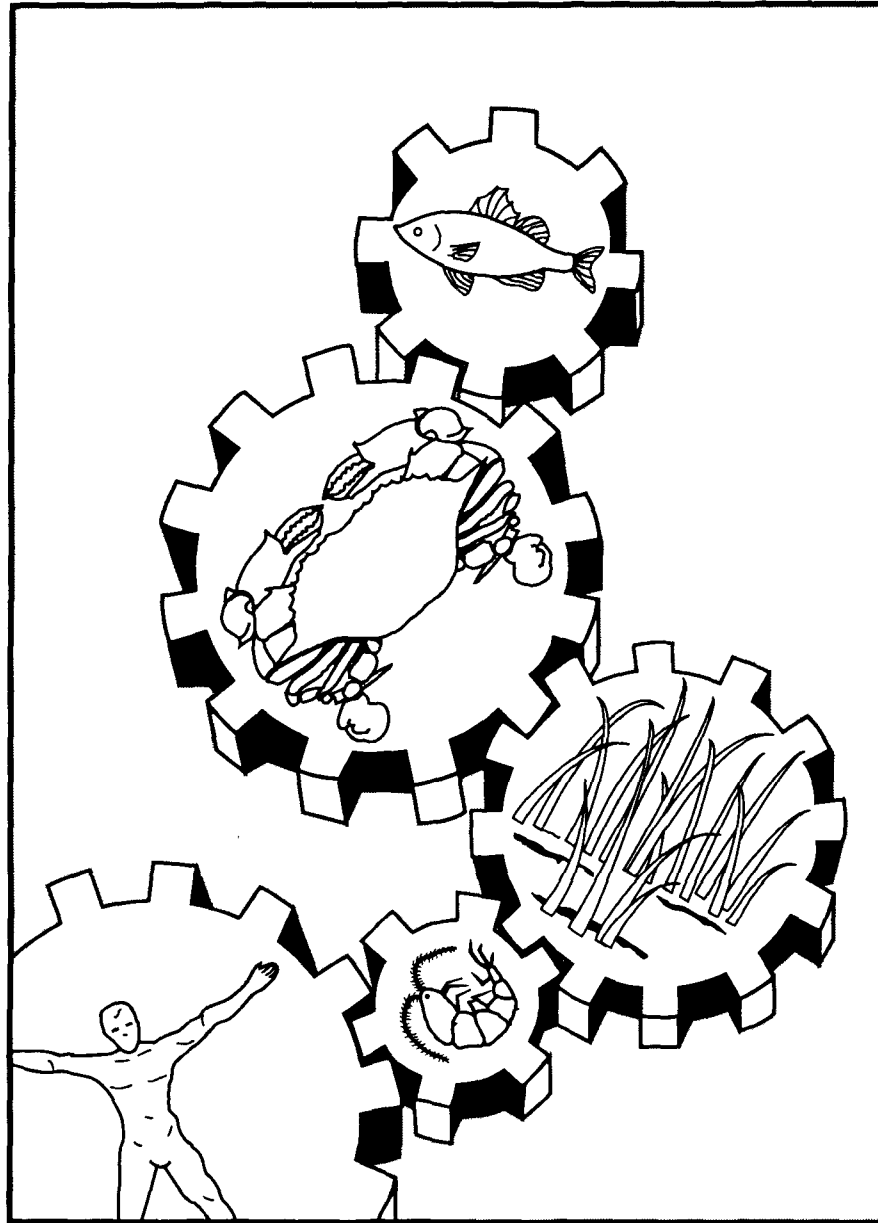


Current Approaches for Modeling Estuarine Ecosystem Processes

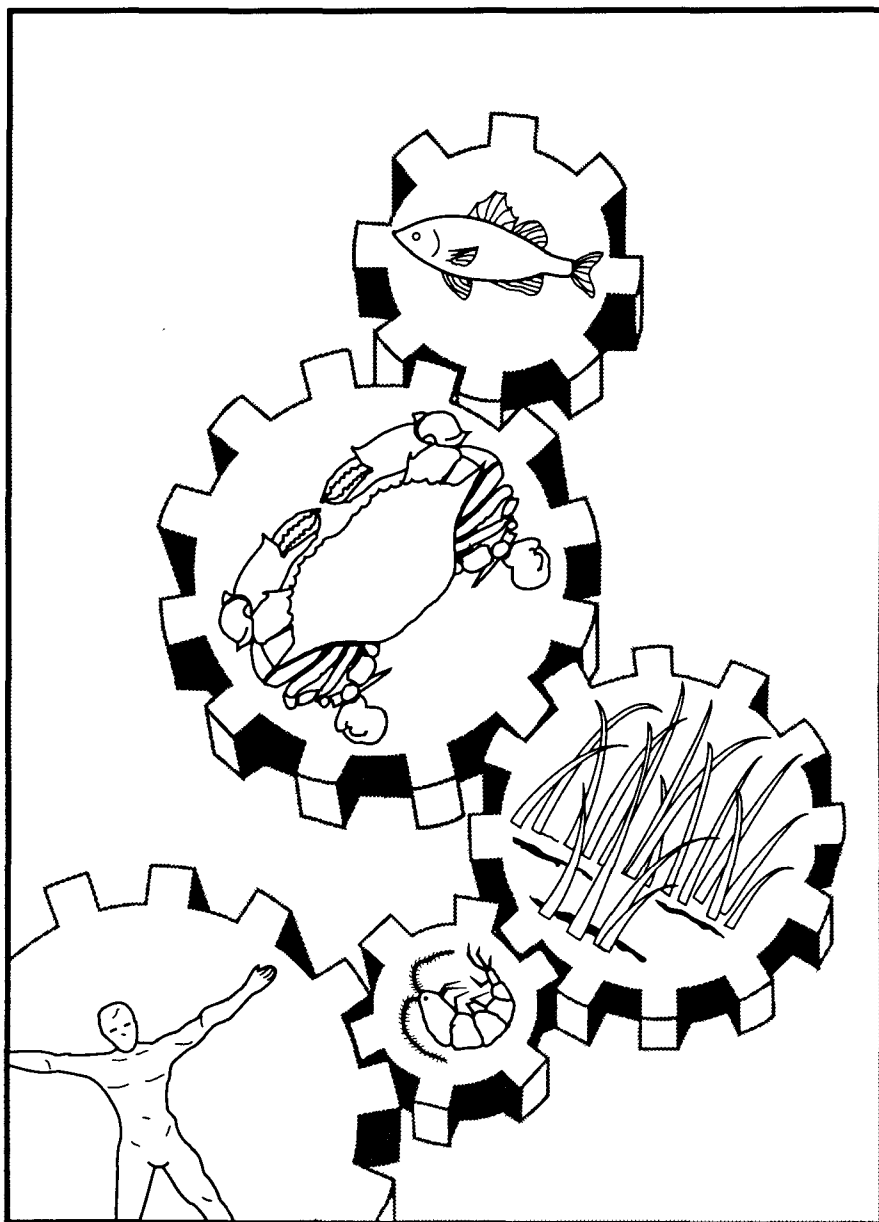


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Scientific and Technical Advisory Committee
Chesapeake Bay Program

Current Approaches for Modeling Estuarine Ecosystem Processes



Scientific and Technical Advisory Committee
Chesapeake Bay Program

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Table of Contents

Section		Introduction <i>Objectives and Organization of Workshop1</i> - Background - Format of the executive summary
Section		State of the Art <i>Contemporary Approaches to Estuarine Modeling2</i> - Introduction - Ecosystem process models - Water quality models - Spatially explicit fish bioenergetic models - Individual-based fishery management models - Ecosystem regression models - Ecosystem network analysis models - Landscape spatial models
Section		Linkage and Coupling <i>Toward an Integrated Modeling Framework17</i> - Overview - Conceptual issues - Physical process issues - Water quality model issues - Submerged aquatic vegetation model issues - Ecosystem feedback and control issues - Fishery management and recruitment issues
Section		Methodology and Technology <i>Factors in Concept, Design, and Implementation21</i> - Introduction - Scales of ecological systems - Aggregation and scale - Predictive versus experimental - Specific scale problems - Limits of technology - Physics: fine-scale versus coarse-scale - Feedbacks, trophic interactions, and time - Data availability - Model development: formulation, calibration, and sensitivity analysis
Section		Recommendations <i>An Agenda for Action27</i> - Recommendations

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** Invited but unable to attend.

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Introduction

Objectives and Organization of Workshop

Background

A group of estuarine scientists and managers met in March 1992 in St. Michaels, Maryland, to discuss a variety of issues relevant to modeling estuarine ecosystem processes in Chesapeake Bay. Sponsored by the Chesapeake Bay Program Scientific and Technical Advisory Committee (STAC), the three-day workshop brought together leading researchers and modelers from across the United States to investigate and to compare a range of numerical ecosystem approaches and to evaluate relevant applications for managing estuarine resources in Chesapeake Bay.

The workshop featured plenary presentations by leading modelers who are working on various approaches to ecosystem modeling. These presentations summarized state-of-the-art methodologies and technologies used in several important areas, including:

- Ecosystem process models
- Water quality models
- Spatially explicit fish bioenergetic models
- Individual-based fishery management models (IBFMs)
- Ecosystem regression models (ERMs)
- Ecosystem network analysis models
- Landscape spatial models

After the plenary presentations, the group divided into smaller subgroups to address a range of technical and philosophical questions pertaining to ecosystem process modeling. Each subgroup focused on the same basic questions of appropriate scales and levels of aggregation, and technical issues associated with model development, sensitivity analysis, calibration, and documentation.

Other discussions focused on coupling and integration questions: How do models integrate scientific research into a coherent framework? What are the best approaches for linking ecosystem process models with physical transport and fish population models? What are the technical and philosophical issues regarding links between such key components as water quality, submerged aquatic vegetation (SAV), fish, and habitat?

On the final day, the group reconvened to summarize its recommendations and to outline an agenda for action.

Format of the executive summary

After the workshop, STAC staff prepared this document—a technical executive summary of the presentations and discussions. To cover issues more effectively, the executive summary does not follow the chronological events of the workshop; rather, it borrows from all presentations, discussions, and papers to summarize essential points. In this way, the executive summary outlines important modeling approaches, reviews conceptual issues, and provides specific recommendations to the Chesapeake Bay Program.

Moreover, readers should be reminded that any good discussion contains a range of opinions and alternative viewpoints. In this context, any statement presented herein as consensus or fact, upon closer scrutiny, will reveal a full spectrum of scientific interpretation and emphasis.

State of the Art

Contemporary Approaches to Estuarine Modeling

Introduction

Workshop participants described a wide range of modeling approaches in use to simulate various processes, populations, and communities in Chesapeake Bay and other coastal ecosystems. Moreover, participants recognized the importance of complex interactions in relating human activities to estuarine resources. There was general consensus that linking or coupling hydrodynamic, water quality, ecosystem, and fish models into an integrated Bay-system framework is a major objective for the future. (See Figure 1.)

To achieve this goal, participants endorsed the idea of developing a suite of coupled (directly or indirectly) models to describe Bay-system processes, populations, and communities. However, they also agreed that because the models are based on different assumptions and attempt to quantify processes at different spatial and temporal scales and at different levels of biological organization, it would be a considerable challenge to overcome the problems inherent in developing a fully integrated model. The following initial steps were proposed: (1) generate output of biologically relevant variables from traditional water quality models; (2) use ecosystem models to explore feedback effects on water quality; (3) apply ecosystem models to examine water quality effects on lower trophic-level organisms (e.g., zooplankton, benthos) and SAV habitat; and (4) repeat the process and get better.

Although there are many approaches to modeling estuarine systems, several types of models stand out for making important contributions to Chesapeake Bay science or for potentially making such contributions in the future. They include:

- Ecosystem process models:
 - Plankton/benthos of Chesapeake Bay
 - Plankton dynamics of Narragansett Bay
 - Seagrass photosynthesis/growth
 - Salt marsh production
- Water quality models
- Spatially explicit fish bioenergetic models
- Individual-based fishery management models (IBFMs)
- Ecosystem regression models (ERMs)
- Ecosystem network analysis models
- Landscape spatial models

The rest of this section summarizes the chief characteristics of these model types. It is based largely on the papers presented at the workshop.

