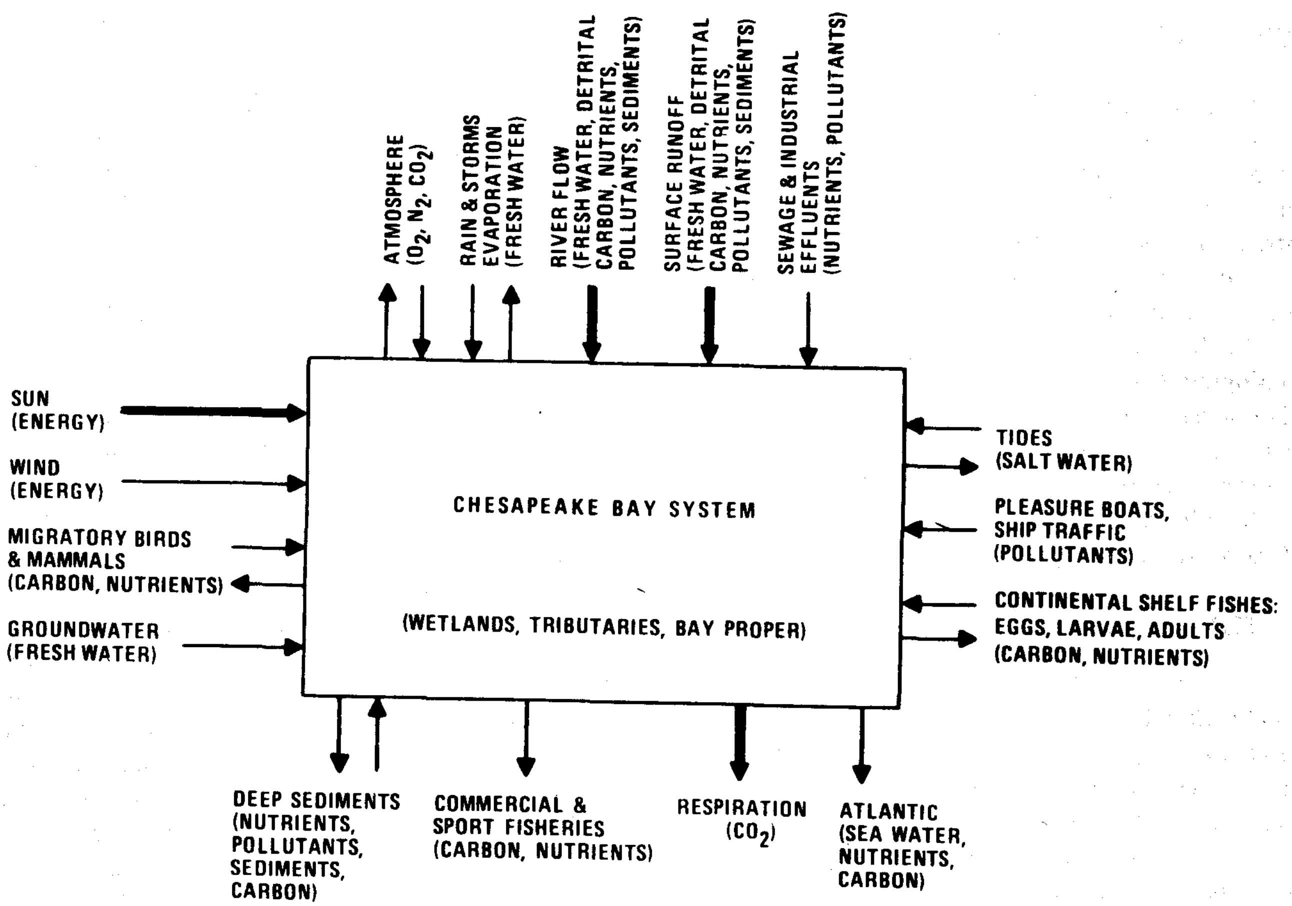


Figure 1. Exchanges between the Chesapeake Bay System and its environment.

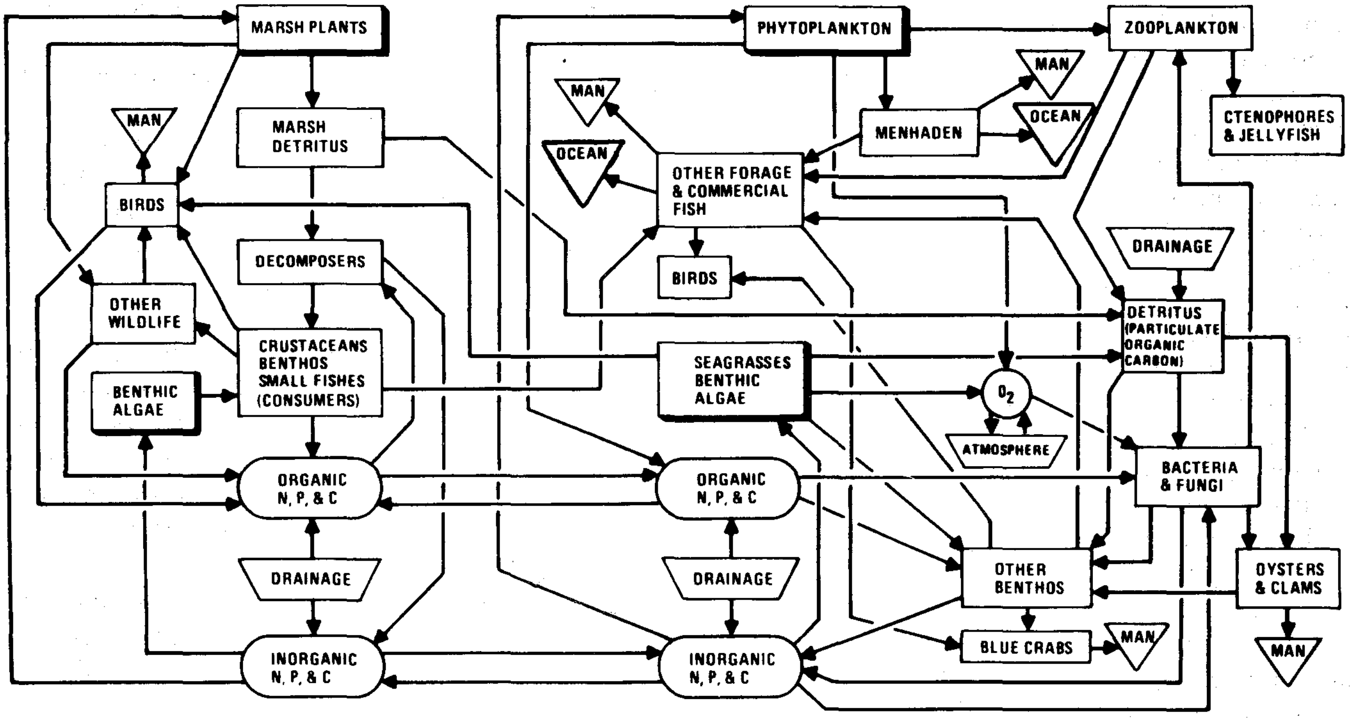


Figure 2. Major processes in a general conceptual model of the Chesapeake Bay system.

RESOURCES OF THE BAY

The Chesapeake Bay provides a variety of resources. The most obvious are commercial and recreational fisheries for clams, oysters, blue crabs, menhaden, striped bass *(Morone saxatilis)* and other species. Other resources are habitat for wildlife and migratory birds, waste treatment, and water of quality that is suitable for recreation.

Each of these resources is dependent on the ecological functions of the Bay system. One objective of these conceptual model diagrams is to indicate the supporting biology for the various resources. Many ecological processes involve loops or cycles within the system, which are vulnerable to disturbance at any point.

WETLANDS

The wetlands considered part of the Chesapeake Bay system are tidal mudflats and marshes that experience tidal flushing (fig. 3). Most wetlands are above mean low water, but some emergent wetlands extend to shallow (2 m) depths.

Marshes can be divided into several types on the basis of plant communities. Through their function as sediment traps and nutrient absorbers, marshes play a role in maintaining water quality of the Bay. Fresh- and brackish-water mixed vegetative marsh communities, salt marsh cordgrass communities, and arrow-arum/pickerel weed communities are the most valuable marsh types in terms of production, habitat, and erosion buffering (Silberhorn et al. 1974).

Some marshes provide a spawning area for fishes, and marsh invertebrates serve as fish food (Wass and Wright 1969).

Marshes also provide food and habitat for migratory waterfowl, resident birds, and other wildlife (Wass and Wright 1969). Migratory geese, whistling swans, and ducks use adjacent farmlands, as well as the marsh, as food sources during part of the year (L. E. Cronin, pers. comm.). Herons, egrets, and ibises nesting in the marshes are important consumers of fish and crustaceans. Gulls, during the winter, and terns, during the summer, eat fin- and shellfish in the marshes (R. Andrew, pers. comm.)

By feeding in farmlands and defecating in the marsh, birds may import carbon and nutrients. The magnitude of such imports is not known. Birds also export some material when they leave the marshes to migrate. Results from studies of the role of birds in other ecosystems suggest that the quantity of carbon and nutrients cycled by migratory birds during feeding and elimination within the system is much greater than that of material imported to or exported from the system.

Mammals which use the marsh habitat include nutria (*Myocastor coypus*), muskrat (*Ondatra zibethica*), mink (*Mustela vison*), and raccoon (*Procyon lotor*) (Wass and Wright 1969).

