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Simulation Models of an Estuarine Macrophyte Ecosystem^{1,2}

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A model is a synthesis of microhypotheses, i.e., a synthesis of information about structure and function of the system [Van Dyne, in *Ohio J. Sci.* 78, 197 (1978)].

Final simulation models are complex in appearance, but they are built up from simple mathematical statements and statistical distributions which represent the functions, interrelationships, and values attributed to the real world ecosystem. Numerical simulation is important; it is the only known technique which is capable of representing the complexities of real ecosystems [Van Dyne, in *Proc. XI Int. Grasslan. Conf.*, p. A142 (1970), U. Queensland Press].

INTRODUCTION

Estuaries are complex and dynamic ecological systems that interact with human societies. These coastal ecosystems provide a bountiful source of fisheries products, commercial and recreational opportunities. Natural biogeochemical processes within

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are also capable of transforming many wastes emanating from human activities into useful components of regional and global cycles. Excessive waste inputs can, however, overwhelm the natural cycles. In such cases, alternative uses of estuarine resources may conflict with one another. In general, environmental research in estuarine systems has contributed significantly to both the basic understanding of ecological processes and the resolution of these natural resource conflicts.

In recent decades, many estuaries have undergone substantial modifications in species composition and ecological relations. One such change, which has occurred in Chesapeake Bay since the mid-1960s, is the drastic decline of the submersed vascular plants that once dominated the estuary's littoral region. Coincident with this loss of aquatic plants, there have been significant changes in water quality (Stevenson and Confer, 1978), as well as declines and shifts in various fisheries in the Bay (Boynton et al., 1979).

An extensive research effort, involving field and laboratory experiments, combined with ecological modeling and quantitative resource assessment, was undertaken to investigate this problem for upper Chesapeake Bay (Kemp et al., 1980). These studies documented the importance of macrophyte communities as habitats and feeding areas for diverse fish and waterfowl, as "filters" which trap and bind suspended sediments, and as storages and sinks for plant nutrients (Ward et al., 1984; Kemp et al., 1984). Research results have also suggested that continuing increases in sediment and, especially, nutrient loading from the bay's watershed have led to serious deterioration of light conditions needed for macrophyte growth; other anthropogenic wastes, such as agricultural herbicides, may have added additional (but lesser) stresses leading to the macrophyte decline (Kemp et al., 1983a).

In this chapter, we describe the simulation modeling framework that was used to organize, focus, and elaborate a broad empirical research program investigating the loss of macrophyte communities in upper Chesapeake Bay. We provide selected results of modeling studies to illustrate the wide range of conditions the models were capable of simulating, the ability of models to provide insight into complex ecological relations, and the utility of model hindcasts and forecasts in developing resource management strategies.

RESEARCH ORGANIZATION AND DESIGN

This research program addressed three broad questions. What factors were responsible for the macrophyte decline? To what extent do such macrophyte communities influence the overall estuarine ecosystem and which ecological interactions are most critical for maintenance of the macrophyte populations? What resource management options are most likely to succeed in restoration of the macrophyte communities? We established at the outset the following philosophical objectives for our research design (Levins, 1966): to use "controlled" experiments for discerning mechanistic relations among ecological factors, to interpret these experimental results in relation to "realistic" conditions actually occurring in nature, and to extend these results into a "general" context relevant for the whole estuary and other related ecosystems (Kemp et al., 1980). To meet these broad objectives, we employed a hierarchical array of research methods, combining bench-scale bioassays with laboratory microcosms, outdoor mesocosms, and descriptive field studies.

A variety of conceptual and simulation models were utilized to integrate this research program. It was reasoned that models could facilitate the coupling of experimental findings on relationships of causality or influence (Patten, 1985) with the inherently holistic perspective of descriptive in situ observations (Odum, 1984). Furthermore, simulation models were used to confer generality upon specific results at either end of the controllability-realism spectrum (Kemp et al., 1980). This was done by constructing, calibrating, and verifying models with data from a variety of systems. Thus, for example, simulation models were used to examine the ecological effects of various changes in water quality conditions characteristic of different regions of Chesapeake Bay. These models were

also used to interpolate and extrapolate the experimental results over a wide range of environmental conditions observed (past or present) in nature.