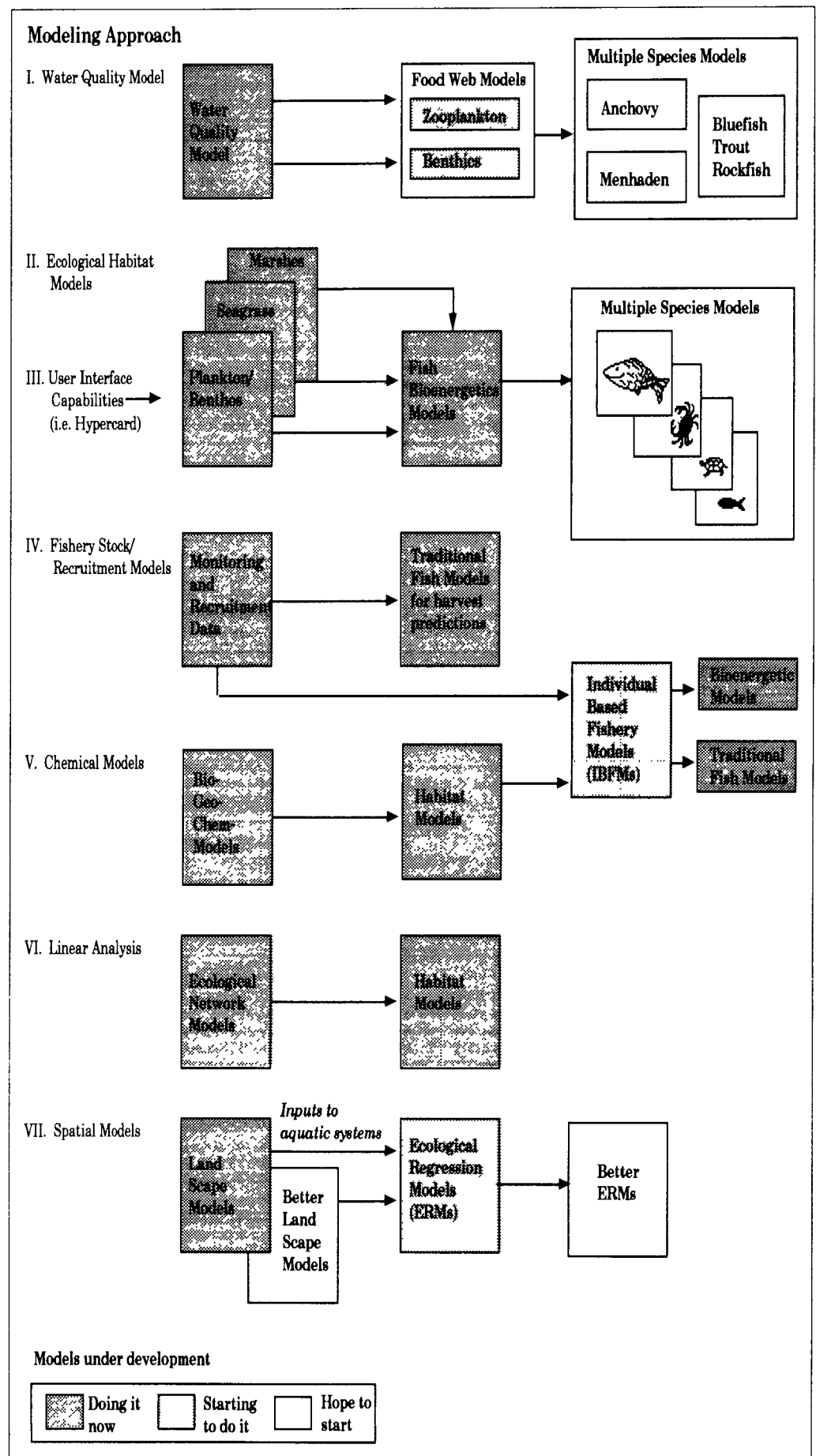
Ecosystem process models

Ecosystem process models address the mechanistic interactions that control the flow of nutrients and organic materials in coastal systems. Based on earlier models used to describe nutrient cycling between sediments and phytoplankton, some current ecosystem models explicitly simulate the effects of organic matter on benthic animals and bacteria. They often emphasize complex biogeochemical processes and interactions with higher trophic species.

Plankton/benthos of Chesapeake Bay

One ecosystem process model that simulates the trophic and biogeochemical processes that control the vertical exchanges of material between sediments and euphotic waters of Chesapeake Bay is Mike Kemp's planktonic/benthic model, which he described in this workshop. The model was designed to answer a range of specific scientific questions about the deposition of particulate organic matter (POM) and the factors controlling the process; for instance:

Figure 1. This diagram summarizes the types of models discussed at the workshop. Dark shading represents models currently in use, light stipling describes models under development, and clear boxes show approaches to future models. Connecting lines represent links between current and planned or potential modeling activities. This simple diagram reveals a great diversity in modeling approaches being developed for estuarine systems. It also shows that there are multiple, but largely untested, approaches for linking different parts of the ecosystem—such as water quality and living resources—into a unified whole.



- How do zooplankton grazing and fish predation affect POM deposition?
- How does nutrient enrichment influence POM deposition and oxygen consumption in bottom waters?
- To what extent does the microbial loop affect POM deposition?
- What controls the balance between denitrification and ammonia recycling in sediments?
- How do benthic suspension-feeders affect plankton dynamics and associated benthic-pelagic coupling?

This benthic-pelagic ecosystem process model includes 36 state variables interacting according to equations well-established in the scientific literature (depicted in Figure 2). Based on well-understood relationships, such equations have a high degree of generality and can be applied to a broad range of conditions and Bay regions. The model spatially averages ecosystem processes in a stratified water column over an area of approximately 200 km². To simulate sediment processes, the model includes the upper 10 cm of sediment and uses a pore-water oxygen pool as a state variable to separate the sediment into two distinct redox zones. It simulates time frames ranging from a day to a decade and uses Apple Macintosh STELLA simulation software to integrate finite difference equations that describe the temporal rates of change in state variables (time-step equals 2-4 h). Simulation time for an annual cycle of the model is about 15 minutes.

Initial model experiments have been used to investigate the seasonal effects on nutrient inputs, the effects of zooplankton and fish grazing, and the interactions between denitrification and bottom water dissolved oxygen concentrations. Moreover, these models have been used to evaluate the effects of nutrient reductions on summer bottom water dissolved oxygen conditions and the results are broadly comparable to the output from the hydrodynamically driven, time-variable, Chesapeake Bay water quality model.

Mike Kemp suggested that, in general, ecosystem process models offer several strengths in that they:

- Provide a framework for empirical research
- Simulate functional attributes of the system
- Can be reasonably calibrated
- Simulate nonlinear ecological feedbacks
- Can be linked to fishery bioenergetic models

Ecosystem process models, however, also tend to have certain weaknesses in that they:

- Often have limited spatial articulation
- Require expensive ecological process data for calibration
- Present calibration difficulties owing to high dimensionality
- Seldom include higher trophic organisms with complex life cycles (e.g. fish and birds)

Plankton dynamics of Narragansett Bay

In reviewing the Narragansett model, Jim Kremer described this classic estuarine ecosystem process model. The model simulates interactions between nutrients, phytoplankton, zooplankton, benthos, and small carnivores in eight spatial elements subject to daily tidal variations. In this approach, two phytoplankton subdivisions grow as an exponential function of temperature; Monod hyperbolic functions define nutrient limitation for nitrogen, phosphorus, and silicon, and Steel's curve specifies light levels for optimal growth. Both zooplankton and benthos graze phytoplankton, thereby controlling the realized increase in phytoplankton biomass.

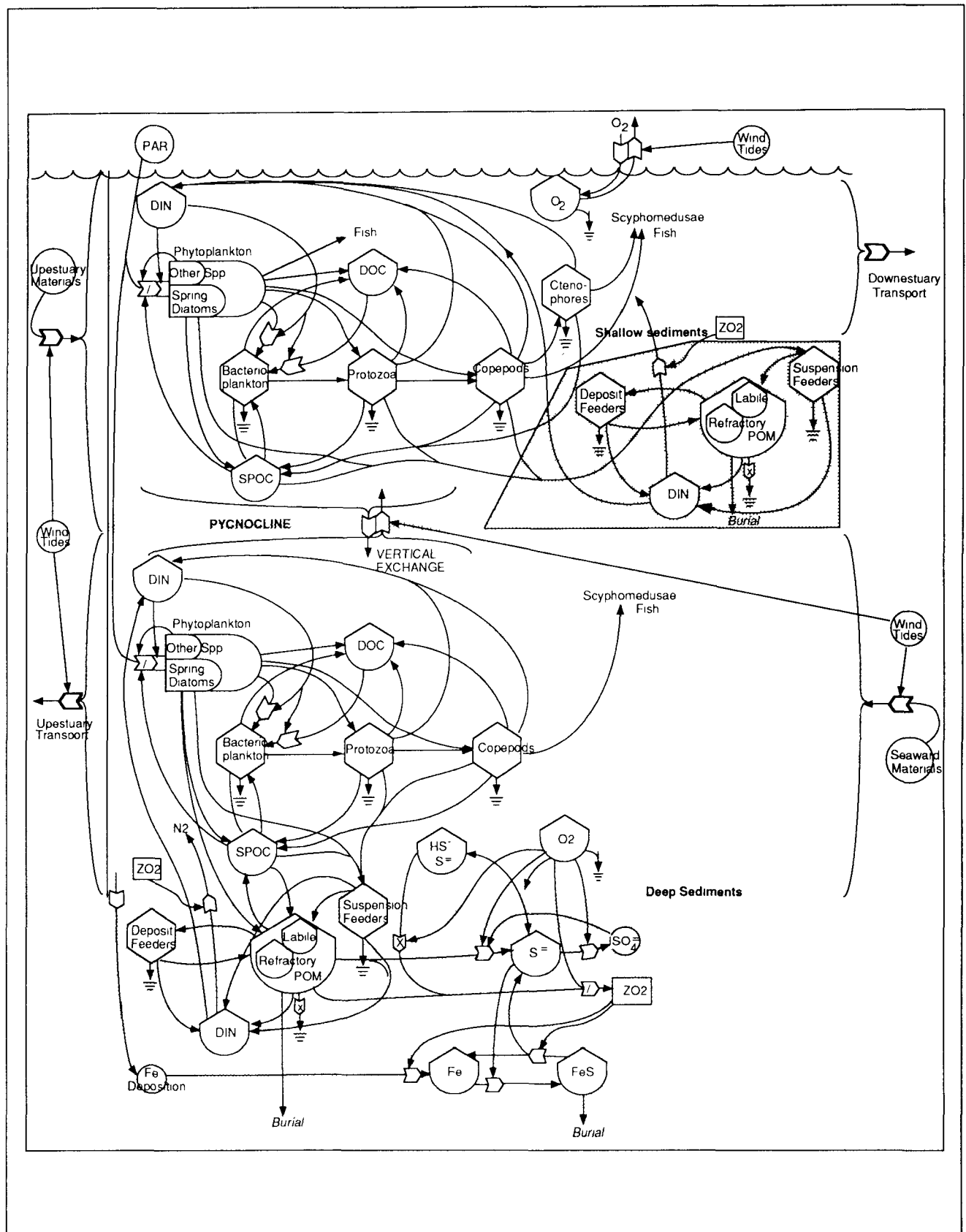


Figure 2. Ecosystem process model of Kemp and Bartleson. Based on Odum's symbols, it is a conceptual model of ecosystem processes in Chesapeake Bay. Arrows indicate flow of either carbon, oxygen, nitrogen, sulfur, or iron, except those from the sun, tides, and wind. Many functional compartments contain more than one biotic or chemical species.

In the Narragansett model, zooplankton are divided into two groupings with algorithms for egg production, growth, respiration, and feeding efficiencies. By comparing preferred respiration activity with available food, the model calculates a filtering rate for phytoplankton. The model assumes unique rates for adults and juveniles and its small carnivores include larval fish, ctenophores, and menhaden. According to formulations for grazing and excretion, these carnivores graze zooplankton, but not algae.