Marshes with sufficient tidal flushing export some of their annual carbon production to the Bay (R. Wetzel, pers. comm. based on salt marsh model research). Most export occurs in the winter, by ice scouring and tidal flushing when standing dead material is greatest (Heinle et al. 1976). Poorly flooded marshes may not exchange any carbon with the estuary on the Patuxent River, although dissolved nitrogen and phosphorus are exported to the estuary (Heinle and Flemer 1976). After Teal (1962), it has been widely assumed that marshes enhance the productivity of estuaries by exporting much of the carbon produced. While it is probable that there is a net export of carbon from marshes along the Chesapeake, there is still disagreement among scientists as to the role of marshes as contributors to Bay production.

Another unresolved aspect of the relationship between the estuary and adjacent marshes is nutrient exchange. Marshes trap nutrients (both natural and pollutants) from tributaries and upland drainage (Silberhorn et al. 1974). Nutrients can be temporarily stored in the marshes, and released gradually to the Bay. The buffering capacity of marshes is, however, limited and can be lost if large nutrient inputs from sewage effluent saturate the marsh (R. Wetzel, pers. comm.).

Organic and inorganic nutrients also enter marshes from the Bay. Nutrient exchange between marshes and Bay waters involves changes in the chemical forms of N and P, superimposed on a probable net export of N and P to the Bay (Axelrad 1974). The role of marshes in nutrient exchange is debated among scientists and requires further research.

The primary producers in coastal wetlands are marsh plants with attached periphyton and benthic algae (fig. 3). Species vary with the type of marsh or mudflat. Most marsh plants enter the marsh

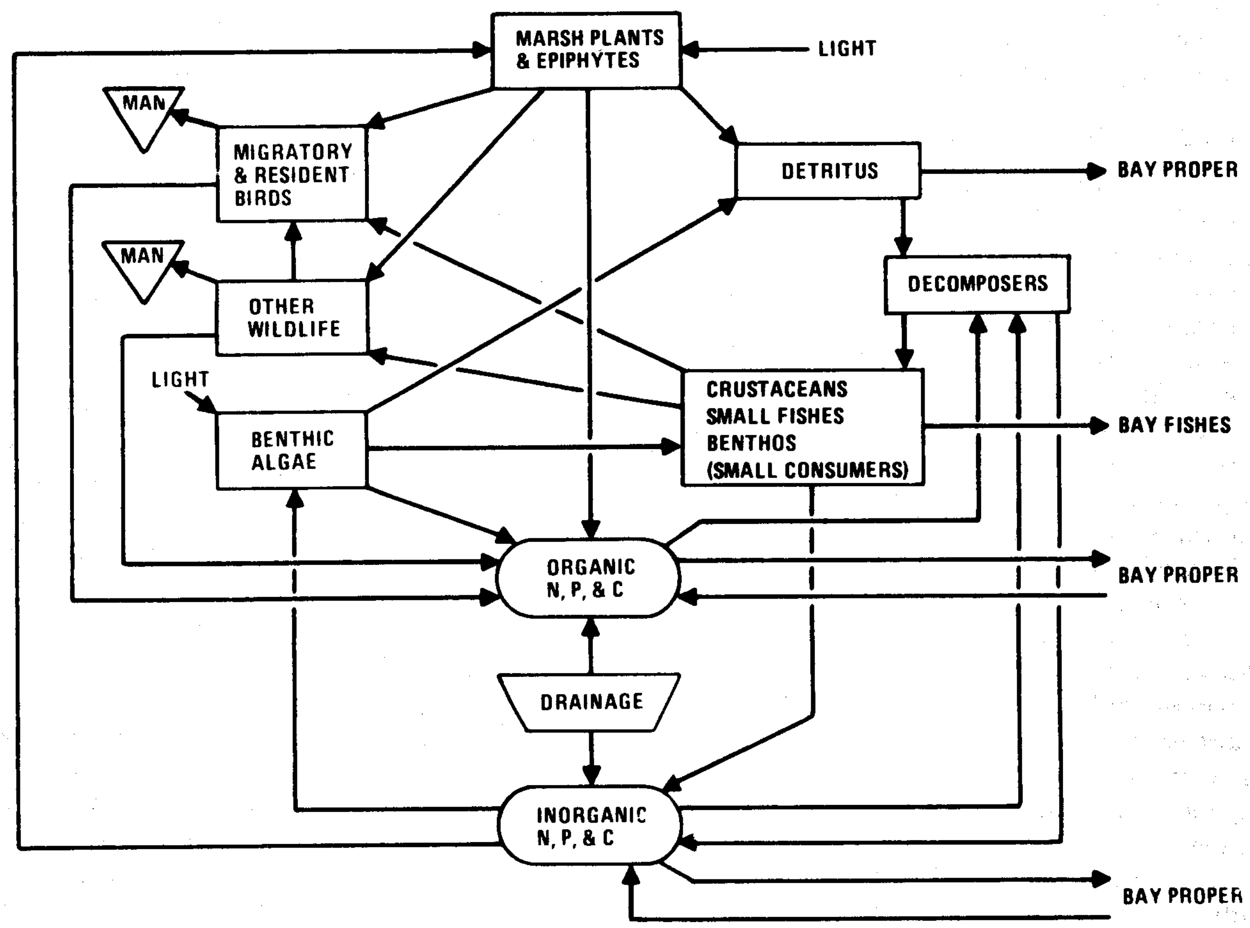


Figure 3. Conceptual model of wetlands.

food web through the detrital pathway, and decomposers are consumed by crabs and other benthic crustaceans, bivalves, mollusks, and small fishes. In any particular marsh, the small (in physical size) marsh consumer box will be dominated by one particular species (R. Wetzel, pers. comm.), e.g., fiddler crabs, insects, or small fishes. However, the dominant consumer member of the compartment will vary with the type of marsh and perhaps with the time of year. Small consumers of marsh detritus and benthic algae play a role in any marsh food web. In turn, these small marsh consumers support fishes which enter from the Bay during high water, birds, and other wildlife.

Material enters the Bay system with runoff over lands which are not classified as wetlands. This flow appears in figure 2 as drainage to the Bay (organic and inorganic N, P, and C). Runoff introduces a variety of substances into the Bay. Pollutants include herbicides and pesticides from agricultural land, and toxic substances impregnating wooden bulkheads, as well as natural (as opposed to man-induced) nutrients and detrital material.

River flow brings natural nutrients, trace metals, and detritus, as well as chlorine and nutrient loads from partially treated sewage, effluents from power plants, and chemicals from industrial activities, into the Bay system. Trace metals and petroleum hydrocarbons are introduced from shipping traffic, Baltimore Harbor, and storm-sewer runoff.

I found no estimates of the relative inputs of natural and pollutant materials from rivers, land runoff, pleasure and commercial boats, and Baltimore Harbor. Some work along this line has been done at Chesapeake Bay Institute at Johns Hopkins University. Point sources such as sewage treatment plants are monitored (A. J. Lippson, pers. comm., Potomac River survey). Nonpoint sources such as land runoff are much more difficult to measure or estimate.

Pollutants have reached all parts of the Chesapeake Bay system (L. E. Cronin, pers. comm.).

BAY AND TRIBUTARIES

Those parts of the Bay system that are permanently under water exhibit a marked salinity gradient from fresh water in the more landward locations of the estuary to approximately 30 o/oo salinity at the mouth of the Bay. At any given location in this partially mixed estuary, salinity is highest in the summer and fall when river runoff is low, and lowest in the winter and spring when rainfall and runoff are high. Pritchard (1968) provides a general description of water movement in the Bay. Storms can produce abrupt changes in salinity distribution.

The salinity regime affects the distribution of species from plankton to benthos to fishes. An ecological structure appropriate to any salinity region within the Bay is illustrated in figure 2. However, species composition inside the boxes varies with salinity and season; for example, net zooplankton species are dominated by copepods: *Eurytemora* in fresh and brackish water, and *Acartia* in more saline water. Net phytoplankton dominants vary from blue-green algae in fresh water to diatoms in more saline waters. The distribution of fish species (eggs, larvae, juveniles, and adults) depends upon the salinity regime as well as the time of year. Species of benthic infauna and epifauna vary with salinity; oysters and clams are found in the middle salinity regions of the Bay (Lippson 1973).

A second gradient in the Bay system is that of depth. Community structure changes from emergent wetlands to shallows to deeper waters.

The upper Bay derives most of its carbon from allochthonous sources; particulate organic carbon is transported into the system by the Susquehanna River. Only about 10 percent of new carbon is derived from primary production in situ; in contrast, most new carbon in the middle Bay is fixed by phytoplankton and relatively little is imported from upstream (Biggs and Flemer 1972). Total annual carbon inputs to the whole Bay from river transport, marshes, seagrasses, and phytoplankton production are estimated roughly in appendix B. Phytoplankton carbon production appears to be the most important, followed by that of marshes and seagrasses, and then by river transport. Inputs from land runoff have not been estimated.

Primary producers in emergent wetlands are marsh plants, epiphytes, and benthic algae. Most of this carbon enters the food web by the detrital pathway. Shallow regions receive carbon from three sources: transport of detrital material from marshes and rivers; production by seagrasses; and production by phytoplankton. In waters too deep for seagrass growth, phytoplankton production in situ and transportation from upstream are the carbon sources.

Much of the biological activity in the Bay occurs in the shoal or shallow waters that are most directly influenced by runoff from the land. Sediment-trap areas may remove sediments, nutrients, and toxic materials from the water column in shallow waters, preventing much of that material from reaching deeper waters.

PLANKTON

Figure 2 was originally planned to distinguish shallow and deeper water communities in the Bay. However, for plankton and some nekton, the distinction is not clear. Plankton species have not been found to vary from shallow to deeper water (Heinle, pers. comm.), although they do vary with salinity (Lippson 1973). The following discussion of the plankton community applies to all Bay waters (fig. 4).