Two distinctly different strategies for simulation modeling were central in this research program. One strategy was directed primarily toward understanding the dynamic behavior of the macrophyte ecosystems, including carbon and nutrient flux and cycling, resource competition, and trophic interactions. A hierarchical perception was used to decompose the complex macrophyte ecosystem into a cluster of simplified subsystem models. This allowed sufficient ecological detail to be maintained against conceptual and computational limitations. The second modeling approach emphasized the role of these plant communities in a larger context of the entire estuarine system, including socioeconomic considerations. In this case, an aggregated version of the overall macrophyte ecosystem model was developed, emphasizing interactions with human systems. This model was placed into a sequence of cascading connections of influence, relating human uses of the estuary for waste disposal to macrophyte ecosystem dynamics, to human uses of the estuary as a source of fisheries harvest and recreational activities.

MACROPHYTE ECOSYSTEM MODEL

Ecosystem Modeling Framework

An initial step in developing a simulation model of the macrophyte ecosystem involved identifying both an appropriate level of aggregation and the essential state variables. Population time constants (Goodall 1974; Schaffer, 1981), as well as life histories, trophic relations, and habitats (Boling et al., 1975), were considered in defining aggregated biological state variables. Other simplifications include consideration of only one plant nutrient as potentially rate limiting.

In an effort to retain the essential ecological features of this system while maintaining computational tractability, the macrophyte system was decomposed into six subsystem models. Similar approaches have been used by previous investigators (Goodall, 1974; Overton, 1975; McIntire and Colby, 1978). These subsystem models contain between six and ten state variables, a total similar to the size of previously reported macrophyte simulation models (Titus et al., 1975; Belyaev et al., 1977; Ferguson and Adams, 1979; Short, 1980; Weber et al., 1981; Verhagen and Nienhuis, 1983; Van Montfrans et al., 1984).

Subsystems were defined so as to maximize internal interactions and minimize connection with external variables and feedbacks from other subsystem models (Simon, 1973). The resulting subsystems are (1) the autotroph model, which considers competition for light and nutrients among major photosynthetic groups of organisms; (2) the epibiota model, which describes the habitat on macrophyte leaf surfaces; (3) the water/plankton model, which includes suspended and dissolved substances; (4) the benthos model, which includes organisms, sediments, and biogeochemical processes; (5) the mobile invertebrates model, which simulates populations moving among other subsystems; and (6) the nekton model, which includes higher trophic levels supported by production from other subsystems. There are 45 state variables contained in all six subsystem models; however, 8 of these reappear in more than one subsystem. This redundancy of variables means that the state spaces overlap, and it further ensures consistency in the overall behavior of the macrophyte ecosystem model and its subsystem simulations. The number of common variables in subsystem models decreases away from the autotroph model, suggesting a reduction in the number of direct interactions among variables at higher trophic levels.

These models were designed to represent a unit area of water and sediment in an estuarine macrophyte ecosystem, with spatial averaging implied. Both carbon (C) and nitrogen (N) are modeled in this scheme, where N is conserved within the model during all transactions, while C is transformed (with CO₂ making the difference) as needed according to prescribed C:N ratios for all biological

state variables. Flows of both C and N are crucial to the behavior of this ecosystem. However, to include both with completely conserved materials would require nearly twice the number of variables. Several previous modeling studies have explicitly considered both C and N (e.g., Walsh, 1975 a,b; Kremer and Nixon, 1978; Hopkinson and Day, 1977; Najarian and Taft, 1981). However, most ecosystem models have been confined to tracing the flows of either carbon (energy) or nutrients, but not both (Najarian and Harleman, 1977; Wetzel and Wiegert, 1983).

The mathematical structure of this model uses nonlinear, first-order, differential equations simulated by finite difference techniques. There is one equation for each state variable, and each term in an equation represents an interaction between variables. The time step for rectangular integration was set at 2 hours. In the following section, we describe the structure and report selected simulation results for one macrophyte subsystem, the autotroph model.