Similar respiration and grazing rates can be calculated for benthic organisms, which are subdivided into filter feeders and deposit feeders. Available particulate food determines rates for filter feeders, while deposit feeder rates depend on sinking phytoplankton and zooplankton feces as food sources. Microbial decomposition occurs as first order decay of particulate organic carbon (POC) in the sediments; phytoplankton, zooplankton, and filter feeders contribute to the POC pool.

Describing this approach as mechanistic, Dr. Kremer stressed the need for detailed understanding of the processes and species controlling the ecosystem. Early versions of the model failed due to a poor understanding of sediment denitrification and zooplankton populations controlled by overwintering eggs. By making the appropriate scientific adjustments, the current model provides better results for nitrogen balances in the estuary.

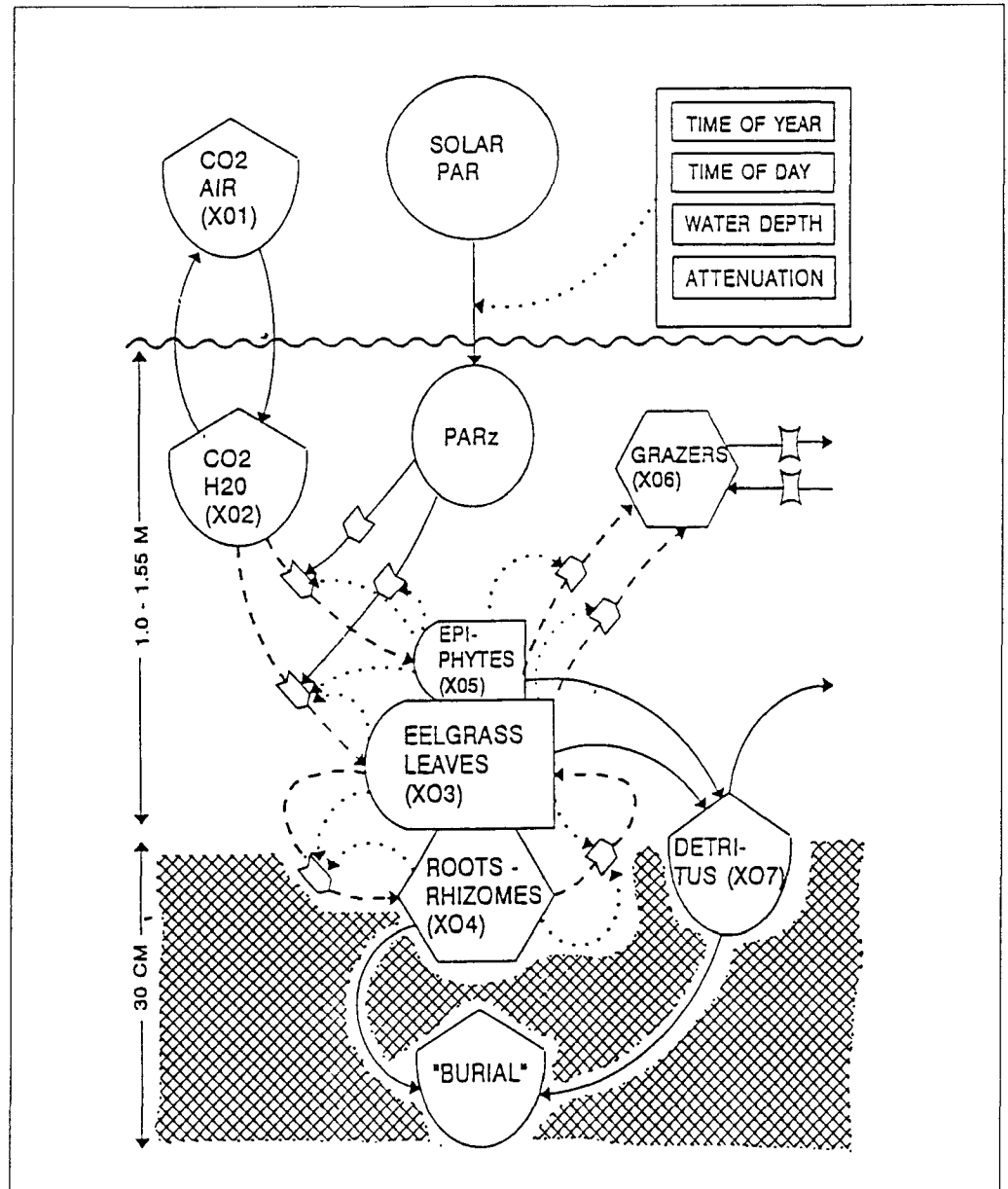
Seagrass photosynthesis/growth

Models of seagrasses and other SAV typically simulate photosynthesis and growth of macrophytes, epiphytes, and phytoplankton. Some seagrass models also include important nutrient cycling pathways and grazing by herbivores. Based on physical forcing functions and biotic interactions in plant and grazer communities, these models have shown the importance of light, epiphytic colonization, and temperature on plant growth and survival. Irradiance, or photosynthetically active radiation (PAR), is attenuated in the water column owing to the scattering and absorption by particulate and dissolved organic compounds. Epiphytes also attenuate radiation and act as a limiting boundary for the exchange of nutrients and gases. Temperature controls specific physiological processes and limits the geographic range of sea grass distribution.

In this workshop, Dick Wetzel described a seagrass model where many statistical or empirical equations were defined using physical/environmental forcing functions, such as temperature, solar insolation, water depth, light attenuation, and photoperiod. However, for biotic interactions the model applies nonlinear, density-dependent feedback mechanisms to limit biological processes. These density-dependent effects include shading, crowding, and nutrient limitation. For instance, the model defines carbon dioxide availability and leaf biomass as limiting factors which keep photosynthesis to less than full physiological capacity. In this model, nonlinear equations describe biological processes like photosynthesis, nutrient assimilation, and other enzyme reactions with relations such as hyperbolic, exponential, and sigmoid functions. In addition to SAV leaf photosynthesis, the model includes biotic components for microflora epiphytes and for isopod and amphipod grazers of both leaves and epiphytes. A conceptual diagram of this model is depicted in Figure 3.

Based on simulations for one, four, and ten years, the model indicates that small changes in irradiance or temperature, or their combined interaction, result in decreased plant productivity and the eventual loss of the eelgrass community. Moreover, the model shows that epiphyte colonization, losses owing to grazing, and other factors controlling the epiphytic community affect long-term eelgrass survival.

Figure 3. These models simulate photosynthesis and plant growth. Epiphytes and particulate and dissolved organic matter limit light availability and control growth of the seagrasses.



Salt marsh production

Daily tidal cycles give salt marsh ecosystems unique spatial and temporal variability. Bidirectional tidal movements can both deposit organic material in the marsh and/or transport carbon in an outwelling flux to surrounding coastal areas. Dick Wiegert reviewed salt marsh models and showed how they can simulate different processes in a coastal Georgia salt marsh. His model was initially designed to test hypotheses about (1) the net flow of carbon into and out of salt marsh systems, and (2) which biological components are most important in influencing this process. The model was also constructed to identify significant information gaps in order to improve predictive accuracy by guiding research priorities.

Wiegert's model describes a marsh environment composed of both the marsh proper, with its resident organisms, and the water-borne tidal system, which carries migrant organisms and materials into and out of the marsh. The 23 compartments of the model are made up of 15 biotic and 8 abiotic components, including *Spartina* roots and shoots, decaying plant material, dissolved organic carbon (DOC), particulate organic carbon (POC), aerobic and anaerobic microbes, benthic algae, phytoplankton, zooplankton, benthic infauna, meiofauna, filter feeders, particle feeders, and top carnivores.

Within this ecological framework, model simulations can be used like experiments to determine how different processes and mechanisms affect each other. In one series of simulations, Wiegert changed values associated with:

- migration of particle feeders and top predators (fish, shrimp, and crabs) into and out of the marsh;
- net primary productivity differences between high marsh and creek bank vegetation; and
- threshold limits controlling rates of anaerobic and aerobic microbial degradation.

Because of the complexities of the interrelationships of the components, some results generated by these manipulations were counterintuitive. For instance, simulations that doubled the number of migrants moving into and out of the salt marsh produced results similar to those that eliminated the migrants: a decrease in aerobic bacteria, benthic infauna, and meiofauna.

Wiegert's model demonstrated that important whole system changes can result from relatively small changes in one of the compartments, particularly the biotic components. One of the key findings was that feedback mechanisms, which control rates of aerobic microbial degradation, can determine whether the marsh impounds or exports carbon, based on small variations in the standing stock of microbes. The model indicated that this is one of the most important processes in determining the spatial and temporal variation in salt marshes. It also presents the possibility that relatively small perturbations could significantly alter a seemingly stable system.

Water quality models

Dominic DiToro reviewed the development of water quality models and described several applications of these models to lakes and estuaries. Summarizing the evolution of water quality models, he outlined important developments in physical transport phenomena, nutrient loading estimations, and chemical/biological kinetics.

Essentially, water quality models predict chemical and biological responses to dynamic spatial distributions of nutrients, light, temperature, and organic material. Current water quality models rely on sophisticated mass balance equations to model physical transport phenomena and to evaluate chemical/biological kinetics in each segment of the water column. Under the mass balance assumptions, closed cycles account for all materials in the system as they move through water and sediment.

These finite-segment, mass balance models use advective and dispersive transport phenomena to simulate the flow of materials to and from adjoining segments. Specifically, the hydrodynamic component of the model predicts water velocity, diffusion, surface elevation, salinity, and temperature on an intratidal, five-minute scale. It formulates turbulence closure for vertical dispersion and thus replaces the Pritchard kinetics and salt-dispersion coefficients used in earlier efforts.

Nonlinear differential equations simulate the exchange of materials among various components (state variables) in each segment in the water column. The Chesapeake Bay water quality model contains 22 state variables (See Table 1) and 4029 segments, or cells. (See Figure 4)

Inputs of nutrients and other materials come from external sources, including point and nonpoint source loadings, and from internal sources, especially the sediments. Current models include sediment fluxes in mass balance calculations and consequently close the nutrient cycle within the modeled system. Sediment loadings are driven by the settling of particulate organic matter from the phytoplankton community.

Phytoplankton taxa include two functional groups—winter diatoms and a summer group of green algae and cyanobacteria—with different nutrient requirements and metabolic processes. Under model assumptions, phytoplankton are considered to be particles of carbon, nitrogen, phosphorus, and silica;

Table 1. The Chesapeake Bay Program model uses 22 state variables to simulate changes in water quality.

Chesapeake Bay Water Quality Model State Variables	
Temperature	Total phosphate
Salinity	Dissolved organic phosphate
	Labile particulate organic phosphorus
	Refractory particulate organic phosphorus
Diatoms	
Green algae	
Cyanobacteria	Particulate biogenic silica
Dissolved organic carbon	Available silica
Labile particulate organic carbon	
Refractory particulate organic carbon	Total active metal
	Chemical oxygen demand
Ammonium	Dissolved oxygen
Nitrate-nitrite	
Dissolved organic nitrogen	
Labile particulate organic nitrogen	
Refractory particulate organic nitrogen	

these materials circulate through completely closed cycles in the water column, in the sediments, and in phytoplankton biomass. Moreover, these materials are categorized as either labile or refractory components and as either particulate or dissolved matter. Such distinctions allow the model to quantify specific aspects of phytoplankton-nutrient kinetics and to predict the status of state variables in each water column segment.