In Chesapeake Bay, phytoplankton standing stock is apparently limited by availability of P in the spring and inorganic N in the summer (Taft and Taylor 1976). In the winter, biomass is limited by light or temperature (Taft, pers. comm.). Sediment-water interactions in oxygenated and anoxic waters, as well as regeneration by organisms, determine abundance and chemical form of available P and N in the system.

Primary production rates may be determined by nutrient regeneration rates. While total nutrients place an upper limit on standing stock during the summer, turnover rates may be as rapid as every 2 days (Heinle, pers. comm.). It is possible that summer primary production is limited only by the physiological capabilities of plant cells (Taft, pers. comm.). Nannoplankton (plant cells less than 10 microns in diameter) contribute at least two-thirds of total primary production on an annual basis (Van Valkenburg and Flemer 1974).

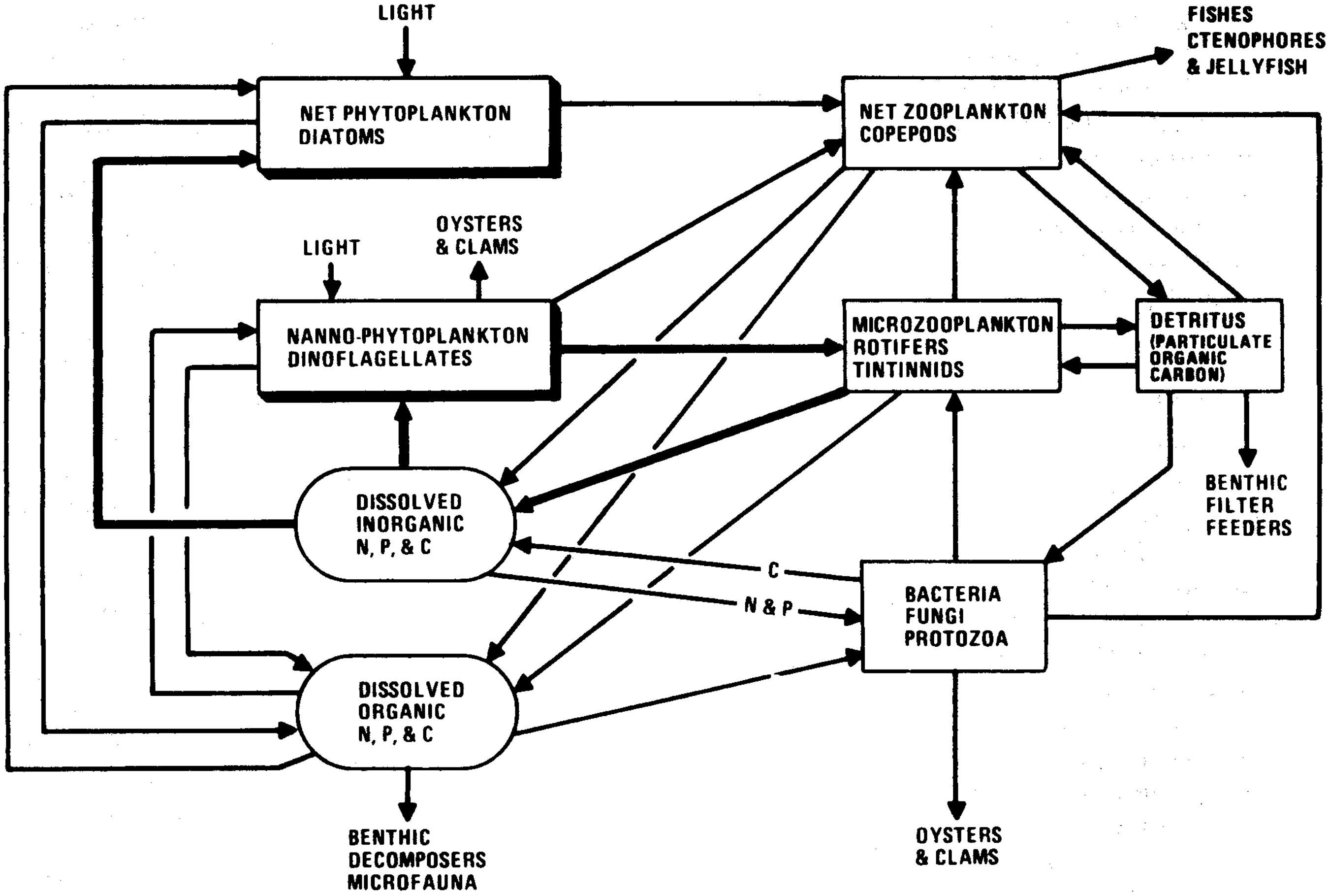


Figure 4. Conceptual model of plankton and nutrient interactions.

Zooplankton also can be considered in two size classes, the larger or net zooplankton such as copepods, and smaller or microzooplankton such as tintinnids and rotifers. In the upper Patuxent River, zooplankton must consume detritus because plant production in situ is not sufficient to support them (Heinle and Flemer 1975); in the middle Bay, larger zooplankton eat only about 10 percent of daily net primary production (Heinle, pers. comm.). What happens to the rest of the production? Figure 4 shows one possible microzooplankton-dissolved inorganic N, P, C-nannoplankton loop whose mechanism for consumption and rapid regeneration of nutrients in the euphotic zone would facilitate rapid turnover of the plankton community, but its existence has not been demonstrated (Heinle, pers comm.).

Zooplankton tend to maximize living material in the diet, and can eat bacteria (Heinle, pers. comm.). Bacteria and protozoa can take up inorganic (as well as organic) N and P, and may be competing with phytoplankton for nutrients (Webb, pers. comm.). Bacteria and fungi can break down cellulose and chitin, the main components of detritus (Webb, pers. comm.).

Plankton must be viewed in the context of organic and inorganic nutrient dynamics. Nutrients are affected not only by plankton, but also by excretion by larger organisms, absorption and regeneration through chemical processes in sediments, regeneration by biological processes in the euphotic zone and benthos, and by physical transport. There are still many questions about nutrient dynamics in the Bay system, and figure 4 should be regarded as expressing present hypotheses. Plankton are usually viewed as the starting point of a food web, but they are one step in a nutrient-cycling loop that involves the whole Bay system.

One other aspect of plankton and nutrient dynamics involves tidal exchange of water between the Atlantic Ocean and the Chesapeake Bay at the Bay mouth. Studies of the tidal exchange are under way at Virginia Institute of Marine Science. The relative magnitudes of inputs and losses are not yet known, but some nutrient losses are probable.

The zooplankton compartments of the conceptual Bay model also contain icthyoplankton and larvae of benthic organisms. Any animal feeding on zooplankton can also consume larval fishes and benthos, thus playing a role in regulation of those populations. All larval fishes are zooplankton feeders, and may be a very significant factor in the trophic dynamics of the Bay system.

BENTHOS

Benthic organisms are important in the flow dynamics of C, N, and O_2 in the Bay (D. Boesch, pers. comm.).

Eelgrass (*Zostera*) communities cover much of the shallow bottom from mean low water to about 2 m depth in the upper mesohaline and polyhaline areas of the Bay (Orth 1975). Other seagrass species, generally more abundant on the eastern shore where there are wide shallow areas, include *Potamogeton* and *Vallisneria* in fresh and brackish water, and *Ruppia* in middle and higher salinities (Lippson 1973).

Seagrasses (fig. 5) provide structure and habitat for epiphytic plants and a diverse epifauna of amphipods, isopods, barnacles, tunicates, polychaetes, and gastropods (Marsh 1973, 1976). Macrofauna consume about 55 percent of the net production of eelgrass, phytoplankton, and benthic algae of a *Zostera* community, with the rest available to bacteria, microfauna, and meiofauna (Thayer et al. 1975). There is little grazing pressure on the leaf blades (Zieman 1975, Marsh 1970), which enter the food chain as detritus. Benthic infauna densities are higher in *Zostera* communities than any other benthic habitat in Chesapeake Bay since the grass stabilizes the sediments (Orth 1973). Seagrass communities also provide protection for larval and juvenile fishes and blue crabs in soft and peeler stages, as well as food for fishes, crabs, shrimps, and water birds. Fishes associated with eelgrass [e.g., anchovies (*Anchoa* spp.) in summer, spot (*Leiostomus zanthurus*) and silversides (Antherinidae) in winter] feed on detritus, planktonic copepods, and epifaunal crustaceans, deriving about half of their nutrition from the seagrass community (Adams 1976a, b, c).

The cownose ray (*Rhinoptera bonasus*) tends to uproot seagrasses as it grubs for benthic organisms (Orth 1975).

Oyster reefs constitute another type of benthic community (Larsen 1974). Oysters feed on dinoflagellates and detritus, and possibly bacteria and lipids; clams feed on coarser particles (D. Haven, pers. comm.). Oysters, clams, and other filter feeders remove sediments and detritus from the water column much faster than possible through sinking alone. Fecal pellets make the material available to benthic grazers. Biodeposits on the sediment surface are enriched by bacteria, and turned over by sediment mixers, such as shrimp and worms (D. Haven, pers. comm.).

Benthic organisms also are present in sandy and muddy bottoms without seagrasses or oyster-reef structure (see fig. 6). Standing stocks are lower, but turnover may be very rapid. Exclosure studies indicate that blue crabs and some demersal fishes are voracious predators, and may control benthic standing stocks on unprotected bottoms (Boesch et al. 1976, Virnstein 1976). Benthic populations may also be partly controlled by predation on planktonic reproductive stages during the summer. A bimodal spring and fall setting pattern is common, with setting reduced during the summer when predation by ctenophores and fishes on zooplankton is highest (D. Boesch, pers. comm.).