Autotroph Model Structure

A major objective in developing the autotroph subsystem model was to examine the consequence of different environmental conditions on the competitive balance among the primary producers in a macrophyte-dominated community. The general structure of this model is depicted in Fig. 9.1, where phytoplankton, epiflora, macrophytes, and benthic microalgae all compete for limited availabilities of light and nutrients. Competition for light occurs through direct shading, while nutrient competition involves two separate sources of nitrogen (water column and sediment pore waters), which undergo periodic depletion of supplies. Only the rooted vascular plants have direct access to both nutrient sources. The original versions of this model included only seven state variables connected to numerous external factors (Kemp et al., 1983b); however, the current model includes both inorganic and organic detritus, as well as sessile (colonial) epifauna, as part of the total epiphytic community inhabiting macrophyte leaf surfaces.

The nature of mathematical formulations used in this and related models can be illustrated with the primary production term in the macrophyte growth equation:

$$P = [C/N][ATTEN][LKIN][TEMP][NKIN][LAI]. \quad (9.1)$$

Here, production (P) is a multiplicative function of six auxiliary variables: $[C/N]$, the nitrogen-to-carbon conversion; $[ATTEN]$, the light attenuation relation; $[LKIN]$, the photosynthesis-irradiance function; $[TEMP]$, the temperature kinetics; $[NKIN]$, the nitrogen uptake relation; and $[LAI]$, an index of leaf area representing the ability to absorb photons. Light attenuation follows a simple Beer-Lambert relation, with various materials contributing to the effect (e.g., Parsons et al., 1977):

$$I_z = I_0 e^{-kz}, \quad (9.2)$$

where I_z and I_0 are light levels at depth z and at the water surface, respectively. The attenuation coefficient k is taken as the sum of individual k 's for seston, phytoplankton, epiphytic material, and vascular plant leaves, where each k is a linear function of the amount of material per square meter, with the overall intercept attributable to dissolved substances and the water itself. The photosynthesis-irradiance relation is approximated by a rectangular hyperbola (Parsons et al., 1977):

$$P = P_m \frac{I_i}{I_k + I_i}, \quad (9.3)$$

where P_m is the light-saturated (maximum) photosynthesis, and I_i is the light level at the intersection of P_m and the initial slope. Data for all the light relations were obtained from experiments in our laboratory using the macrophyte species *Potamogeton perfoliatus* (Goldsborough, 1983). The temperature (T) function used is a simple Arrhenius relation,

and McRoy, 1984). The formulation used here was analogous to the Michaelis–Menten relation, with a single, overall maximum uptake rate [$V_m = f(P_m)$], but differing half-saturation constants for each of the two uptake routes:

$$V = V_m \frac{N_a + k^*N_b}{K_s + (N_a + k^*N_b)} \quad (9.5)$$

where N_a and N_b are water-column and pore-water nitrogen concentrations (primarily NH_4^+), K is the half-saturation constant for uptake of N_a , and (K_s/k^*) is the half-saturation for N_b . The need to calibrate this kinetic expression and the absence of information in the literature motivated us to conduct appropriate experiments with *P. perfoliatus* (Kemp et al., 1981, 1984). Similar expressions were used to describe light, nutrient, and temperature interactions in primary production of other autotrophic groups in this model.

Autotroph Model Results

The dynamic behavior of the macrophyte ecosystem was simulated for three different physical environments (Figs. 9.2 and 9.3): an open embayment characterized by rapid exchange with external estuarine waters, a protected cove with more restricted tidal flushing, and experimentally fertilized