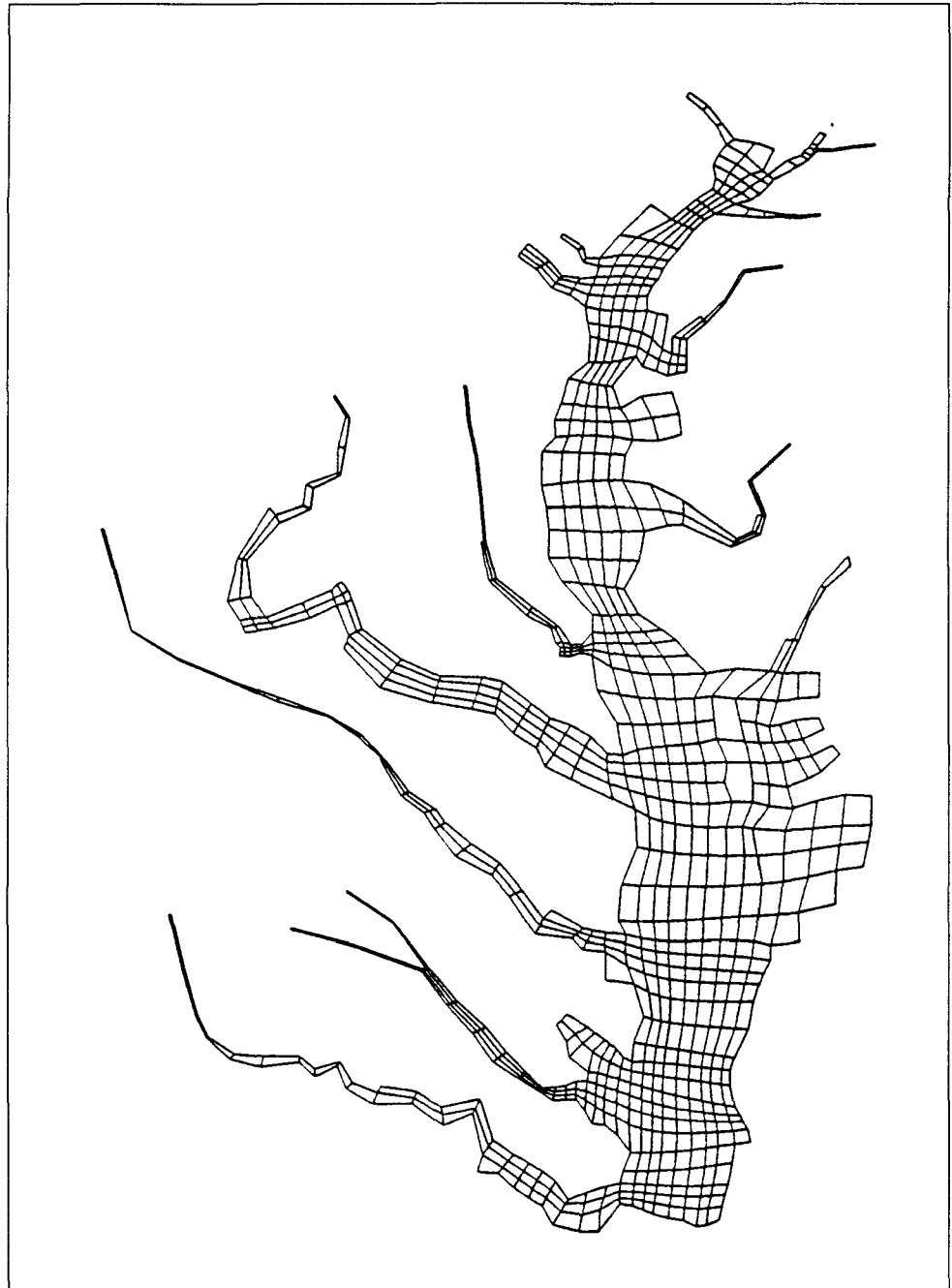
The status, or amount, of state variables depends on the flow of materials through the closed system; process formulations control system flow and determine the importance of sources and sinks for each variable. For example, algae production (source) depends on available nutrients, temperature, and light; while algal loss (sink) results from settling, basal metabolism, predation, and benthic grazing. Oxygen production (source) results from photosynthesis and reaeration; while oxygen loss (sink) is due to algal respiration, nitrification, and the oxidation of organic carbon.

For management purposes, water quality models have often been used to predict changes in dissolved oxygen concentration in response to changes in nutrient loading to the system. However, estuaries present especially difficult modeling problems due to complex intratidal transport processes and the variable phytoplankton-nutrient kinetic interactions controlled by salinity gradients.

DiToro went on to review the predictive capability of other models and showed how certain assumptions can modify model results. For example, a water quality model in San Francisco Bay was used to predict the effects of agricultural runoff on phytoplankton and dissolved oxygen in the estuary. Although the model correctly predicted salt and freshwater flows, it did not consider the effects of freshwater flushing on the benthic community, nor did it predict the significant effect of benthic filter feeders on phytoplankton concentration. In other words, the model simulated the physics correctly, but it missed important biological processes. Subsequent model corrections were made to account for densities and filtration rates of benthic filter feeders and their effect on water quality parameters.

In another example, DiToro explained how a Lake Erie water quality model correctly predicted a required reduction in total phosphorus necessary to achieve a 4.0 mg/L level of dissolved oxygen. The Lake Erie model included a sediment component that calculated internal sediment oxygen demand (SOD) based on diagnosis mechanisms in anaerobic and aerobic sediments. In this example, the model correctly determined allowable loads of phosphorus required to achieve a specific dissolved oxygen goal.

Figure 4. The Bay Program model is an integrated compartment box model; boxes correspond to cells in three-dimensional space. The surface plan contains 729 cells, roughly 10 km by 5 km by 1.7 m. The vertical dimension contains two to fifteen cells for a total 4,029 cells, or boxes.



As a final example, DiToro described the failure of the Potomac eutrophication model (PEM) to predict a large *Microcystis* algal bloom in the summer of 1983. Based on dynamic, nonlinear nutrient-phytoplankton interactions, the model outlined the need for phosphorus reduction efforts. With reduction efforts well underway, a major algal bloom occurred, which raised questions over the cause and doubts about the model. However, scientists used the model to investigate bloom conditions and performed sensitivity analysis to identify the source of additional phosphorus loading to the system.

As a result of these investigations, scientists determined that increased algal production raised pH in the water column, which subsequently led to a release of sediment phosphorus, thereby further fueling the bloom. In this case, increased algae, increased pH, and increased sediment flux of phosphorus presents a positive feedback to the nutrient-phytoplankton kinetic loop. The Potomac estuary example shows how a failure to correctly portray natural processes in the model formulation leads to erroneous predictions.

Spatially explicit fish bioenergetic models

Spatially explicit fish bioenergetic models determine volumetric maps of fish-growth potential. They identify specific areas, or volumes of water, with favorable prey populations and water temperature. In this context, bioenergetic models define the habitats with the highest potential for fish growth. Moreover, they predict fish growth based on consumption of prey species, and they attempt to quantify the functional responses of fish to their physical and biological environment.

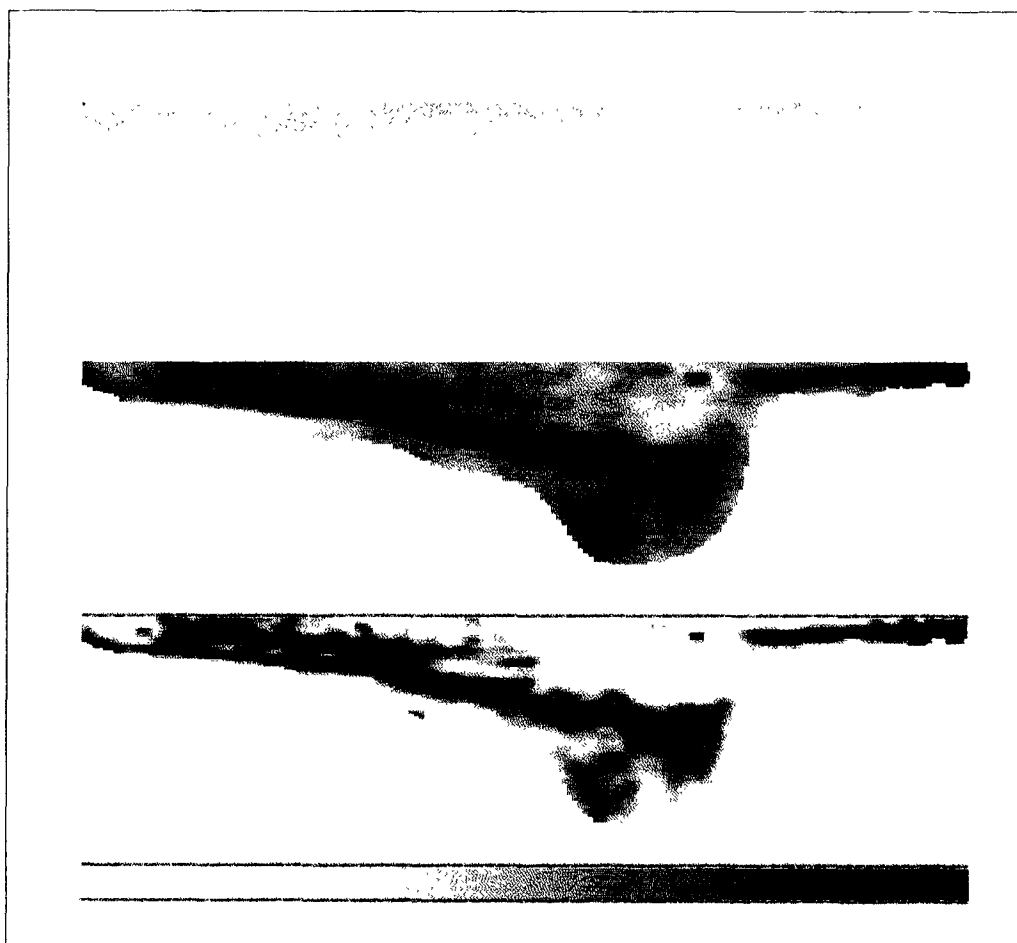
Steve Brandt presented an example of such a spatial bioenergetic model in this workshop. The model, which describes estuarine populations of striped bass, divides the water column into horizontal and vertical grids and estimates prey size and densities and water temperature in each cell. Prey densities (e.g., bay anchovies) are measured with acoustic sampling procedures, while temperature is measured by field observations. A foraging submodel translates prey size and density data into prey availability and consumption by predators. Physiological growth equations relate prey consumption to striped bass fish production. By integrating predator fish movement, or behavior/migration, through the cells and by adding potential growth rates for all the cells, modelers can obtain a bioenergetic estimate for total system predator fish production. Figure 5 contains an example of striped bass bioenergetic model output.

Individual-based fishery management models

Individual-based fishery models (IBFMs) describe population dynamics based on the characteristics of the individual fish. The IBFM uses physiological and behavioral attributes of the individual to ascertain day-to-day survival and growth through various life stages. Such a model, therefore, uses a reductionist approach to infer population status by tracking the characteristics of individual survivors.

IBFMs are appealing because they are conceptually simple and because they account for the many stochastic events, density-dependent factors, and nonlinear processes that control fish populations in particular and many other biological

Figure 5. Bioenergetic model output. Map of water temperature (top panel), fish biomass density (middle panel), and growth rate potential (bottom panel) of a 1.9-kg striped bass across a 7.5-km section of the mesohaline, middle portion of the Chesapeake Bay at night on 2 May 1990. Maximum bottom depth is 34 m. Scanned from color graphics. Color representations from blue to red are linear for water temperature (9 to 28°) and fish growth rate (-0.004 to 0.019 $\text{g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$) but logarithmically-spaced for fish biomass density (0 to 158 $\text{g} \cdot \text{m}^{-3}$). Graphic by Jiangang Luo.



systems in general. For example, such models can predict growth based on prey consumption and estimate mortality based on starvation, predation, and temperature fluctuations. To model such random and episodic phenomena, IBFMs use Monte Carlo simulation to distribute events according to relevant stochastic probability functions.

In this way, IBFMs provide a mechanism for modeling the intense variability in fish recruitment, growth, and reproductive success. Because they are based on the rules of individual survival, IBFMs account for the genotypic fact that the survivor is not the average, but rather the exceptional individual.

In this workshop, Ken Rose described an IBFM for Potomac River striped bass. The IBFM uses population data for length, weight, and age, along with data for zooplankton, and white perch as a food competitor. By varying the combinations of factors, this model was able to estimate how each factor and the interaction among factors control the variability in each yearclass.

Despite their heuristic advantages, IBFMs are data-hungry; they require comprehensive data on the recruitment, growth, and survival of individual species. Moreover, IBFMs ignore foodweb interactions and do not account for spatial heterogeneity. Nonetheless, IBFMs are important because of their straightforward approach to modeling recruitment variability.