The distinction between shallow and deep parts of the bay is more obvious for benthos. Benthic communities are characterized by surface and suspension feeders in shallower waters, and deposit feeders in deeper waters. Predation on infauna may be the most important controlling factor for shallow populations, and competitive interference is a controlling factor in deeper waters. Species also tend to be associated with sediment type; shallow sediments are usually sand, and deeper sediments are usually mud. In the deep channels experiencing anoxic conditions due to stratification of the water column, benthos are depauperate (D. Boesch, pers. comm.). Presumably, low oxygen conditions also exclude fish and other mobile organisms from some of the deeper waters of the Bay during the summer (Haefner 1971).

Biological and chemical processes in the sediments are thought to be important in regulating the abundance and chemical form of N and P in the water column. More research is necessary to elucidate the mechanisms as well as the magnitude of these processes (K. Webb, pers. comm.).

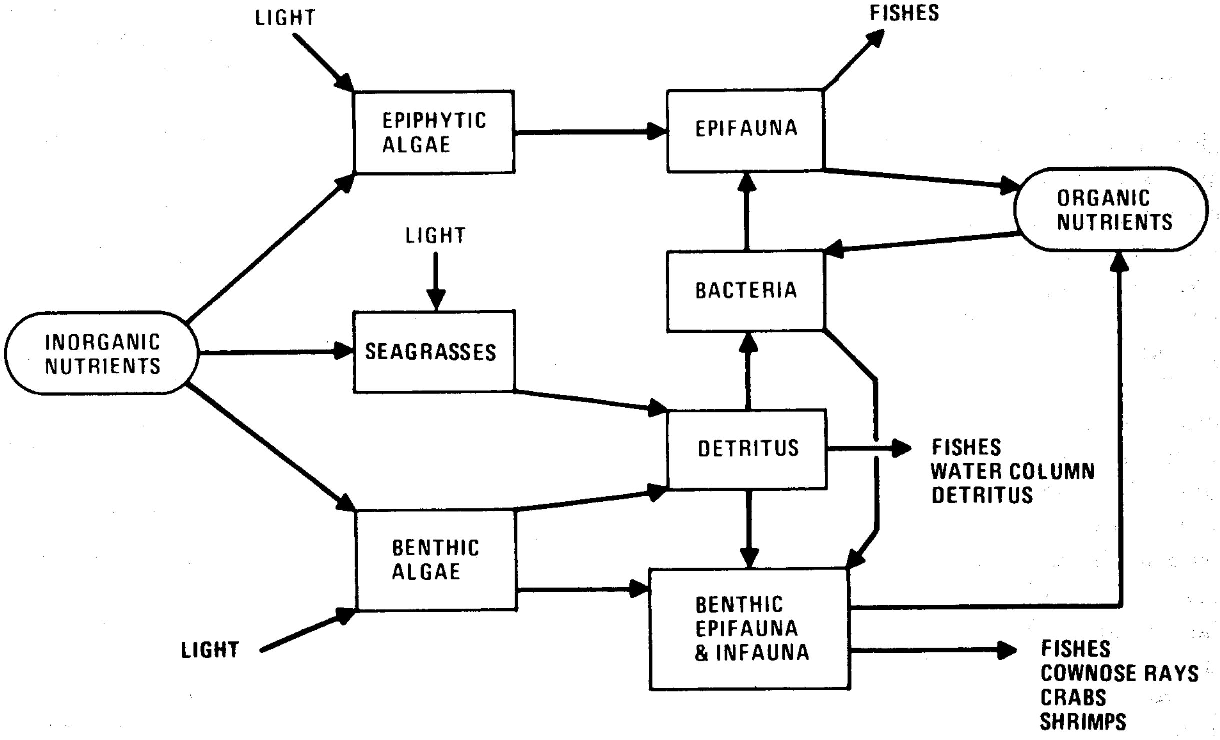


Figure 5. Conceptual model of seagrass communities.

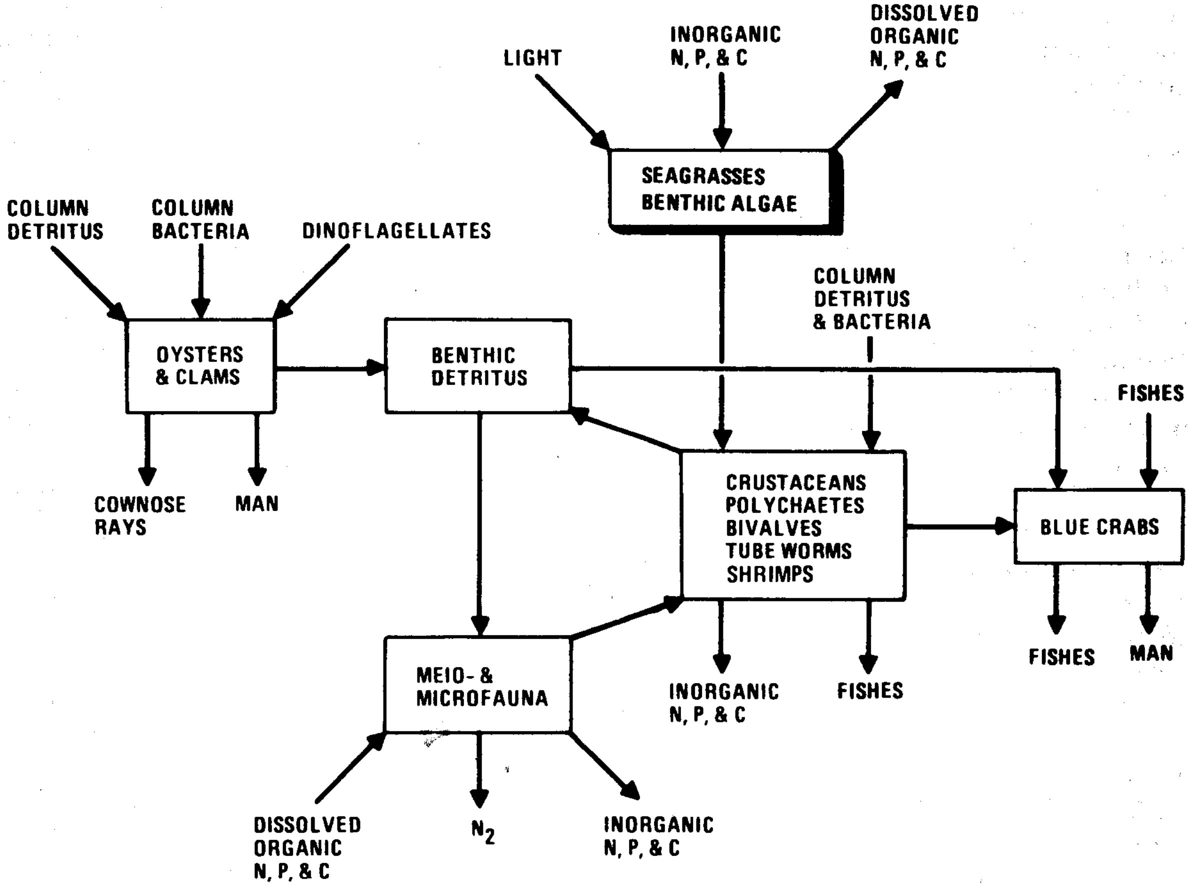


Figure 6. Conceptual model of other benthic communities.

NEKTON

Ctenophores and jellyfish are a nuisance to swimmers in the Bay, and can be extremely abundant in certain areas in the summer time. Their abundance is controlled by salinity, temperature, and possible unidentified factors, as well as the breaking up of their tissues by high wave activity in the fall and winter. They are a major predator of zooplankton, but are apparently a dead end in terms of trophic dynamics; they are not known to provide a major food source for any other group.

The fish community of the Bay can be considered to be dominated by the Atlantic menhaden which as an adult consumes phytoplankton, and during the larvae stages, consumes zooplankton. In fresh waters, the menhaden are replaced by other clupeid fishes. In the diagram of major Bay processes (fig. 1), fishes are considered in two groups, Atlantic menhaden and all others. This indicates the importance of menhaden in grazing on the phytoplankton and in providing food resources for other fishes. Menhaden also support a large commercial fishery and are the main resource removed from the Bay in terms of fishery yield. Removal of menhaden is also removal of fish food; menhaden feed other populations of commercial and recreational fishes in the Bay.

The dominance of fishes by menhaden is presented as a simplifying perspective on the fish community. Some Bay scientists disagree with this view.

There are approximately 200 fish species in Chesapeake Bay. Figure 7 shows a generalized trophic dynamics model of this diverse fauna (Hildebrand and Schroeder 1928, Bigelow and Schroeder 1953, Reintjes 1969, Markle and Grant 1970). Adult menhaden and anchovies, and all fish larvae are primarily plankton feeders. At various times of the year, however, the larvae of most of the fish species in the Bay will be included among the plankton. Some fishes such as bluefish (*Pomatomus saltatrix*), weakfishes (*Cynoscion* spp.), and striped bass are piscivorous. Bluefish are particularly voracious predators, feeding on the juveniles and adults of all other fishes found in the Bay. There is a middle group of omnivores, such as eels and Atlantic croaker (*Micropogon undulatus*), whose diets may include the planktonic crustaceans (copepods, amphipods, and mysids); benthic crustaceans such as crabs or shrimps; bivalves; small forage fishes such as killifishes (Cyprinodontidae); mummichog (*Fundulus heteroclitus*); silversides, anchovies, and menhaden; and benthic fauna from marshes. They may also feed on the epifauna and epiphytes of seagrass communities.