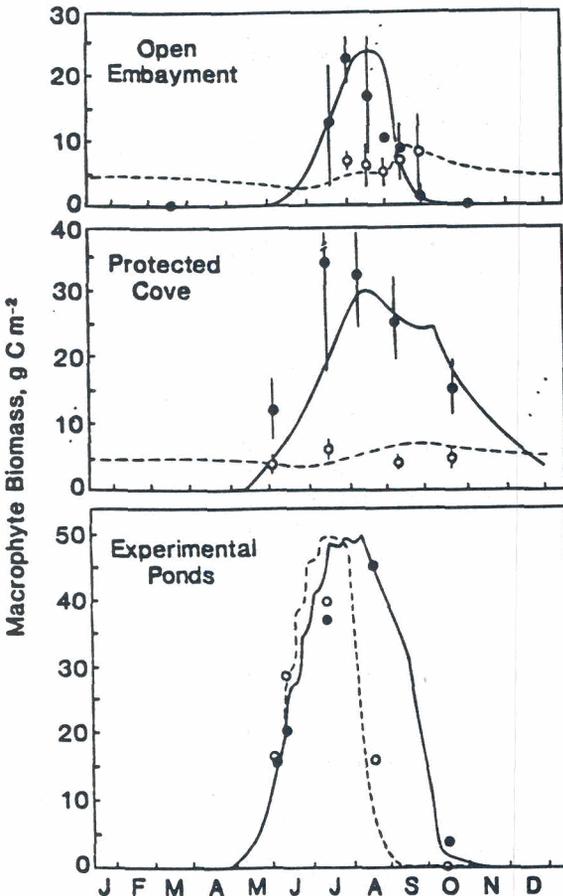


Figure 9.2 Annual distributions of macrophyte biomass in an open embayment and a protected cove in upper Chesapeake Bay and the experimental ponds receiving bay water. Lines represent output from the autotroph ecosystem model, while circles and intersecting vertical bars are means \pm standard errors for field data. In the upper and middle panels, solid lines and filled circles are for shoot (leaf and stem) biomass, and dashed lines and open circles are for root (plus rhizome) biomass. In the bottom panel, solid lines and filled circles are for ponds receiving low fertilization rates, and dashed lines and open circles are for ponds receiving high fertilization rates.

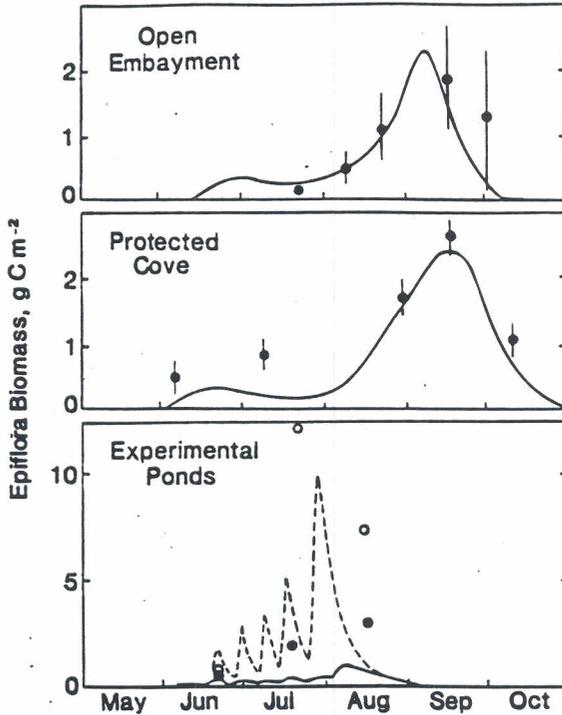


Figure 9.3 Temporal distributions of epiflora biomass on macrophyte leaves from May through October as estimated from the autotroph model and field data. See Fig. 9.2 for further explanation.

ponds with limited exchange and no tidal mixing. The model was originally calibrated with data from the open embayment; it was then verified for the protected cove situation, changing only the external forcing functions. Finally, the model was used to predict the outcome of fertilization experiments conducted in pond "mesocosms" contemporaneously with model simulations.

In general, the correspondence between model output and empirical data for standing stocks of autotrophic groups was very good. Simple linear regressions between model and data means for macrophyte shoot biomass were highly significant in all three cases, with the model explaining 89%, 62%, and 95%, respectively, for the three conditions. Model output correlated well with data means for epiflora also (Fig. 9.3), with r^2 values of 0.99 and 0.89 for the two field conditions (only three data points were available for pond experiments). Where an estimate of the sampling variance was available for empirical measurements, the model trace generally fell within one (always within two) standard errors about the mean.

Qualitative differences for autotroph abundances among the three sites were also captured in the simulation. Peak biomasses for macrophytes and their associated epiflora were slightly higher (20% to 30%) for the protected cove site compared to the open embayment (Figs. 9.2 and 9.3). Standing stocks reached levels two to five times greater in the experimental ponds than in the embayment. The length of the macrophyte growing season (defined by the presence of shoot biomass) increased from about 4 months in the open embayment to 7 or 8 months at the cove and pond sites (Fig. 9.2). Sensitivity analyses indicated that these differences in maximum abundance and growing season duration were largely the result of differences in flushing and mixing rates. Higher rates of water exchange between the model ecosystem and the external estuary allowed higher phytoplankton, seston, and nutrient concentrations, which stimulated epiflora and phytoplankton production, but inhibited macrophyte growth. With increased mixing rates, particulate matter tended to remain in suspension more readily, leading to greater attenuation of light available for macrophyte growth. These and related results are discussed elsewhere in greater detail (Kemp et al., 1981).