Ecosystem regression models

Avoiding the mechanistic details of ecosystem processes, ecosystem regression models (ERMs) use regression analysis to identify strong relationships in systems. ERMs typically correlate a chosen environmental forcing function, such as nutrient loading or river flow, with a selected ecosystem response, such as primary production or fishery yield. Based on these regressions, modelers can identify patterns in the whole system and test hypotheses based on various cause-and-effect assumptions. Because ERMs evaluate relationships without specific mechanistic details, they are holistic rather than reductionist; because they correlate large-scale trends rather than facilitate analysis of processes, they are empirical rather than analytical. Walter Boynton described several ERMs, an example of which can be found in Figure 6.

ERMs provide ecologists tools to establish and measure basic rules of thumb for estuarine response to a given causative agent or predictive variable. For example, although we can correlate loading with eutrophication, we know little about how individual estuary morphology and hydrology affect the status and responses of areas within an estuary or different types of estuaries. ERMs help ecologists answer questions about the relative status of particular estuaries, including:

- What kinds of estuaries are most susceptible to eutrophication?
- What regions are most vulnerable to the effects of excess nitrogen or phosphorus nutrients?
- What level of nutrient decrease is necessary to achieve restored conditions?

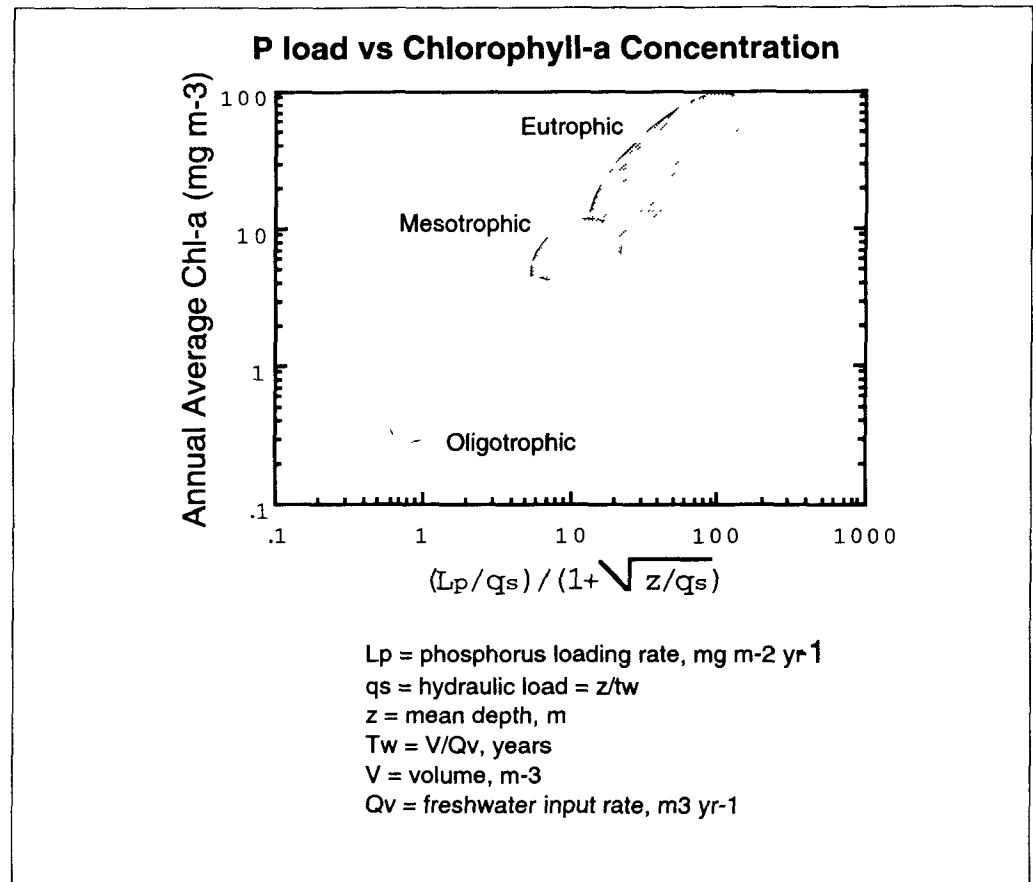
The availability of the many good databases developed to assess and monitor water quality provides an important advantage for the ERM approach. When scaled appropriately, these data make it possible to compare processes and trends in a large number of estuaries.

Some of the disadvantages of ERMs stem from problems associated with time lags, averaging errors, and spatial shifts that occur in large-scale systems. Nonetheless, numerous ERM applications have been successful.

Ecosystem network analysis models

Ecosystem network analysis models allow investigators to examine the indirect connections between species in an ecosystem. These models use linear algebra techniques to assess the interactions between species, or components, not in direct trophic communication. Network analysis was developed by Robert Ulanowicz and his colleagues as a tool to improve the predictive power of complex ecosystem process models and to analyze indirect ecosystem effects in nonlinear trophic interactions.

Figure 6. Ecosystem regression model (limnological model).



Network analysis requires data on the connections and magnitudes of all trophic transfers occurring within an ecosystem. Such data rarely come from a single study; rather, they are collected from various studies of the relevant ecosystem. Using estimation techniques, trophic interactions can be assembled and averaged to create a snapshot of ecosystem function over some convenient time interval. For example, Figure 7 shows the average annual transfers of carbon (mg/yr) moving through 36 major components of the Chesapeake Bay ecosystem from 1984 to 1985.

In network analysis, matrix manipulation techniques can be used to quantify trophic interactions and to characterize features of an ecosystem. Based on such techniques, investigators can:

- identify indirect feeding relationships
- determine trophic position and status
- calculate trophic efficiencies
- elucidate material and energy pathways
- determine measures of ecosystem health

Consider some examples. By examining material flow through several species, investigators can identify feeding relationships between species not in direct predator-prey relationships. For example, although striped bass do not directly consume microzooplankton, analyses reveal that over 25 percent of the carbon in the striped bass diet once passed through microzooplankton biomass.

In the same way, network analysis can trace the number of trophic interactions food undergoes on the way to each species. This allows the investigator to determine the trophic status of each species and the average trophic position of the entire system (the so-called "average-path length"). This latter averaged value can serve as a useful indicator of system response to applied stress. In one such analysis, Ulanowicz used information theory to compare indices of the Chesapeake Bay network to corresponding values in the Baltic Sea in order to assess the metaphorical "health" of the two systems. He showed that the Bay faces more intensive stress than its high-latitude counterpart.

Moreover, analysis techniques can be used to map elements of a complicated food web into a linear series of transfers in order to calculate the trophic efficiencies associated with transitions at each consecutive level. Analyses show that drops in trophic efficiencies, as may occur under community perturbations, often result in dramatic decreases in the amounts of material and energy reaching higher levels.

Algorithms also can be used to enumerate and quantify recycling pathways for the circulation of energy and materials within the ecosystem. When applied to the Chesapeake Bay ecosystem, network analysis reveals a bipartite carbon cycling structure. In this structure, carbon recycling pathways in the planktonic section of the ecosystem do not overlap with the more substantial recycle pathways between the benthic and nektonic sections. Only the filter feeding species were common to both domains. This analysis revealed for the first time the ecological role filter feeding species (oysters, soft clams, menhaden, and alewives) play in the overall carbon processing in the ecosystem.

Ecological network models offer a powerful analytical tool. They are not, however, designed to predict or examine causal relationships. Although network models do not depict dynamic ecological relationships, they can portray sequential changes in ecological relationships over time.

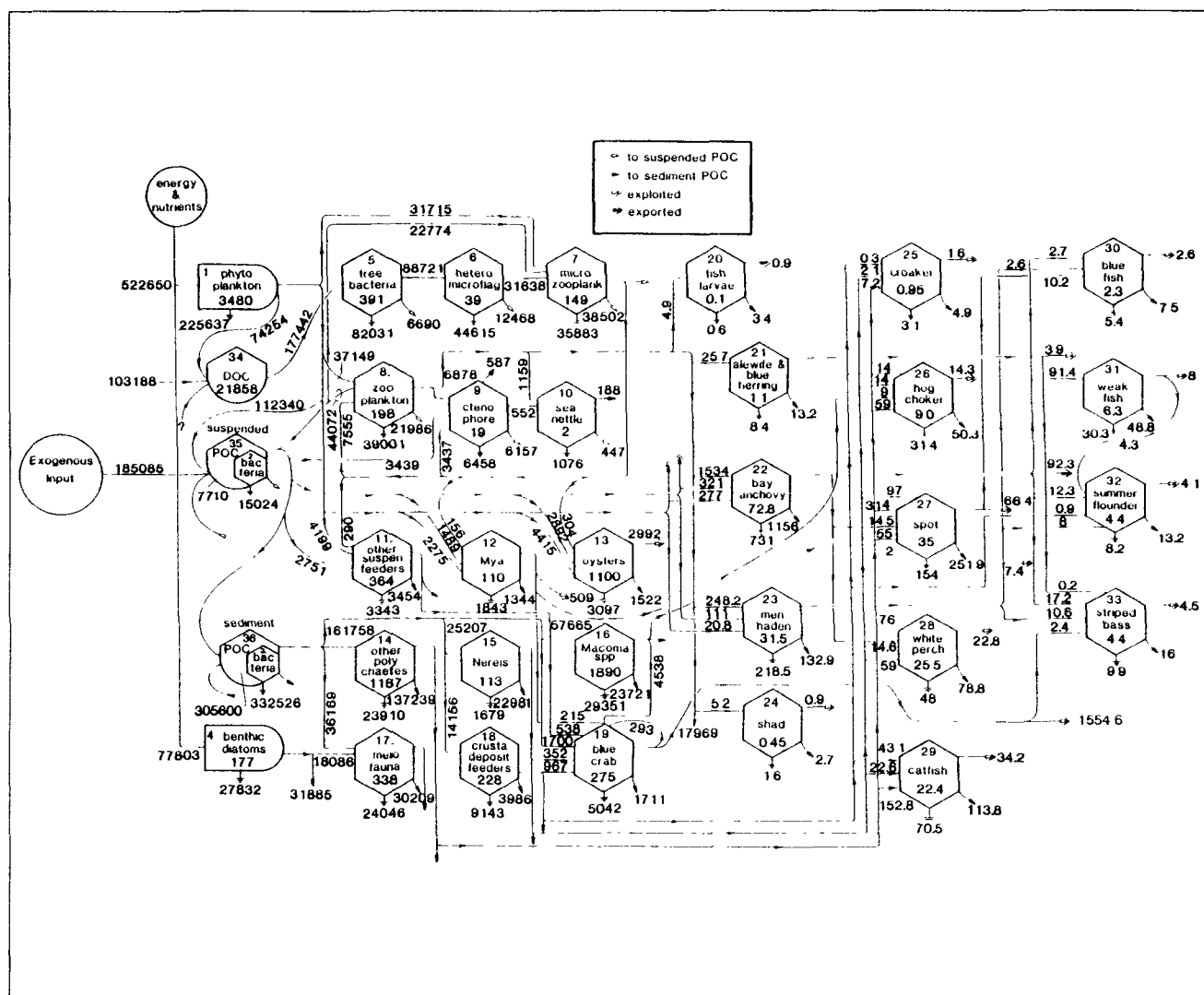


Figure 7. Network analysis model simulate trophic transfers occurring in the ecosystem. This figure shows the average annual carbon transfers among 36 major components of the Chesapeake Bay ecosystem.

Landscape spatial models

Most ecological models simulate processes occurring at a point in space and extrapolate findings to the entire landscape by assuming the environment is homogeneous. Such models provide little or no spatial articulation. However, landscape models incorporate space as well as time to a level of resolution that is meaningful to a given management question.

In general, landscape models can be used to predict the temporal evolution of landscapes and to quantitatively describe landscape phenomena. More specifically, these models can:

- map flows of energy, matter, and information in space
- designate source, sink, and receptor areas
- predict succession in two and three-dimensional space
- determine cumulative use thresholds for anthropogenic substances
- address questions of scale

Process-based landscape models simulate spatial structure by compartmentalizing the landscape into a geometric design and then describing the flows between and within compartments. Specific algorithms determine spatially explicit processes controlling material and energy flow, including inputs from outside the system, transfers within the system, outputs of useful material, and energy dissipation.

Bob Costanza outlined process-based landscape models and described recent efforts to model landscape dynamics in a Louisiana marsh complex and the Patuxent River watershed. He stressed the spatial characteristics of landscape models and showed how dimensions of scale affect interpretation of model results.