A diagram of food-web dynamics for Bay fishes is very difficult to construct. To attempt accuracy only produces a diagram which is too complex to be useful, with arrows from every box to every other box, or with dozens of boxes. In developing figure 7, fishes were grouped by major food habits. A different set of simplifying assumptions would produce a different diagram of fish trophic dynamics. Common names in the compartments indicate adults or late juveniles. Larval fishes are all plankton eaters. Production of larvae contributes to Bay zooplankton, which includes icthyoplankton. Larvae in the Bay system are indicated by broken arrows; spawning may occur in the Bay or outside the Bay mouth, with larvae then coming into the Bay.

As a broad overview, Chesapeake Bay supports resident and migratory fishes, with planktivorous, omnivorous, and piscivorous feeding habits. Menhaden, striped bass, and anchovies can be found in the Bay year round even though they may not necessarily spend their entire life cycle there. Menhaden are most abundant in the spring and summer. Other small forage fish such as killifishes, mummichog, silversides, hogchoker (*Trinectes maculatus*) and gobies (Gobiidae) are found in the shallow waters, among seagrasses, or feeding out of the marshes throughout the year. In the spring (approximately March), adult fishes migrate into the Bay from the Atlantic. The anadromous alosines, or shad and river herring, migrate to fresh water to spawn, and feed as they return to sea. White perch (*Morone americana*) and striped bass, which are resident in the Bay, migrate into fresher water to spawn. This wave is followed by a migration of the sciaenids, or croaker, drum, weakfish, and spot, entering the Bay to feed after spawning in nearshore shelf waters of the Atlantic. Then their larvae also enter the Bay. Bluefish spawn in the ocean and enter the Bay only for feeding. Bluefish are a major fish predator as well as an important recreational fish. They can be found up to the fresh water limits in the Bay system, although they are more abundant in waters of higher salinity. In the fall the migration process is reversed as many of the fishes

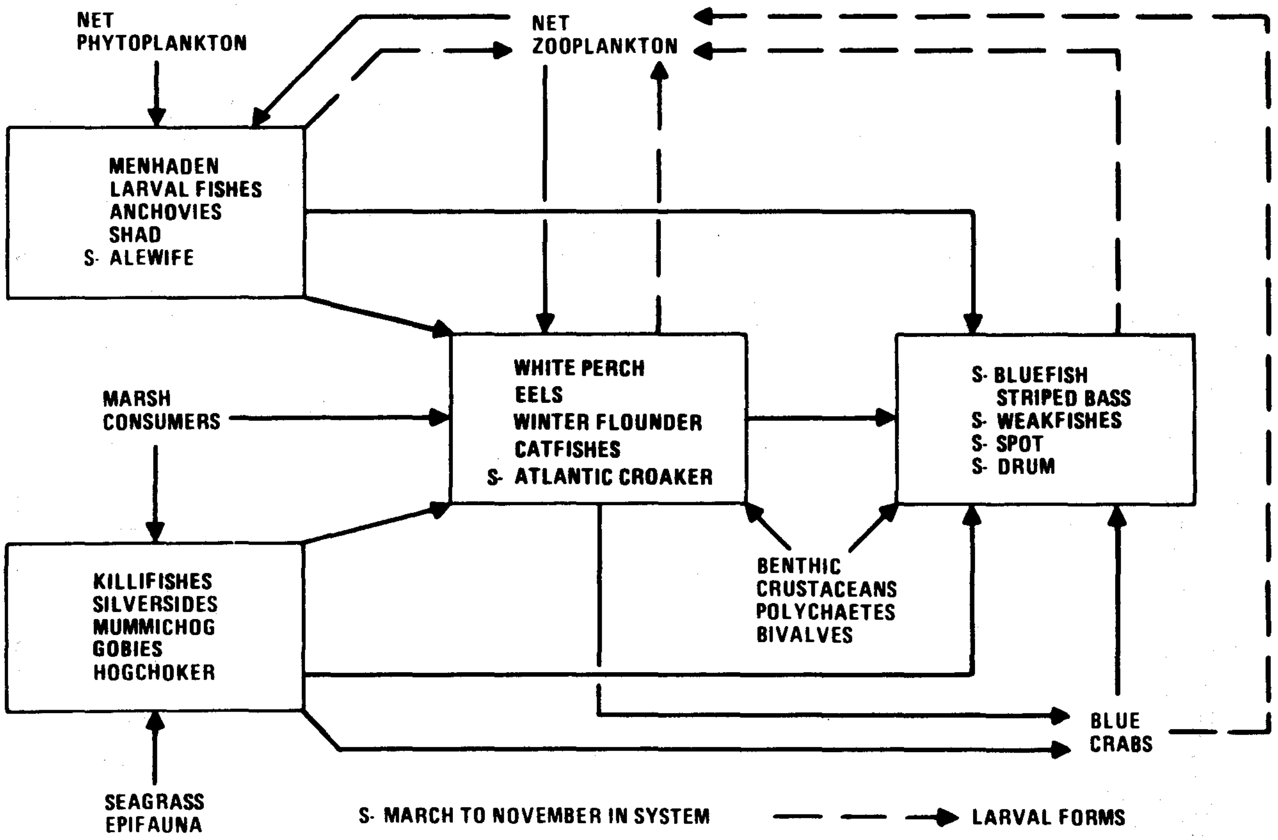


Figure 7. Trophic dynamics of fish.

leave the Bay for the ocean (Cronin and Mansueti 1971).

Dominant fish fauna of the Bay, in terms of biomass present and food consumed or material flow, are the Atlantic menhaden, the sciaenids, and the bluefish (Merriner, pers. comm.).

Fishes feed on plankton and other fishes in the water column, on bivalves, mollusks, crustaceans, polychaetes and other benthic organisms, on the epifauna and epiflora of seagrass communities, and on consumers in the marsh. Thus all portions of the Bay are important for the feeding ecology of fishes. While spatial variations are not indicated in figures 2 and 7, they may be very important in terms of overall fish population dynamics because of the need for suitable spawning areas. Different areas of the Bay are crucial for different fishes, but every part of the Bay serves as a spawning area for some species.

The bottle-nosed dolphin (*Tursiops truncatus*), which consumes fishes, is found in the Bay. Other dolphins, porpoises, and the smaller toothed whales are rarely recorded (Wass 1972).

Migratory waterbirds feed in open water. Diving ducks such as scaup (*Aythya* spp.) or canvasback (*Aythya valisineria*) feed primarily on mollusks; scoters (*Melanitta* spp.), oldsquaw (*Clangula hyemalis*), goldeneyes (*Bucephala* spp.), and ruddy ducks (*Oxyura jamaicensis*) eat crustaceans. Loons (*Gavia* spp.), mergansers, (*Mergus* spp.) and nesting ospreys (*Pandion haliaetus*) feed on fish. Fin- and shellfishes are consumed by gulls (Laridae) in the winter and terns in the summer (R. Andrew, pers. comm.).

DETAILED BAY MODEL

To integrate the wetlands, plankton and nutrients, seagrass community, other benthos, and fish trophic dynamics submodels (fig. 3 through 7) into one model more detailed than the system overview in figure 2, the connectivity matrix of figure 8 was constructed. This matrix model contains the same information as a combined box and arrow diagram, but in a different format. With a little practice, the matrix format is easier to read than the diagrams.

Compartments in the connectivity matrix

	FROM:	WETLANDS									WATER COLUMN															BENTHOS											ENVIRONMENT					
	TO:	1 PLANTS & EPIPHYTES	2 BENTHIC ALGAE	3 SMALL CONSUMERS	4 BIRDS	5 OTHER WILDLIFE	6 DETRITUS	7 DECOMPOSERS	8 ORGANIC N, P, & C	9 INORGANIC N, P, & C	10 NET PHYTOPLANKTON	11 NANNOPLANKTON	12 NET ZOOPLANKTON	13 MICROZOOPLANKTON	14 CTENOPHORES & JELLYFISH	15 WATERBIRDS	16 MENHADEN, LARVAL FISH, ETC.	17 KILLIFISH, ETC.	18 CROAKER, ETC.	19 BLUEFISH, ETC.	20 DETRITUS	21 BACTERIA, PROTOZOA	22 ORGANIC N, P, & C	23 INORGANIC N, P, & C	24 DISSOLVED OXYGEN	25 SEA GRASSES	26 EPIPHYTES	27 BENTHIC ALGAE	28 EPIFAUNA	29 INFAUNA	30 OYSTERS & CLAMS	31 BLUE CRABS	32 CRUSTACEANS, ETC.	33 DETRITUS	34 MEIO- & MICROFAUNA	35 POLLUTANTS	36 RIVER DRAINAGE	37 LAND RUNOFF	38 ATMOSPHERE	39 ATLANTIC OCEAN	40 DEEP SEDIMENTS	41 MAN
WETLANDS	1 PLANTS & EPIPHYTES									●																																
	2 BENTHIC ALGAE									●																																
	3 SMALL CONSUMERS		●					●																												●						
	4 BIRDS	●		●																																●						
	5 OTHER WILDLIFE	●		●																																						
	6 DETRITUS	●	●	●	●																																●	●				
	7 DECOMPOSERS						●		●	●																																
	8 ORGANIC N, P, & C		●	●	●	●																															●	●				
	9 INORGANIC N, P, & C							●																													●	●				
WATER COLUMN	10 NET PHYTOPLANKTON																						●	●												●						
	11 NANNOPLANKTON																						●	●												●						
	12 NET ZOOPLANKTON										●	●		●											●											●						
	13 MICROZOOPLANKTON											●										●			●											●						
	14 CTENOPHORES & JELLYFISH												●												●											●						
	15 WATERBIRDS																																			●						
	16 MENHADEN, LARVAL FISH, ETC.												●												●											●				●		
	17 KILLIFISH, ETC.			●																					●				●							●						
	18 CROAKER, ETC.			●									●				●	●							●					●		●	●			●				●		
	19 BLUEFISH, ETC.																●	●	●						●							●	●			●				●		
	20 DETRITUS						●				●		●	●	●	●	●	●	●	●						●						●	●				●	●				
	21 BACTERIA, PROTOZOA																				●		●	●	●																	
	22 ORGANIC N, P, & C								●		●	●	●	●												●	●	●									●	●			●	
	23 INORGANIC N, P, & C									●			●	●	●	●	●	●	●	●		●							●	●		●	●		●		●	●	●		●	
	24 DISSOLVED OXYGEN		●								●	●														●	●	●											●			
BENTHOS	25 SEA GRASSES																																			●						
	26 EPIPHYTES																																			●						
	27 BENTHIC ALGAE																																			●						
	28 EPIFAUNA																								●		●									●						
	29 INFAUNA																								●			●								●						
	30 OYSTERS & CLAMS											●									●	●			●											●						
	31 BLUE CRABS																	●	●						●					●			●	●		●						
	32 CRUSTACEANS, ETC.																								●			●							●	●						
	33 DETRITUS																				●					●	●	●	●	●			●									
	34 MEIO- & MICROFAUNA																						●		●									●								
	35 POLLUTANTS																																				●	●	●			
ENVIRONMENT	36 RIVER DRAINAGE																																									
	37 LAND RUNOFF																																									
	38 ATMOSPHERE																							●	●																	
	39 ATLANTIC OCEAN																●		●	●																						
	40 DEEP SEDIMENTS																																			●						
	41 MAN				●	●										●	●	●	●	●											●	●										