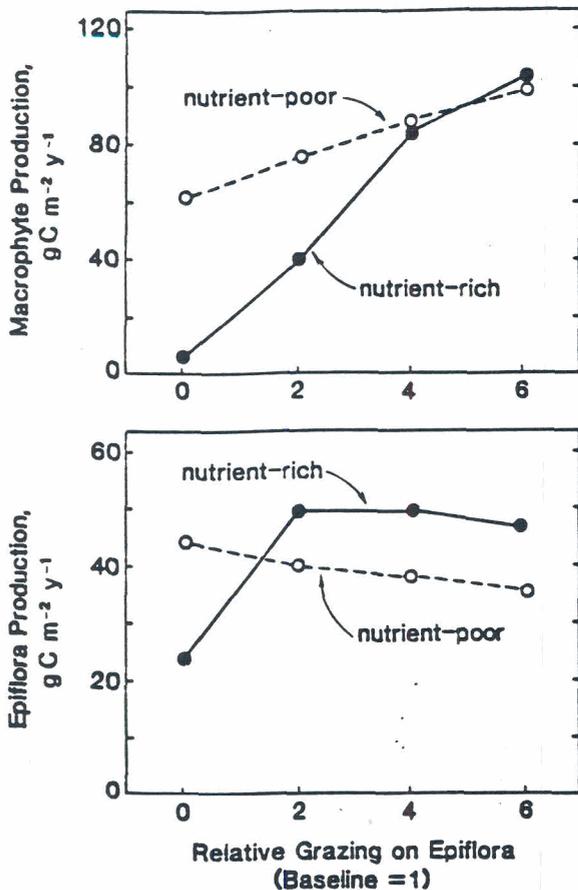


Figure 9.4 The autotroph model's simulated effects of changing rates of herbivorous grazing on epiflora in terms of production by macrophytes (upper panel) and epiflora (lower) under nutrient-poor and nutrient-rich conditions.

Simulation studies with this model revealed that the four autotrophic groups would coexist under unperturbed conditions of nutrient and seston concentrations. Temporal separation of peak growth periods and spatial separation of habitats effectively ameliorated the competition for light and nutrients among these autotrophs. Nutrient enrichment of estuarine waters, however, led to enhanced growth of phytoplankton and epiflora at the expense of the macrophytes, which were inhibited by increased light attenuation. Herbivorous grazing by invertebrates on epiflora allowed coexistence of epiflora and their macrophyte hosts even under extreme nutrient enrichment (Fig. 9.4). Although increased grazing pressure had relatively little effect ($\pm 30\%$ to 50%) on either epiflora or macrophyte production with low nutrient inputs, under nutrient-rich conditions grazing led to substantial increases in production of both epiflora ($2\times$) and macrophytes ($10\times$). The potential importance of grazing on epiflora in the competition between epiflora and their hosts has been discussed previously (Van Montfrans et al., 1984); however, potential interacting effects of grazing and nutrient enrichment have not been considered. In this situation, grazers function much like "keystone predators" by removing the advantage of one competitor over another (Paine, 1980).

MACROPHYTE MANAGEMENT MODELING

Management Modeling Framework

Parallel to the macrophyte ecosystem modeling effort, a system of resource management models was developed for focusing on the multiple interactions between socioeconomic systems and the estuarine macrophyte ecosystems. The objective of this management modeling was to assist in

utilizing scientific information toward the protection and management of submersed vascular plants in Chesapeake Bay. These models were intended to be used both in assessing factors potentially contributing to the decline in macrophyte abundance and in estimating the consequences of this decline in terms of changes in fish production, sedimentation, and nutrient fluxes.