For example, the Coastal Ecological Landscape Spatial Simulation (CELSS) model is a process-based simulation of the Atchafalaya marsh area in southern Louisiana. (See Figure 8.) It compartmentalizes the marsh complex into 2479 interconnected cells, each representing 1 square kilometer. Under the control of connectivity parameters, the model simulates the movement of water, salts, nitrogen, and organic and inorganic sediments between adjacent cells. Water movement from one cell to another is modeled as a function of water storage and connectivity, which in turn depend on various landscape characteristics including habitat type, drainage density, waterway orientation, and levee height.

Each cell in the CELSS model contains a dynamic, nonlinear ecosystem simulation model with eight state variables. Based on parameter values for these variables, each cell is defined as one of six marsh habitat types:

- Fresh marsh
- Brackish marsh
- Salt marsh
- Swamp forest
- Upland
- Open water

Habitat succession occurs when environmental variables fall outside the range of values specified for a designated habitat type. For example, changes in elevation, salinity, water level, and primary productivity could convert a cell habitat from fresh to brackish marsh. By evaluating the transition of ecosystem types due to natural and anthropogenic changes, managers can use these spatial, process-oriented models to predict the impacts of events such as sea-level rise or levee and canal construction in a coastal area.

Dr. Costanza also described a Patuxent landscape model that was designed to estimate nutrient and sediment loads resulting from various land use practices in the Patuxent watershed. Containing approximately 6,000 spatial cells, 10 state variables, and 22 land uses, the model predicts the effect of natural vegetation associations (wetlands, riparian forests, grassed buffer strips, etc.) on nutrient and sediment loadings to the aquatic environment. It also simulates the effects of vegetative growth, buffers, and retention ponds on rates of soil erosion and nutrient retention. Moreover, the terrestrial Patuxent landscape model is designed to link directly with a Patuxent estuarine ecosystem model.

Early versions of landscape models ran on supercomputers due to the intensive data requirements for modeling dynamic, spatial processes and to the many simulations required for parameter estimation. For example, a typical run of the CELSS model simulates 22 years of landscape dynamics based on weekly time steps for 2479 cells with eight state variables, each with 19,832 simultaneous difference equations. Although initial simulations required 15 minutes of Cray X/MP supercomputer time, recent software and hardware developments now allow these simulations to run on Macintosh II computers using parallel processors.

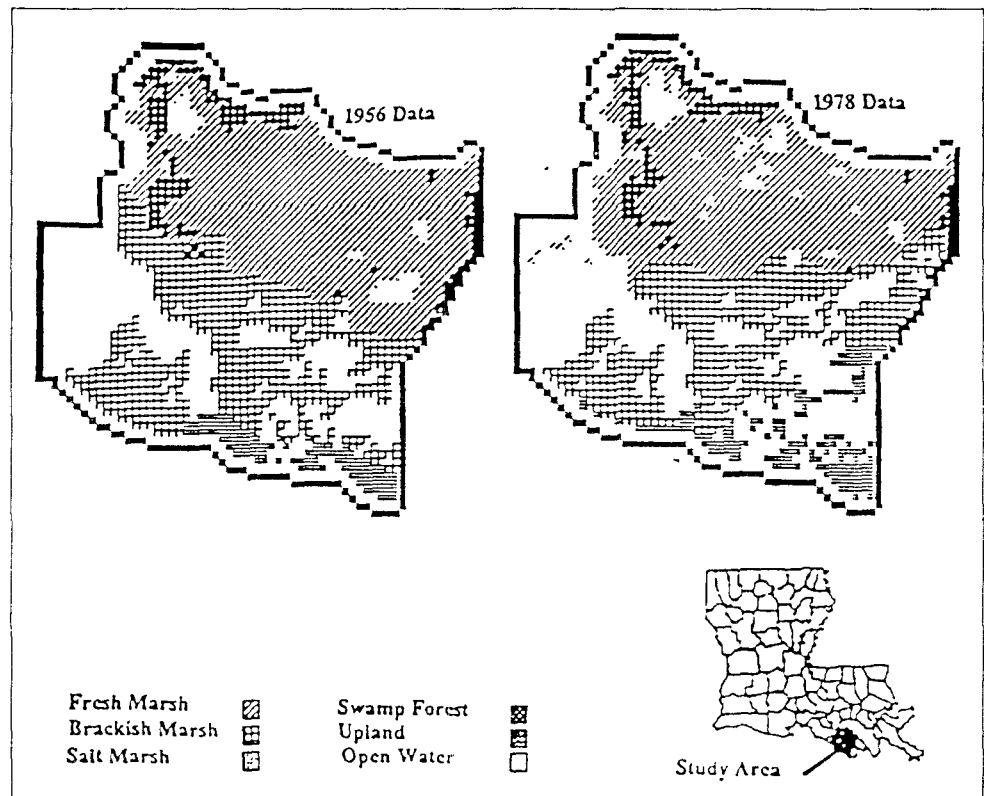


Figure 8. Landscape spatial models can be used to show land use changes over time.

Section 3

Linkage and Coupling *Toward an Integrated Modeling Framework*

Overview

Section 3 characterizes conceptual issues to address before building an integrated modeling framework. It describes important linkage problems inherent in coupling hydrodynamic and water quality models to various ecosystem and fishery models.

In considering linkage problems, the workshop participants discussed specific issues for key components of an integrated modeling strategy, including:

- Conceptual issues
- Physical process issues
- Water quality model issues
- Submerged aquatic vegetation model issues
- Ecosystem feedback and control issues
- Fishery management and recruitment issues

Conceptual issues

Clearly, there are difficulties inherent in trying to link models that range from hydrodynamic models to traditional fishery management models. The general problems include the choice(s) of appropriate time and space scales. The more specific problems revolve around the difficulties of linking water quality models to biological phenomena often characterized by discontinuities, thresholds, rare events, behavior, recruitment success, and counterintuitive feedback mechanisms. Other conceptual linkage problems arise in trying to incorporate feedback mechanisms operating between water quality models and foodweb processes.

Most participants agreed that modeling fishery recruitment—the fish that survive early life history stages to enter into the adult population—was the greatest obstacle to incorporating fishery models into an integrated ecological framework. Moreover, there are scale problems to consider in linking diverse processes at various levels of aggregation in time, space, and biological detail. The participants agreed that in choosing appropriate scales, modelers should not necessarily copy scales used for the water quality models. Scaling problems are treated in more detail in Section 4.

Some of the linkage problems have been addressed by making broad assumptions about the relevance of using one model variable as a simple surrogate for processes in other models. For example, dissolved oxygen concentrations are often used as an indicator of habitat conditions. Although this loosely links the water quality model to fish populations, it fails to account for the highly variable and complex factors controlling fish behavior, recruitment success, and trophic interactions.

Despite the importance of the linkage issue, most participants agreed that linkage problems should not be overemphasized at this early stage of model development, simply because so much basic biology remains unknown. The group agreed that to make ecosystem models more accurate, research was needed to provide additional biological details, especially at higher trophic levels. In this context, the workshop participants emphasized two important roles of modeling: (1) to identify gaps in our understanding of estuarine ecology, and (2) to integrate and synthesize diverse research results.

Physical process issues

Most participants agreed that current physical process models can describe material transport and hydrodynamic phenomena to an acceptable degree of precision and accuracy. Recent advances have been particularly exciting and useful. Methods are currently being developed to adjust detailed hydrodynamic model output to time and space scales appropriate for specific ecosystem process models. Appropriate time-space scaling of these models will make them useful to a diversity of modeling efforts.

The participants raised the need for finer resolution, or segmentation, of current Chesapeake Bay hydrodynamic models for shallow estuarine areas, such as SAV habitat. Such an improvement would provide a link to the important ecological processes and living resources along shorelines and in shallow areas.

Output from physical/chemical models also provides important habitat data for fishery bioenergetic models. Because output variables such as dissolved oxygen and temperature directly link to such bioenergetic models, these data may be enhanced to suit the specific needs of a model of higher trophic organisms. For example, dissolved oxygen concentration and temperature fields predicted from water quality models provide limits on striped bass habitat and control fish growth and production. In this way, the development of a spatially articulated database of physical parameters allows better modeling of fish populations.

Water quality model issues

The Chesapeake Bay Program has developed a three-dimensional, time-variable water quality model that describes the concentration of nutrients and dissolved oxygen throughout the main Bay. As described in Section 2, the Bay model is based on physical transport, closed nutrient cycles, mass balance, and a distinction between summer and winter algae. The participants endorsed the Bay Program water quality model as a robust technology for predicting dissolved oxygen and nutrient concentrations in the Bay mainstem. The hydrodynamics have been sufficiently resolved to describe most transport and distribution phenomena relevant to other ecosystem processes.

To be useful as a tool for managing living resources, water quality models must generate biologically useful output. Models should be able to generate useful chemical and physical information corresponding to the habitat requirements for key species. For example, submerged aquatic vegetation (SAV) habitat requirements are described based on water quality parameters, such as light attenuation and the distribution of total suspended solids, chlorophyll *a*, dissolved inorganic nitrogen, and dissolved inorganic phosphorous.

To meet these habitat requirements and to provide better links to living resources, it was recommended that time steps for water quality model output should match the averaging periods used to define habitat parameters. Participants also recommended the development of finer scales for temporal and spatial distribution of water quality output.

The Chesapeake Bay time-variable water quality model currently does not receive feedback input from biological processes occurring in or at the borders of the water column; in reality, however, zooplankton, benthos, SAV, filter feeding fish, and many other organisms can affect water quality. These organisms may graze phytoplankton, shift carbon flow, alter microbial processes, or in other ways indirectly control aspects of water quality.

The workshop participants endorsed incorporating ecological feedback models into the water quality model. The first step in such an effort is to carefully choose appropriate organisms to model and integrate them into the water quality model; in this context, the group recommended three important criteria:

- Sensitivity—organisms and/or processes should be suitably responsive to environmental changes and/or capable of altering environmental conditions
- Trophic importance—organisms should be important in the Bay's foodweb
- Data sufficiency—adequate data should exist for realistic simulation of a species in a model.

Based on these criteria, the participants agreed that zooplankton and benthos should be the first groups of organisms to be integrated into the water quality model. In both cases, there is a good monitoring database and both hold a key trophic position between primary producers and large fish. Some participants warned, however, that because of their relative instability in the environment, zooplankton would be difficult to model.

Submerged aquatic vegetation model issues

Currently, SAV models provide the most direct link to water quality models. Several of the habitat requirements for SAV, such as chlorophyll *a*, dissolved inorganic nitrogen (DIN), and dissolved inorganic phosphorus (DIP), can be simulated by the Chesapeake Bay Program (CBP) water quality model. However, the CBP model does not explicitly extend to littoral areas; before linking to SAV models, the CBP model must be able to simulate habitat requirement parameters in these shallow areas. The participants pointed out, however, that parameters for habitat requirements are not species-specific, nor do they fully account for the enormous temporal and spatial variations in SAV communities. SAV models will also require better information about the grazer communities. Moreover, links between SAV and water quality models will have to incorporate feedback mechanisms—the effects of the grasses on the ambient water conditions.

Ecosystem feedback and control issues

Currently, the Chesapeake Bay Program water quality model incorporates linked physical processes and can simulate the dynamics of chemical parameters relevant to ecosystem models. However, the outputs from ecosystem models do not link into the water quality model. To anticipate linkage problems, the participants discussed interactions, controls, and feedbacks relevant to linking components.

Numerical models of marine processes have existed since the late 1930s, but not until 1949 did researchers begin to incorporate phytoplankton and zooplankton equations into a system of equations with feedback control. Current ecosystem models attempt to quantify feedback interactions and incorporate controls to more accurately describe actual ecological phenomena. The microcomputer, coupled with the diagrammatic languages of Odum and Forrester, has enabled modelers to easily simulate ecosystems by solving a system of nonlinear, differential equations.