Figure 8. Connectivity matrix for a detailed conceptual model of the Chesapeake Bay ecosystem.

model are plants and epiphytes, benthic algae, small consumers, birds, other wildlife, detritus, decomposers, and organic and inorganic N, P, and C for wetlands; net phytoplankton, nannoplankton, net zooplankton, microzooplankton, ctenophores and jellyfish, water birds, menhaden and fish larvae, killifishes, etc., croaker, etc., bluefish, etc., detritus, bacteria and protozoa, organic and inorganic N, P, and C, and dissolved oxygen for the water column; seagrasses, epiphytes, benthic algae, epifauna, and infauna for seagrass communities; and oysters and clams, blue crabs, crustaceans, etc., detritus, and meio- and microfauna for benthos; pollutants are also part of the system. The environmental elements are river drainage, land runoff, atmosphere, Atlantic Ocean, deep sediments, and man.

Each compartment appears as a heading for one column in the matrix. Cells of the matrix indicate material flow between compartments. For example, the element in row 12 (net zooplankton) and column 10 (net phytoplankton) indicates flow from net phytoplankton to net zooplankton, or grazing on phytoplankton by zooplankton. Processes covered by elements of the matrix include grazing, predation, respiration and mineralization of nutrients (from animals to inorganic N, P, and C), heterotrophy (from organic N, P, and C to plants), migration (between fishes and Atlantic Ocean), waterborne inputs of detritus, nutrients, and pollutants, gas exchange between water and the atmosphere, chemical exchanges between sediments and the water column, etc. Empty cells represent exchanges that do not or are not known to occur.

The matrix format shows interactions within and between the submodels for wetlands, water column, and benthos. In a hierarchical study approach to the Bay, with research focused on subsystems, connections between the system under study and other parts of the Bay ecosystem should also be addressed.

For any compartment, elements in its row indicate the inputs to it, and elements in its column list its losses. The diagram does not show the relative magnitudes of such inputs and losses. Information on magnitudes will be useful in assigning priorities for research and environmental concerns.

MODEL INTERPRETATION

WATER QUALITY AND ECOLOGICAL CONCERNS

The Chesapeake Bay estuary is a very dynamic environment in which organisms must continually cope with changing conditions. Many researchers are concerned that human activities such as increasing sediment loads from land development; nutrient loads from sewage disposal; herbicides and pesticides from agriculture; other toxic chemicals from industrial effluents; refined petroleum hydrocarbons from pleasure boating, commercial shipping, or runoff from storm sewers (oil changes, etc.) may be altering the Bay environment too rapidly. If the limits of organisms to adapt or adjust to environmental change are exceeded, then the ecological structure of the system could change, with the loss of desirable species and introduction or increase of undesirable ones. The Bay system is self-cleaning to some extent, but if its capacity to recover is exceeded, water quality will continue to deteriorate.

The shallow waters of the Bay system are most likely to be affected by pollutants from river flow, land runoff, or sewage and industrial effluents. The sediment-trap function of some shallow waters also serves to keep pollutants in the shallower areas. But shallows are regions of the greatest biological activity and concentration of biomass, and so are most affected by pollutants. Pollutants are here defined as materials introduced into the system, as a result of human activities, that are excessive or harmful to the system.

Toxic substances that have entered the Bay system can be found in the water column, the sediments, and the biota. Material-flow pathways in the Bay model indicate potential routes for bioaccumulation of toxic materials and concentration up the food chain. Physical transport processes affect the distribution of toxic materials and their availability to biota. Chemical processes in the sediments and water column also influence the availability of such materials.

An example of a system response to changing environment is the recent decline of seagrass communities. The present decrease in abundance may be within the range of normal variation for the system; one of the problems in evaluating observable changes is the tremendous natural (i.e. undisturbed) variability of the Chesapeake Bay system. It is difficult to attribute the changes in the seagrasses to man-related causes when large population fluctuations have been observed historically. Within the model framework, however, are pathways that may contribute to the decline. First, some researchers argue that nutrient loading (from sewage inputs and land runoff of fertilizers) has increased the phytoplankton standing crop, which has in turn increased turbidity and reduced the light available for seagrass growth. A second hypothesis is that herbicides from land runoff may be responsible for killing seagrasses. Current research indicates that there are toxic concentrations of herbicides in the Bay (D. Correll, pers. comm.).

Another observed change is the great reduction in oyster spatfall since Hurricane Agnes. The cause is unknown. Model processes and pathways that affect plankton or benthic community conditions are possibilities.

Aspects of water quality affecting the ecology of the Bay include water transparency, dissolved oxygen concentration, chemical forms and concentrations of N and P, presence and concentrations of trace metals and toxic chemicals, rates of biological activities such as plant growth or nutrient regeneration, and abundance of desirable or undesirable species. Each aspect is affected by biological, chemical, and physical processes within the Bay system. In interpreting the model for the ecosystem, remember that where directions of flow are indicated by arrows, the rates along those pathways depend on the environmental parameters of temperature, light, nutrient or pollutant concentrations, mixing, water and sediment chemistry, transport, and salinity and oxygen distribution, as well as on the abundance of the donor and receiver compartments for each flow.

The fishery, estuarine habitats, waste treatment, and recreational resources of the Bay system are supported by its underlying ecology as indicated in the conceptual models for the system.

Fishes appear as larvae and as adults in the conceptual model. Production of fishes sufficient for a commercial or recreational fishery requires suitable habitat for spawning, survival of some larvae through juvenile stages to adult and recruitment size, and availability of fish food. For species spawning inside the Bay, suitable unpolluted habitats are required. The model indicates fish food requirements as well. Nutrient concentrations affect phytoplankton and other plant growth, which in turn provides food for the zooplankton and epifaunal and infaunal benthic communities supporting forage fishes, which are then fed upon by fish of commercial importance. Many components of the food web are necessary to sustain the fishery. Larval fishes in the plankton are especially vulnerable to pollution or other changes in water quality. Even though the biomass represented by larvae is low, they are essential to the continuation of the fishery. Fish habitats are more difficult to pull from the model, since each species uses a different part of the Bay, and spatial relationships are not indicated.

The Bay system functions naturally in waste treatment, as indicated by the nutrient uptake and regeneration cycles, the role of decomposers in the water column and benthos, and sediment chemistry. Loops need emphasis, since cycles for nutrient import, regeneration, and export involve the whole food web, as well as chemical and physical processes. Toxic substances that interfere with organisms, particularly plants and decomposers, interrupt the nutrient cycle and hence the self-cleaning action of the system. The conceptual models indicate the nutrient cycles and the presence of pollutants as potential rate modifiers. Nutrient inputs from river drainage and land runoff are also indicated in the model. Sewage disposal, if input rates are too great, may overload the system with nutrient concentrations higher than biological turnover rates can handle.

The maintenance of habitat for fishes, birds, and other wildlife is indicated indirectly by the conceptual models. Food supply and the ecological mechanisms for its continuance are indicated. Species diversity, and the abundance of desirable species for different habitats are indicated only indirectly. With sufficient pollution stress, the structure of the food web might change, so that the one presented in the models no longer applies.

To be suitable for recreational purposes, water should be clear, have a pleasant smell, be free of weeds or stinging jellyfish; in short, be aesthetically pleasing. It is the ecology of the whole system that produces these qualities; the entire system needs to be healthy to maintain them. Plants, nutrients, and decomposers affect water chemistry. Biological as well as physical processes control the abundance of weeds or jellyfish. Spawning habitat, acceptable conditions for larval development, food availability, and predation pressure (including commercial fishing) influence recreational fisheries.