The management modeling framework consisted of a network of interconnected models that traced the influence of human activities on macrophyte populations, which in turn affect fisheries and other resources valued by society (Boynton et al., 1981; Kemp et al., 1983b). In this scheme, a hydrologic-chemical runoff model (Holtan and Yaramanglou, 1979) combined meteorological conditions with agricultural practices to calculate delivery of nutrients, sediments, and herbicides from fields to the estuary. The transport, flushing, and transformations of these substances in the estuary were estimated using simple, steady-state, box models (Officer, 1980). A macrophyte management model was used to simulate the behavior of submersed vascular plants, other autotrophs, nutrients, sediments, invertebrates, and fish in relation to these inputs from adjacent land and water (Kemp et al., 1981). The benefits and costs of alternative agricultural or waste-treatment practices that influence fisheries and other resource values via changes in water quality and macrophyte growth were assessed using resource evaluation models (Kahn and Kemp, 1985; Boynton et al., 1981).

Connections between submodels in this management modeling framework are generally unidirectional, with feedback occurring only indirectly through the management decision process. For example, materials enter the estuary from the watershed, and the estuary, per se, has little direct influence on watershed activities. In this scheme the modeler serves as the interface between connected submodels, and piecewise simulations can be performed with no loss of information since feedbacks are weak. In other words, the output information from simulations in one submodel is used by the modeler to define input conditions for the next submodel in the sequence.

Macrophyte Management Model Structure

At the focal point of this resource management framework is the macrophyte management model. This model emphasizes interactions between macrophyte ecosystems and human systems (Fig. 9.5). Specifically, water quality effects on macrophyte production and abundance are included along with the habitat and food-chain factors by which macrophytes influence fish production. The structure of this model aggregates much of the complexity that had been emphasized in the macrophyte ecosystem submodels (Kemp et al., 1983b). Sensitivity analyses performed for the ecosystem submodels provided some guidance on appropriate strategies of aggregation, wherein crucial variables and pathways were preserved, and less sensitive factors were either omitted or combined.

The general structure of the macrophyte management model is comprised of 15 state variables organized into five groups: (1) the three major primary producers or photosynthetic groups, all competing for limited light and nutrient resources; (2) the sediments and their associated chemistry; (3) the water with its dissolved nutrients (DIN) and herbicides (HCD), as well as suspended particulate matter (SPM); (4) the herbivorous invertebrate secondary producers at the lower end of the food chain; and (5) the fish, which are generally tertiary producers at the top of the ecological food chain. These state variables are driven by 11 seasonally varying, external forcing functions. This model also includes new state variables (viz., dissolved and adsorbed herbicides) not occurring in the ecological submodels, but included here because of their potential importance in resource management. The differential equations defining this model are essentially similar to those used in the autotroph model. However, these equations tend to be less mechanistic and more linear. These forms are consistent with the concept of increasing linearity of systems with increasing degree of aggregation (e.g., Patten, 1975; Odum, 1983).