Currently, several nonlinear ecological feedback mechanisms occurring in estuaries have been studied and incorporated into ecosystem models, including:

- Benthic suspension feeding
- Seagrass nutrient assimilation
- Seagrass sediment trapping
- Grazing on seagrass epiphytes
- Oxygen effects on denitrification/nutrient recycling
- Benthic bioturbation effects on nutrient cycling

Incorporating diverse nonlinear ecological responses into an integrated framework presents both a conceptual and a mathematical challenge. In the conceptual context, control mechanisms and feedback interactions are difficult to determine and often are counterintuitive to an initial understanding of the ecosystem. The piecemeal nature of existing data makes it difficult to gain a comprehensive understanding of the complex interactions of biological, physical, and geochemical processes that govern the cycling of nutrients and organic matter in estuaries. Moreover, averaging nonlinear responses across diverse time and space scales presents a difficult mathematical challenge. Averaged fine-scale phenomena may accumulate and propagate through the system to make aggregated results inaccurate.

To help clarify the influence of control processes, one can apply sensitivity analysis techniques to ecological models to reveal indirect feedbacks that may seem unimportant but actually exert great control over ecosystem phenomena. When such techniques identify processes previously thought to be unimportant or when the results do not adequately follow observed field data, alternative hypotheses can be developed to account for the predicted behavior. In this context, models can be used to guide new research or to refine monitoring programs. Also, they can be used to test new hypotheses or to obtain additional information about controlling processes.

Fishery management and recruitment issues

Fishery models have been widely used by fishery managers since the 1950s to generate maximum sustainable yield (MSY) and yield-per-recruit. However, fishery models have been marked by numerous failures and deficiencies, and they have lost credibility in recent years.

(Fishery
management cont'd)

To some managers, linking the water quality model with fishery models represents the ultimate challenge in building an integrated ecological modeling framework. As one workshop participant pointed out, "We manage the Bay from two points—nutrient input and fishery harvest—and we need models to explicitly address this strategy." Others commented that water quality models and fishery models were at opposite ends of the spectrum; the best ecological modeling strategy would be to "meet in the middle."

Population models usually fail owing to their inability to predict recruitment variability. According to some workshop participants, the problem of quantifying the intense variability in recruitment success remains the single greatest obstacle in linking ecological processes with traditional fishery management models.

Recruitment success is often a random event based on biological phenomena, such as fish behavior and predator-prey interactions, and on physical characteristics, such as temperature and river flow. Modeling recruitment success is complicated by episodic perturbations in the environment and the density-dependent characteristics of many fish populations. Models work best with averages, but in the context of population genetics, survival often depends not on the average, but rather on the exceptional individual, because larval survival itself is a rare event.

There are other problems with traditional fishery models. For example, fishery management models based on surplus production and yield-per-recruit assume a population in equilibrium with predictable or constant recruitment. In addition, the critical interactions of fish populations with other components of the estuarine ecosystem are not included in traditional fish population models. Typically, such factors as food abundance, habitat (e.g., refuge) availability, disease, and predation losses are either ignored or implicit within empirical coefficients used for natural mortality, growth, and fecundity.

To address these problems, current stock recruitment models attempt to predict the number of progeny from the size of the spawning stock. But such relationships are poorly understood, and recruitment models require long time-series data of all environmental parameters (e.g., temperature and river flow), biological factors (e.g., mortality rates, fecundity, and growth rates), and fishing characteristics (e.g., annual harvest and catch composition). Even with available data, unpredictable natural and anthropogenic environmental changes remain as obstacles to the reliable prediction of recruitment success.

For many species, management agencies solve the recruitment problem by using other quantification approaches, such as virtual population analysis, juvenile indices, or stock recruitment models. But important questions regarding fisheries modeling remain open to further consideration. One such question is whether fish population models can be improved by linking them to other models. For example, physical circulation models and water quality models provide physical and chemical information that could be used to describe fish habitat; ecosystem models also generate information about potential habitat, including food availability and predation pressure. These physical, chemical, and biological data may provide important links to improve fishery models.

The workshop participants discussed how ecological models might add new insights to fishery models. Spatially explicit fish bioenergetic models describe the potential for fish growth based on density of prey species and temperature. Because they evaluate growth conditions, rather than actual populations, fish bioenergetic models can be linked to ecosystem models of fish habitat. Moreover, they can be linked to the water quality model through data on temperature and dissolved oxygen. Individual-based fishery models were also discussed as another approach for handling recruitment variability for specific species.

Methodology and Technology

Factors in Concept, Design, and Implementation

Introduction

In discussions and presentations, workshop participants evaluated the technical issues associated with model conceptualization and construction. Such discussions covered various approaches for addressing scaling and aggregation issues, and they reviewed the evolving methodologies for model development, calibration, and sensitivity analysis. Section 4 provides an overview of these issues based on both plenary presentations and technical discussions in individual subgroups. It summarizes criteria for deciding on appropriate scales, and it outlines trade-offs in aggregation or disaggregation over scales of time, space, or trophic complexity.

Scales of ecological systems

By scales, we mean the fundamental metrics used to describe the dimensions of a system. The divisions, or levels of articulation, are chosen to capture the details of a specific process. To describe ecological phenomena, models must incorporate scales of time, space, and some level of biological organization. Because relevant biological, chemical, and physical phenomena occur on such varied dimensions, ecological modelers must choose scales appropriate to a specific modeling objective. As a result, the degree of articulation in scale and the level of aggregation determine the value of any modeling approach to a specific problem. In other words, scales for time, space, and ecological complexity may be appropriate for one use but not for another. Decisions over appropriate scales should be determined by the objectives of the model, the limits of technology, and the availability of relevant data. The participants generally agreed that the model objective, or question, defines the appropriate scale for each model, and different scales are appropriate for different questions. Others specifically noted that scales used in the water quality model, although appropriate to predicting anoxia, may be inappropriate for questions regarding ecosystem processes or population dynamics.

Distinguishing between types of models and their intended uses is an important step in determining appropriate scales. To emphasize this point by an analogy, Bob Costanza suggested that we compare models to maps. Fine-scale street maps are relevant to some problems, whereas large-scale global maps (aggregated ecosystem models) are relevant to others. Modelers must articulate dynamic models in time, space, and trophic complexity. An important step is to choose the appropriate level of articulation to evaluate the processes defined in model goals.

Aggregation and scale

Modelers aggregate systems to simplify the conceptual framework or to convert myriad and diverse phenomena into more tractable computer simulations. However, by combining fine-scale, nonlinear systems into coarse-scale, aggregated ones, modelers may introduce averaging errors that accumulate and propagate through the entire simulation system. Aggregation errors occur most often when modelers average nonlinear systems into a larger whole; the aggregate average may lose the rich nonlinear features of the natural system. For example, in a forest leaf canopy, the photosynthetic capability of the canopy could be estimated by summing up the individual capabilities of all leaves. Such an aggregation, however, would ignore the interactive effects (shading, etc.) of leaves on each other. In this way, the coarse-scale aggregate does not behave the same way as the sum of its component fine-scale simulations. Important details of fine-scale components with high-frequency, transient behavior may be lost or damped in aggregation. Thus, a coarse-scale model can fail even though it was assembled from well-understood, accurately modeled, fine-scale processes.

Predictive versus experimental

In one presentation, Jim Kremer outlined a continuum of modeling strategies ranging from the highly aggregated, holistic ecosystem models to the detailed, mechanistic models used to describe microbial processes in the sediments. Large-scale holistic models are highly aggregated relative to the phenomena to be explained; although extremely predictive, such models are often so broad they preclude direct experimental measurement. In other words, they seldom fail, but often they are right for the wrong reasons. Such models are accurate; they are not precise.

Large-scale, aggregated models may best be applied to management applications in which predicting system response is more important than describing detailed mechanisms. Managers use predictive models to extrapolate the structure or behavior of a system outside the existing data boundaries. Moreover, such models can be used to support pollution abatement strategies based on broad assumptions— such as limiting nutrient input to raise levels of dissolved oxygen. It might be argued that large-scale landscape models, such as those outlined by Bob Costanza, provide practical scales because pollution and environmental policy occur at the large, landscape scale.

In contrast, small-scale, mechanistic models are best applied in experimental approaches in which hypotheses about causal relationships can be tested and rejected. Indeed, models can play a role analogous to experiments in the scientific method. But models can be seen as rejectable alternative hypotheses if their compartments are defined on scales appropriately small relative to the question being asked. Such descriptive models are used to test hypotheses and they often fail because of limited understanding of processes controlling the system. In this context, small-scale models can be used to guide research.

Problems of scale ultimately require making decisions as to the appropriate level of aggregation/disaggregation, and the best solution depends on making trade-offs between accuracy, precision, and generality. Ultimately there must be a compromise between model resolution and model predictability; finer resolution lowers predictability.

Specific scale problems

Between the two extremes of aggregated, holistic, predictive models and disaggregated, mechanistic, descriptive models, there are many practical scale problems to address before building an integrated modeling framework. Consider some examples involved in creating an integrated model for the Chesapeake Bay. In the Chesapeake Bay water quality model, the Bay is divided into 57,871 cells each measuring 1 km² in area and 1 m in depth. Mass or concentration values of dissolved oxygen are calculated based on statistical interpolation from nearby sampling sites. Steve Brandt presented a striped bass bioenergetics model that uses 18,000 water column cells to describe fish growth and survival. To integrate his model with the water quality model, Brandt would need to use dissolved oxygen and temperature information at other scales. The SAV models of Dick Wetzel operate on a spatial scale of 1 m². These smaller scales are more realistic for SAV growth and survival than the km² scales of water-column models. Other participants raised other scaling problems, including the integration of groundwater transport phenomena into mainstem Bay hydrodynamic models and the large-scale problems associated with atmospheric deposition and sea-level rise.

Limits of technology

Numerical ecosystem modeling requires the use of computers. The participants agreed that, although limited, the technology is available to support the development and integration of ecosystem process models. In fact, hardware development has catalyzed the ecological modeling field. Computers enable modelers to organize complex ecosystem information, simulate possible outcomes over time, examine control mechanisms, describe changes, and model uncertainty.

Consider that the time-variable, three-dimensional water quality model of the entire Chesapeake Bay runs an annual cycle on 25 hours of Cray supercomputer time. In contrast, mechanistically complex but spatially-averaged ecosystem process models, such as those outlined by Mike Kemp, can be run on desktop computers with a one year simulation requiring 15 minutes.

As a result, practical concerns over computing power can define appropriate scale. *Increasing scale resolution causes an exponential increase in computing requirements*; some models aggregate scales simply to maximize computing resources. One participant remarked that, “in the early days, we designed our water quality models to run in eight hours computing time.” As a result, we can expect some scales to be determined not by the relevance of the problem, but rather by the size of a workable computer model.

Currently, the Bay water quality model runs push the limits of technology in terms of required supercomputer time. Several participants said that adding ecosystem processes to the present version of the water quality model would strain existing computer resources. In this context, any new biological components added to the water quality model would strain technical resources. For these reasons, the workshop participants stressed that species for initial ecological modeling efforts should be carefully chosen based on a high probability of success (see water quality model issues in Section 3).

Physics: fine-scale versus coarse-scale

Given limited computing resources, the participants discussed trade-offs in fine-scale versus coarse-scale hydrodynamics and the benefits of aggregating cells in the water quality model. According to several participants, in order to save computer power, individual cells in the bottom 6-7 m of the Bay water column could be collapsed into a single cell without changing data for key processes.

Other participants said that the water quality model has too many cells; Chesapeake Bay Program managers should aggregate the Bay into larger segments to interpret results. Dominic DiToro described a successful 2:1 grid collapse in the Long Island Sound water quality models; the aggregation was made to “improve computation tractability.”

On the other hand, some participants warned of the potential problems stemming from coarse hydrodynamic cells. For example, in collapsing small cells into bigger ones, the model may lose important details and gradients in the water column. Dick Wetzel suggested that finer-scale hydrodynamic cells were needed to model SAV phenomena. Most participants agreed that hydrodynamic segments of the current water quality model are too big to model resuspension and turbidity phenomena in tributaries and shoal areas. Participants recommended using finer physical scales in shallow areas.

From the ecological perspective, participants identified transport and diffusion phenomena as the processes that should determine optimal hydrodynamic cell size. Because material inputs are assumed to be instantaneously distributed across the entire cell, the natural rate of transport and diffusion in the water column limits the size of the modeled cell. Steve Brandt pointed out that scale-dependent measurements of prey-fish density also determine optimal hydrodynamic cell size; scales must be small enough to account for the patchy distributions of small schooling fish.