It is the healthy function of the whole Bay ecosystem, not just single parts of it, that allows the Bay to provide abundant resources.

INDICATORS

The conceptual model provides a perspective on the role of the following potential indicators of water quality in the Chesapeake Bay ecosystem.

Seagrasses. Seagrasses, present in some of the shallow areas of the Bay, occupy both sediment and the water column; they can respond to conditions in both. Abundance and distribution of seagrass communities may reflect herbicide concentrations, water transparency, and other factors.

Chlorophyll a. Chlorophyll *a* concentration is proportional to phytoplankton standing stock, but not turnover rate. It can be measured throughout the year in the upper few meters of the whole system for comparison of conditions over space and time. It is related to nutrient abundance and possibly with herbicides or other toxic pollutants.

Dissolved Oxygen. Dissolved oxygen distributions are affected by biological processes (increased by plant production, decreased by animal respiration and decomposition) and physical ones (exchange with the atmosphere, mixing and vertical stratification of the water column). It can be measured at all depths in the system, and provides another parameter for comparison in space and time.

Transparency. Water transparency is easily measured by Secchi disc. It indicates both sediment loading and biological contributions to turbidity.

Blue crabs. Because blue crabs require different habitats during various parts of their life cycle, from the water at the Bay mouth to the tributaries, they can integrate information for the whole Bay system. Abundance may be affected by climate and fishing pressure, as well as water quality, and there may be wide natural variations in abundance. Consideration of additional system information will be necessary to interpret changes in abundance.

Larval forms. Larval forms are potentially good indicators of pollution levels because larvae are much more sensitive to pollutants than adults. Forms that eventually settle on the bottom, such as oyster spat, are the easiest to measure.

Pollutant concentrations in tissues. Concentrations of pollutants in the tissues of commercial fishes and shellfishes can provide indications of bioaccumulation in the benthic and pelagic environments. Concentrations in forage fishes and plankton, while a little more difficult to analyze, would provide earlier indications of dangerous accumulations that could eventually be passed to commercial species.

RESEARCH NEEDS

One problem in assessing the impact of man's activities on the Bay as a system is lack of adequate information on how the Bay system operates, on both short-term and long-term time scales. Short-term information requirements involve such matters as feeding habits, spawning habits, relationships of species to toxic substances, migration patterns, fishing patterns, and so forth. The long-term natural variation in population sizes is more difficult to handle, but the information is important. Since the Bay is a very dynamic system, it is difficult to distinguish between the biological responses to human activities and the undisturbed or "normal" changes which are long-term cyclic or successional phenomena due to the nature of the Bay as an estuary. Spatial scales are also important. Most studies are quite localized, and extrapolation of their results over the whole Bay, a very large system, presents serious problems in interpretation and impact assessment.

Thus one important aspect of research in the Bay is large-scale, long-term work. Parameters which will provide effective monitoring of water quality and ecosystem conditions need to be identified. Some possible indicators have been discussed.

There is also a need for ecosystem-level studies in the Bay. While a great deal of information is available on Bay ecology, it is still difficult to answer definitively such questions as (1) the relative impact of marsh detritus, upland detritus, seagrass production, and phytoplankton production in driving the system; (2) the relative importance of physical processes such as climate, temperature, ice regime, or sediment loading; (3) the importance of biological processes such as reproduction and predation; or of human impact such as the effects of toxic substances on commercially important species in the Bay, or on populations which are important in their food chains; or (4) the relative importance of water column and benthic processes in regeneration of nutrients, which are crucial to the overall productivity of the system. These questions are pertinent to management decisions as to habitat that must be protected, processes to be monitored, and the important aspects of water quality and their long-term economic effects. Answering these questions may be an ambitious undertaking, but coordination among investigators would contribute toward providing answers.

In the conceptual model for the Chesapeake Bay ecosystem, (figs. 1 through 8), about 40 key system components are identified by the compartments or boxes of the diagrams. Their interactions (arrows) and interrelationships are indicated. Physical and chemical processes that affect the biology of the system are identified. The relationships of several system processes to water quality have been discussed. This conceptualization of the system can be debated, compartments redefined, and new interactions included. As understanding of Bay ecology increases, the diagrams will be modified. The conceptualization reflects current hypotheses about Bay ecology.

Even at this simple level of resolution, the relative magnitudes (or importance) of the various flows on a Bay-wide, annual basis are not known. Compartment sizes or biomass measured in carbon units can be estimated easily for only a few of the compartments. One approach to research about water quality of the Bay is to take this or a similar general conceptualization of the system and estimate magnitudes (at least relative magnitudes) of the flows. It will not be easy. An example of the kind of information and calculations required is given in appendix B, a rough attempt to quantify carbon fixed in the Bay system by marsh plants, seagrasses, and phytoplankton, and to compare that quantity to carbon imported by rivers. Relative flow information can be useful for management. The largest inputs to primary production are most important to protect. The largest point or nonpoint sources of pollutants are the most important to regulate. The nutrient regeneration pathways having the highest turnover rate should be measured accurately so that the waste-treatment capacity of the system can be calculated. The ecosystem context provides a perspective on the relative importance of various management problems, if quantitative information can be obtained.

In a hierarchical approach to the Bay ecosystem, such as currently taken, subsystems are studied. Practicality dictates some subdivision of the ecosystem for study purposes, and a community approach (seagrasses, plankton, fishes, etc.) is workable. It is important to include information about exchanges between the particular community under study and the rest of the system (seagrass export of detrital carbon, consumption of zooplankton by fishes, proportions of phytoplankton production consumed by various grazers) as well as interactions within the subsystem itself. Quantitative information, with seasonal and spatial variations or year to year variations, is most useful.

Whenever quantitative estimates of any of the model compartments or flows are made for any part of the Bay system, an attempt should also be made to extrapolate the estimates to the whole Bay for a year. If such an extrapolation cannot be made, the information necessary to complete it should be identified. If an extrapolation is made, the underlying assumptions on spatial and temporal variations should be defined.

The attempt to quantify standing stocks and annual total flows for the conceptualized Bay system may eventually lead to development of a simulation of Bay ecology. In the meantime, it provides a means for examining a variety of assumptions about dynamics of subsystems in the context of the whole ecosystem.

A list of specific research questions of concern to scientists interviewed for this project is presented in appendix C.

REFERENCES

Adams, S. M. 1976a. Feeding ecology of eelgrass fish communities. Trans. Am. Fish Soc. 105:514-519.

Adams, S. M. 1976b. The ecology of eelgrass, *Zostera marina* (L.), fish communities I. Structural analysis. J. Exp. Mar. Biol. Ecol. 22:292.

Adams, S. M. 1976c. The ecology of eelgrass, *Zostera marina*(L.) fish communities II. Functional analysis. J. Exp. Mar. Biol. Ecol. 22:292-311.

Axelrad, D. M. 1974. Nutrient flux through the salt marsh ecosystem. Ph. D. Dissertation. William and Mary University. 134 pp.

Bigelow, H. B., and W. C. Schroeder. 1953. Fishes of the Gulf of Maine. U.S. Fish and Wildl. Serv., Fish. Bull. 53. 577 pp.

Biggs, R. B., and D. A. Flemer. 1972. The flux of particulate carbon in an estuary. Mar. Biol. 12:11-17.

Boesch, D. F., M. L. Wass, and R. W. Virnstein. 1976. The dynamics of estuarine benthic communities. Pages 177-196 *in* L. E. Cronin, ed. Estuarine processes. Vol. I. Academic Press, New York.

Cronin, L. E., and A. J. Mansueti. 1971. The biology of an estuary. Pages 14-39 *in* A symposium on the biological significance of estuaries. Sport Fishing Institute, Washington, D.C.

Dale, M. B. 1970. Systems analysis and ecology. Ecol. 51: 1-16.

Green, K. A. 1975. A simulation of the pelagic ecosystem of the Ross Sea, Antarctica: a time varying compartmental model. Ph. D. Dissertation. Texas A&M University. 187 pp.

Haefner, P. A., Jr. 1971. Avoidance of anoxic conditions by sand shrimp, *Crangon septemspinosa* Say. Chesapeake Sci. 12:50-51.

Heinle, D. R., and D. A. Flemer. 1975. Carbon requirements of a population of the estuarine copepod *Eurytemora affinis*. Mar. Biol. 31:235-247.

Heinle, D. R., and D. A. Flemer. 1976. Flows of materials between poorly flooded tidal marshes and an estuary. Mar. Biol. 35:359-373.

Heinle, D. R., D. A. Flemer, I. F. Ustach, and R. A. Murtagh. 1976. Contributions of tidaly wetlands to estuarine food chains. University of Maryland Water Resources Research Center TR 29. 34 pp.

Hildebrand, S. F., and W. C. Schroeder. 1928. Fishes of the Chesapeake Bay. Bull. U.S. Bur. Fish. 43. 388 pp.

King, C. E., and G. J. Paulick. 1967. Dynamic models and the simulation of ecological systems. J. Theor. Biol. 16: 251-267.

Lane, P., and R. Levins. 1977. The dynamics of aquatic systems. 2. The effects of nutrient enrichment on model plankton communities. Limnol. Oceanogr. 22:454-471.

Larsen, P. F. 1974. Quantitative studies of the macrofauna associated with the mesohaline oyster reefs of the James River, Virginia. Ph.D. Dissertation. William and Mary University. 182 pp.

Levins, R. 1966. The strategy of model building in population biology. Am. Scient. 54:421-431.

Lippson, A. I. 1973. The Chesapeake Bay in Maryland: An atlas of natural resources. Johns Hopkins University Press, Baltimore. 54 pp.