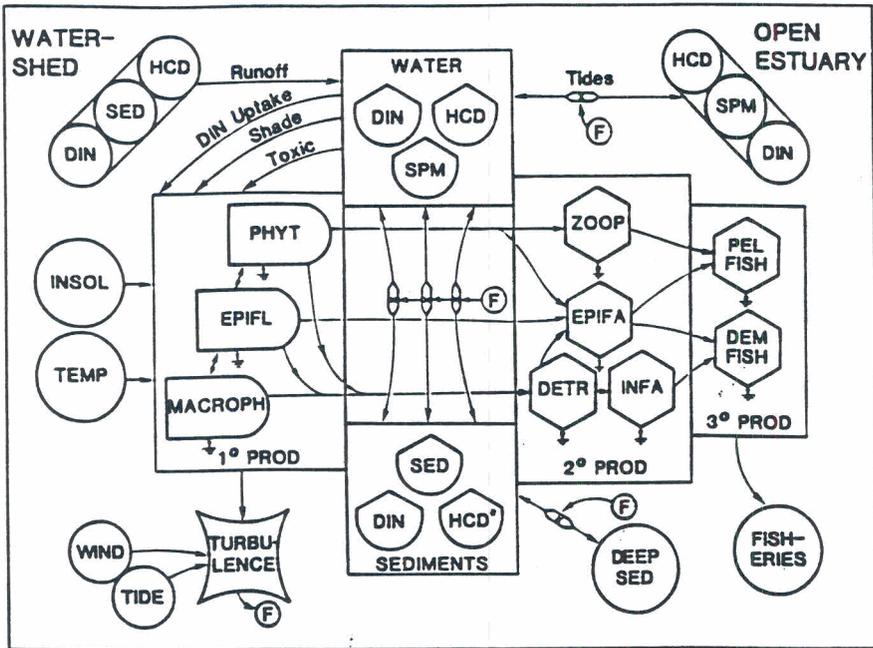


Figure 9.5 Conceptual diagram of macrophyte management model depicting interactions among three major primary producer (1° PROD) groups (PHYT, phytoplankton; EPIFL, epiflora; MACROPH, macrophytes) competing for limited availabilities of sunlight (INSOL) and dissolved inorganic nitrogen (DIN). Autotroph production, which is influenced by shading effects (including suspended particulate matter, SPM), DIN concentrations, and toxicity of herbicides dissolved in water or sorbed to sediments (HCD, HCD*), supports secondary production (2° PROD), including zooplankton (ZOOPL), epifauna (EPIFA), infauna (INFA), and detritus (DETR); and tertiary production (3° PROD), including pelagic (PEL) and demersal (DEM) fish. See Fig. 9.1 for explanation of symbols (adapted from Kemp et al., 1983b).

Macrophyte Management Model Results

The general behavior of the macrophyte management model correlated well with field data from the open embayment site (Fig. 9.6). As with the autotroph model, macrophyte and epiflora biomasses were reproduced reasonably well in simulation. Similarly, simulations of fish and invertebrate population abundances corresponded well with measurements. For this model, we have made no attempt at verification with a second data set, largely because data were unavailable for many key variables. By changing nutrient, sediment, and herbicide loading rates in the model, simulations were obtained corresponding to both pre-1970 and post-1980 water quality conditions (Fig. 9.6). In the later simulation, macrophyte biomass was decreased by about 40%, with a reduction (about 20%) in summer abundance of demersal fishes. Such a small difference in fish biomass would be difficult to detect empirically; however, simulation studies revealed that total loss in macrophytes would result in >50% decrease in demersal fish. Model sensitivity analyses indicated that most of this loss of fish abundance was attributable to reductions in food and refuge from predators, rather than simple loss of habitat where fish produced elsewhere congregate locally. This distinction would be difficult to discern without the aid of the simulation model.