The participants discussed possible rules for aggregation and disaggregation decisions. One suggestion: run models on different spatial and temporal scales to evaluate the effects on model output. Specifically, the Chesapeake Bay Program could run the time-variable water quality model under fine-scale and coarse-scale scenarios to evaluate changes in water quality results. Rules for cell aggregation could evolve from this effort.

To study trade-offs and benefits of various scales and to examine aggregation/disaggregation issues more systematically, Mike Kemp announced that the University of Maryland will soon begin the 10-year Multi-scale Experimental Ecosystem Research Center (MEERC) funded by EPA's Centers for Exploratory Research Program.

Feedbacks, trophic interactions, and time

Trophic interactions and nonlinear biological responses complicate the aggregation of ecological models. By simply aggregating segments into larger wholes, a model may not accurately account for the many nonlinear processes occurring in biological systems. For example, processes such as photosynthesis, nutrient uptake, growth, and some density-dependent population phenomena depend on nonlinear biological responses that are subject to thresholds and feedback mechanisms.

Moreover, biological processes may have unique characteristics that require special temporal considerations. The participants discussed temporal variation in many processes. Fish, for example, have different functional responses during phases of their life cycle—larval, juvenile and adult stages—that may need to be distinguished into separate model variables. Water quality models have evolved that separate winter and summer algae into distinct functional components and account for the relative importance of top-down versus bottom-up control changes over time.

Large scale aggregation can blur many of these important processes; thus, the participants supported flexible time scales to incorporate the temporal variability in many biological systems. The ability to characterize rare or episodic events and tease out such events from seasonal or monthly averages may define appropriate scales for modeling. In reality, aggregated time scales often average long-term data and produce periodic averages too general to describe important episodic phenomena. For example, Ken Rose pointed out that fish larvae may be killed by the rare event, such as a sudden temperature drop, rather than the long-term seasonal temperature average.

To better understand biological events, the participants recommended that selected variables be monitored on finer time scales, particularly for key ecosystem processes or in areas characterized by feedback mechanisms. Several modelers described techniques to dynamically adjust temporal parameters according to seasonal fluctuations.

Data availability

The availability of data may also limit the choice of scales, especially in the temporal dimension. For example, monitoring data may be available only for limited periods, and extrapolation and averaging may be required for application to specific problems.

Although the group acknowledged the good monitoring database available for Chesapeake Bay, there is a need for more comprehensive data, especially for the basic natural history of important species and ecosystem processes.

The group recommended a balance between data gathering and data modeling. According to Dominic DiToro, current modeling efforts cost only about one-third of the cost of data collection and monitoring. Moreover, modeling should not be kept separate from monitoring; to be most useful, choices should be made more carefully over what to monitor and when. Specifically, the participants endorsed more detailed data collection in areas in which nonlinear processes are likely to occur.

Also, the group identified data availability as a key criterion for choosing appropriate and relevant species to model. In addition to having a solid database, a species selected for inclusion in models should also be significant in the foodweb and should be environmentally sensitive. Based on these criteria, the group endorsed macrozooplankton (e.g., copepods) as a key taxonomic group for initial links to the water quality model. Zooplankton, in particular, have a good monitoring database. The group also recognized the existence of good databases for striped bass and Chesapeake Bay water quality.

To make the most of current databases, the participants recommended better communication and exchange of existing databases. In his presentation, Jim Kremer described HyperCard software as an example of a system that makes databases more transparent and easy to use.

Model development: formulation, calibration, and sensitivity analysis

Ecological models begin as tools for addressing specific problems or questions. As such, models must have a purpose, or goal, and must be defined in time and space.

To achieve stated goals, modelers design a conceptual framework to describe relevant natural processes, stocks, or resources. Such a framework usually includes the components of the ecosystem, defined as state variables, and uses equations to control input and output to state variables. State variables are usually connected through material or energy flow.

The process of model building includes six important steps:

- (1) Define and conceptualize the process;
- (2) Express relationships empirically with equations;
- (3) Translate equations into computer code;
- (4) Simulate, calibrate, and validate model results;
- (5) Analyze results and perform sensitivity analysis;
- (6) Apply results.

Define and conceptualize

Before conceptualizing processes and interactions, modelers must clearly define purposes and goals of the model and set boundaries in time and space. Models with different purposes and goals will have different structures and components. Model structure and the interactions between components define a conceptual framework for the model.

Build equations and empirical relationships

Using a conceptual model with clear boundaries and stated goals, modelers mathematically describe the relationships between components and processes with a collection of equations for various ecological processes. Ecological modelers most often rely on standard equations for processes such as photosynthesis, nutrient assimilation, metabolic rates, light irradiance, and predation.

Although these processes are well understood and have solid mathematical descriptions, many natural history processes, such as predator behavior and migrations, are complex and cannot always be described in precise mathematical terms. Often, equations will result from a researcher's own work and subsequent simulations will be used to test the new equation. In any case, modelers must borrow existing equations and/or derive and estimate new formulations.

Generate computer code

Because ecological models run on computers, their mathematical formulations must be translated into computer code. There are several approaches to the problem; most often, modelers either write their own code in FORTRAN or C, or they use modeling software packages such as STELLA to construct heuristic, graphic models that, in turn, are translated into computer code.

Some participants anticipate future difficulties integrating computer code across a standard software platform. Earlier water quality models, including the Chesapeake Bay time-variable, water quality model, have been written in FORTRAN and run on supercomputers; current ecosystem models are constructed in STELLA and run on Apple Macintosh microcomputers. Bob Costanza described a transputer technology using parallel processors that greatly increases computation speed for repetitive calculating with Macintosh-based STELLA models, with the resulting computation systems rivaling supercomputers. Dick Wetzel showed how he planned to integrate SAV data into geographic information systems. Some participants suggested planning ahead to anticipate and thus minimize problems resulting from the integration of varied software and hardware technologies used in ecosystem models.

Simulate, validate, and calibrate

Using ecological equations, computers simulate the interactions among variables in time and space. Normally simulations occur in time; that is, models evaluate ecosystem structure and function as time changes. This capability enables modelers to

predict potential changes to the system based on modified inputs and it invites “what if” comparisons of alternative scenarios.

However, before simulated results can be applied with confidence, simulated data must be validated, or compared with collected data, and calibrated to better fit real-world conditions. Often, validation/comparison and calibration/adjustment constitute an iterative process, as adjustments in forcing functions or equation coefficients produce more accurate or more precise simulation output.

Some participants discussed techniques for improved validation and calibration and the need for a set of standards to judge the “goodness of fit” of various models. For model validation, basic statistical methods, such as the Student *t* test, might be used to compare simulated data with collected data, but participants warned of the difficulties in comparing model averages with actual collected data. Overall, there were suggestions for robust quantitative methods to test whether or not model variables are within a prescribed margin of error relative to collected data.

One approach to model calibration is to adjust standard equation coefficients. In the process, modelers first define equation coefficients, or parameters, based on accepted values in appropriate scientific literature. Coefficients are then adjusted to match model output with actual data. Adjustments normally occur within a range of standard error; if modeled processes and state variables still do not match expected values, equations can be modified or rejected.

Often, historical data are used to validate and calibrate model simulations. For example, Bob Costanza made use of U.S. Fish and Wildlife Service historical data to calibrate a large spatial simulation of 2,479 interconnected cells of 1 km² each, representing the Atchafalaya delta. Historical data were available for 1956 for initial conditions and for 1978 and 1983 for correlation points. The use of historical data to calibrate models foreshadows the need to collect relevant monitoring data for use in future ecological models.

Perform sensitivity analysis

Simulations can be used to explore and determine components and processes controlling ecosystem structure and to evaluate how changes in model structure or inputs affect model results. By using sensitivity analysis or network analysis, modelers can determine the components that have the greatest control over modeled processes and simulation output.

Monte Carlo simulation techniques involve repetitive simulations with coefficients for each variable selected randomly from prescribed confidence intervals. Using these techniques one can determine which variable had the greatest control over some process (e.g., production) and calculate the sensitivities to evaluate how the variance in each component variable controls variance in output variables. Such sensitivity analysis techniques also determine the residual variance owing to nonlinear and interactive effects among components.

Apply results

Well-calibrated models can be used to predict changes, to test hypotheses, to understand mechanisms controlling a system, or to explore how various processes control other processes.

Recommendations

An Agenda for Action

Recommendations In the final session of the three-day workshop, the participants recommended a series of specific steps to guide the ecosystem modeling effort. The plan includes the following steps:

- Define the objectives
- Establish a conceptual framework
- Identify gaps in data and models
- Support consensus and facilitate standardization
- Gain the confidence of model users
- Establish institutional support
- Communicate results and boost credibility

Define the management objectives of a modeling program

A successful ecosystem modeling strategy should address the management objectives of the agencies responsible for restoring and protecting Chesapeake Bay. In this context, managers will be responsible for asking the questions that ultimately guide the ecosystem modeling program with clearly stated goals and objectives.

Establish a conceptual framework

A hierarchy of management questions/objectives can initiate the research/management dialogue necessary to establish a conceptual modeling framework. Such a framework should link ecologically valuable species and important processes (e.g., water quality and habitats) in the Chesapeake Bay ecosystem. Moreover, it should incorporate a continuum of models ranging from traditional water quality models to seagrass models to fishery management models. Several earlier conceptual frameworks were suggested in the 1980s.

Identify gaps in data and models

The workshop participants endorsed the diversity of approaches currently underway to model the Chesapeake Bay ecosystem (see Figure 1). A conceptual framework can put these models in the perspective of an integrated whole and highlight areas in which more work needs to be done. Based on the goals of the ecosystem modeling framework, existing and new models should be identified for further development and refinement. Moreover, because the utility of any model depends on the availability of relevant data, managers and scientists should work to identify data gaps or missing information critical to the modeling strategy. Recognition of required data and information should lead to improvements in ongoing monitoring programs and help guide specific research activities to investigate and/or quantify processes relevant to ecosystem model development, calibration, and validation.¹

¹ See:

Green, K.A. A conceptual ecological model for Chesapeake Bay. Washington, D.C.: U.S. Fish and Wildlife Service, Division of Biological Services, FWS/OBS-78/69, 22 pp.

Kemp, W.M., R.R. Twilley, J.G. Stevenson, W.R. Boynton, and J.C. Mian. 1983. The decline of submerged aquatic vascular plants in upper Chesapeake Bay: Summary of results concerning possible causes. Mar. Tech. Soc. J. 17:78-89.

Support consensus and facilitate standardization

Owing to the complexity of the Chesapeake Bay system, a diversity of modeling approaches remains essential for understanding and/or quantifying ecosystem processes. However, the workshop participants encouraged planning efforts that anticipate integration and linkage issues. Managers and scientists should support the movement toward consensus on technical issues involving appropriate scales, levels of aggregation or disaggregation, linkages between individual models, and recognized standards for model development, calibration, and sensitivity analysis.

Gain the confidence of model users

To streamline development, boost the credibility of model results, and ultimately ensure model acceptance, technical program managers should develop marketing strategies aimed at winning the confidence of management agencies and other potential model users. Specific suggestions included (1) facilitate communication between managers, modelers, and researchers, and (2) carefully choose modeling approaches and/or species with a high probability of success and with direct management implications. Initial modeling efforts should focus on zooplankton, SAV, and benthos.

Establish institutional support

To provide long-term financial support, the Chesapeake Bay Program and other regulatory and resource management agencies should establish a consortium of funding sources. Such a funding consortium would help guide the modeling program through integration and standardization issues, establish mechanisms for technical guidance and peer review, and identify specific monitoring and research needs.

Specific funding agency consortium objectives could include the following:

- Define a hierarchy of objectives and establish a conceptual framework for the ecosystem modeling strategy
- Select principal investigators and technical program managers to direct and coordinate the program
- Establish an independent peer review structure (similar to the Modeling Evaluation Group [MEG] of the Chesapeake Bay Program Modeling Subcommittee)
- Develop a detailed two to three year short-term workplan along with a longer five to ten year strategy for ecosystem processes model development, calibration, and application
- Create a specific list of monitoring and research needs to fill identified data and information gaps

Communicate results and boost credibility

Model developers and model users should actively communicate model results to a wide variety of audiences. Communication strategies should include technologies, documentation, and presentations that explain model assumptions and make them easy to use.