Mann, K. H. 1973. Seaweeds: their productivity and strategy for growth. Science 182:975-981.

Markle, D. F., and G. C. Grant. 1970. The summer food habits of young-of-the-year striped bass in three Virginia rivers. Chesapeake Sci. 11:50-54.

Marsh, G. A. 1970. A seasonal study of *Zostera* epibiota in the York River, Virginia. Ph.D. Dissertation. William and Mary University. 156 pp.

Marsh, G. A. 1973. The *Zostera* epifaunal community in the York River, Virginia. Chesapeake Sci. 14:87-97.

Marsh, G. A. 1976. Ecology of the gastropod epifauna of eelgrass in a Virginia estuary. Chesapeake Sci. 17:182-187.

Orth, R. J. 1973. Benthic infauna of eelgrass, *Zostera marina*, beds. Chesapeake Sci. 14:258-269.

Orth, R. J. 1975. Destruction of eelgrass, *Zostera marina*, by the cownose ray, *Rhinoptera bonasus*, in the Chesapeake Bay. Chesapeake Sci. 16:205-208.

Pritchard, D. W. 1968. Chemistry and physical oceanography of the bay. Pages 49-74 *in* Proceedings of the Governor's Conference on Chesapeake Bay. State of Maryland, Annapolis.

Reintjes, J. W. 1969. Synopsis of biological data on the Atlantic menhaden, *Brevoortia tyrannus*. FAO Species Synopsis 42. USDI Circular 230.

Silberhorn, G. M., G. M. Dawes, and T. A. Barnard, Jr. 1974. Coastal wetlands of Virginia. Interim report 3. Virginia Institute of Marine Science special report in applied marine science and ocean engineering 46.

Taft, J. L., and W. R. Taylor. 1976. Phosphorus distribution in the Chesapeake Bay. Chesapeake Sci. 17:67-73.

Teal, J. J. 1962. Energy flow in the salt marsh ecosystem of Georgia. Ecology 43:614-624.

Thayer, G. W., S. M. Adams, and M. W. LaCroix. 1975. Structural and functional aspects of a recently established *Zostera marina* community. Pages 518-540 *in* L. E. Cronin, ed. Estuarine research. Vol. I. Academic Press, New York.

Van Valkenburg, S. D., and D. A. Flemer. 1974. The distribution and productivity of nannoplankton in a temperate estuarine area. Estuarine Coastal Mar. Sci. 2:311-322.

Virnstein, R. W. 1976. The effects of predation by epibenthic crabs and fishes on benthic infauna in Chesapeake Bay. Ph.D. Dissertation. William and Mary University. 87 pp.

Walsh, J. J. 1975. Utility of systems models: a consideration of some possible feedback loops of the Peruvian upwelling ecosystem. Pages 617-632 *in* L. E. Cronin, ed. Estuarine research. Vol. I. Academic Press, New York.

Wass, M. L. and T. D. Wright. 1969. Coastal wetlands of Virginia. Interim report. Virginia Institute of Marine Science special report in applied marine science and ocean engineering 10.

Wass, M. L. 1972. A checklist of the biota of lower Chesapeake Bay. Virginia Institute of Marine Science special scientific report 65. 290 pp.

Zieman, J. C. 1975. Quantitative and dynamic aspects of the ecology of turtle grass, *Thalassia testudinum*. Pages 541-562 *in* L. E. Cronin, ed. Estuarine research. Vol. I. Academic Press, New York.

APPENDIX A

QUESTIONS ASKED OF BAY SCIENTISTS

1. What is the relative importance of macrophytes and phytoplankton in total primary production?
2. What proportion of primary production goes through the herbivore food chain, and what proportion through detritus?
3. What is the role of detrital feeding in the ecosystem?
4. Why is the estuary productive?
5. What are critical pollution problems, and impacts?
6. What are the main stresses on living resources (harvest, habitat, etc.)?
7. What research is needed on the Bay system?
8. What is the role of jellyfish and ctenophores in the system?
9. How do seasonal variations in salinity, temperature, or other physical parameters affect the biology of the system?
10. How do shallow areas compare with the deeper open bay for primary and secondary productivity, biological activity, resource availability, pollution stress?
11. What are the most important inputs and outputs for each compartment? What are turnover rates?
12. What are the relative importance of physical and biological controls on population sizes and energy and carbon flow rates?
13. What controls biological population sizes?
14. Identify critical habitat types. What are the requirements for their maintenance?
15. What are inputs to and outputs from the system by migratory populations?
16. How does Bay ecology vary spatially? (e.g., shallows vs. deeper waters, upper vs. lower Bay.)
17. What are food resources, competitors, predators, and parasites for commercially harvested species?
18. What are the greatest threats to commercial and sport fisheries, habitats, and aesthetic values of the Bay?
19. What are the greatest threats to water quality?

20. What are potential indicators of water quality, ecosystem health?

21. What has been the impact of power plants on tributaries?

22. What is the impact of pesticides and herbicides on the Bay?

23. What is the impact of commercial shipping, other sources of petroleum hydrocarbons?

24. Are relevant studies on particular questions available from other estuaries?

25. What processes are most important to nutrient regeneration?

26. Are C, N, and P flows all in the same direction?

27. What is the significance of migratory and resident birds on biological populations, nutrient and carbon flow?

28. What historical changes can be perceived in the Bay? Last 10 years? Last 300 years?

APPENDIX B

PRELIMINARY PRIMARY PRODUCTIVITY CALCULATIONS

Carbon input calculations here are intended as an example of information required to quantify the conceptual Bay model. Results are not considered to be realistic.

Annual marsh carbon production

$$300{,}000\text{A}(4000\text{m}^2/\text{A})\ (337.5\text{g/m}^2/\text{yr})=4\text{X}10^{11}\text{g/yr}=400{,}000\ \text{ton/yr}$$

Marsh area and productivity from discussion with R. Wetzel.

Seagrass annual production

$$21{,}000\text{A}(4{,}000\text{m}^2/\text{A})\ (1{,}750\text{g/m}^2/\text{yr})=1.47\text{X}10^{11}\text{g/yr}=147{,}000\ \text{ton/yr}$$

Productivity estimate from Mann (1973) for Nova Scotia. Acreage estimate, roughly 7,000 acres for the western shore at present (R. Orth, reluctant estimate), and assuming 14,000 acres for eastern shore.

Phytoplankton annual production

Estimated in situ carbon production for the Maryland portion of the Bay, 282,000 ton/yr (Biggs and Flemer 1972). Assuming the same rate and similar area for the Virginia portion, total phytoplankton carbon production is roughly 600,000 ton/yr.

River input of carbon

POC (particulate organic carbon) input from the Susquehanna River, which is 85 percent of river flow into the Bay, is 84,000 ton/yr (Biggs and Flemer 1972). Assuming the same input rate for other rivers, total river carbon input is 100,000 ton/yr.

Summary

Carbon sources for the Bay system, and annual totals over the whole Bay:

Phytoplankton	600,000 ton/yr.
Marshes	400,000 ton/yr.
Seagrasses	147,000 ton/yr.
River input	100,000 ton/yr.

APPENDIX C

RESEARCH PROBLEMS IDENTIFIED BY BAY SCIENTISTS

1. Relate commercial harvest of menhaden to that of other species.
2. What is the sustainable yield for Bay fisheries, and where should it be cropped?
3. More information is needed about fish food species, Atlantic menhaden, anchovies, penaeid shrimp, mysids.
4. What eats hogchokers?
5. What are the food web pathways for phytoplankton production if zooplankton only consume 10% of daily net production?
6. What is the Bay nutrient budget, including benthic regeneration?
7. How are changes in nutrient inputs and primary productivity transferred up the food chain?
8. What are food chain consequence of species changes in phytoplankton?
9. What will happen to the ecosystem if nutrient loading is (is not) cleaned up?
10. What is the N vs. P limitation for primary production–seasonal and spatial variations?
11. What are the effects of land-use policies on the Bay?
12. What are the nutrient uptake kinetics in the estuary, or how can productivity be kept down?
13. What is the abundance and distribution of benthic organisms and plankton?
14. Better fisheries monitoring data is needed, both of commercial and recreational catch.
15. What are the synergistic effects of pollutants?
16. Large-scale regional studies are needed rather than very localized studies in the Bay.
17. What is the impact of agricultural pesticides and herbicides?
18. Generally more quantitative work is needed.
19. What are the impacts of PCBs, toxins?

20. How do benthos serve as indicators of Bay health?

21. What is natural variability in Bay populations vs. impacts of human activities?

22. More studies are needed about the Bay edges, where biological activity and control are.

23. What is the role of mudflats in Bay ecology?

24. Mass balance studies of marsh/estuary exchanges are needed.

25. Develop a conceptual model to focus on systems level information.

26. What is the value of benthos as support for other resources, and as a pollution reservoir?

27. Emphasize control of populations and processes.

28. What are the relative values of different bottom types?

29. Information is needed on utilization of shallows, where it isn't deep enough for trawl samples.

30. What eats bacteria?

31. Studies of anaerobic processes and nutrient regeneration are needed.

32. What are the chemical and biological interactions between water column and benthos and sediments?

33. Recent and widely distributed chemical data is needed.

34. More coordination among institutes and research programs is needed.

35. Research the basic biology of eelgrass—physical, chemical environment, recruitment, culturing.

36. What is the importance of seagrasses to the Bay system—protection and food for shrimp, crabs, fish, etc.

37. Bioassay the effects of pollutants and herbicides.

38. What has caused the decline in setting of oysters and other larvae?

39. What are the environmental cues for fish migration?

40. Quantitative information for food webs is needed.