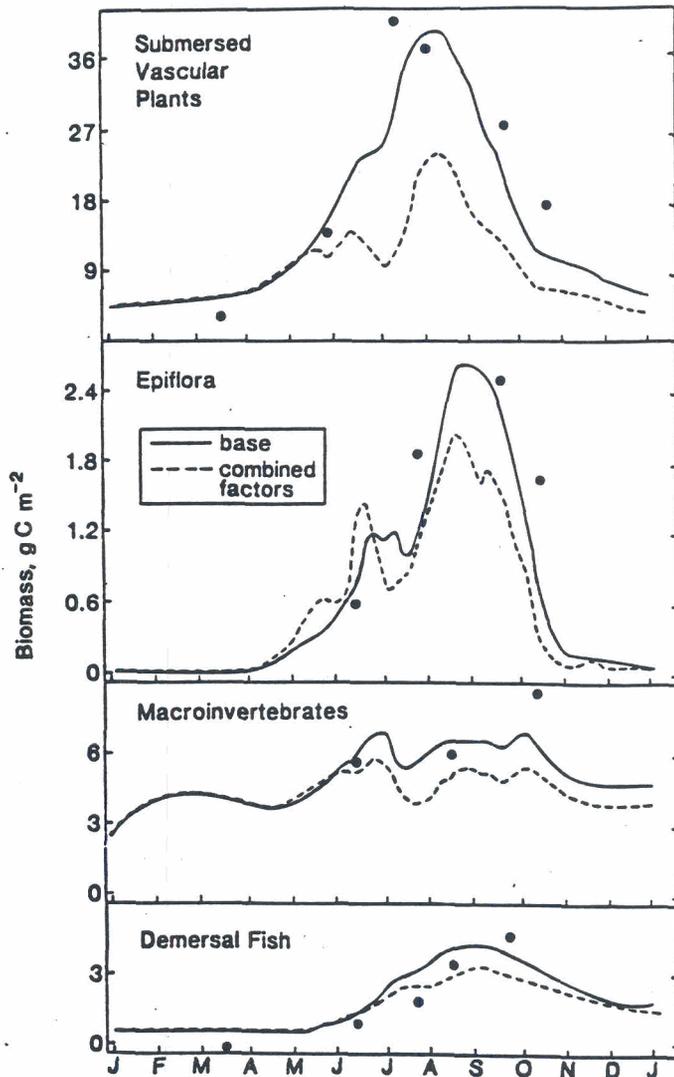


Figure 9.6 Annual distributions of biomasses for submersed vascular plants (shoots and roots), epiflora, macroinvertebrates, and demersal fish. Solid lines and circles represent output from macrophyte management model and data means, respectively, for an open embayment in upper Chesapeake Bay (1970s); dashed lines indicate model output for conditions in the 1980s at the same site.

Multiple simulation experiments with this model allowed consideration of the relative effects of herbicide, sediment, and nutrient loading on macrophyte production (Fig. 9.7). Here, growth of submersed plants exhibits little response to changes in herbicide loading from the watershed. Rapid dilution, degradation, and sorption to sediments by the major herbicides in this region, combined with low toxicity of degradation products and a degree of resistance exhibited by these macrophytes, all contribute to this minimal effect (Kemp et al., 1983a). Sediment inputs produce a more dramatic effect on macrophyte production, following, essentially, an exponential relation. However, much of the total estuarine sediment loading is derived from natural processes, such as shore erosion, which

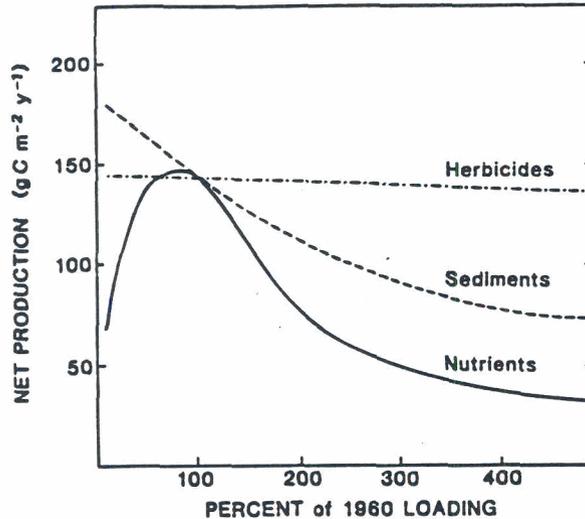


Figure 9.7 The macrophyte management model's simulated effects of changing watershed loading rates for herbicides, sediments, and nutrients on annual net production of macrophytes. Loading rates are adjusted relative to values estimated for 1960 (adapted from Boynton et al., 1981, and Kemp et al., 1983b).

are difficult to manage (Kemp et al., 1984). Nutrient (and in particular nitrogen) loading at low levels causes an enhanced macrophyte growth, whereas reduced production results from inputs greater than estimated 1960 rates. As emphasized above in relation to the autotroph model, decreased vascular plant production at high nitrogen levels results from enhanced growth of planktonic and epiphytic algae, which effectively reduce light available to the macrophytes (Twilley et al., 1985). In combination, historical changes in these water quality variables between 1930 and the present appear sufficient to account for the observed decline in Chesapeake Bay macrophytes (Kemp et al., 1983a).

RETROSPECTIVE CONSIDERATIONS

The roles of ecological modeling in scientific research and natural resource management have been much debated over the last 20 years (Jeffers, 1973; Mar, 1974; Cooper, 1975; Watt, 1975; Wiegert, 1975). Some of the often mentioned utilities of modeling in environmental research include organizing research objectives and methods, identifying missing information or poorly understood relationships, formulating and formalizing scientific hypotheses, interpolating and extrapolating from a given data base, and testing sensitivities of model variables in relation to their real-world counterparts. In her review, Pielou (1981) concluded that many of these points, while conceptually valid, are often overstated. For the research program described in this paper, an attempt was made to utilize models toward most of these objectives. In the following section, we take a retrospective view of this modeling effort (emphasizing the two models presented here) to identify examples of how these models may have enhanced the overall research effort.

Understanding Ecological Interactions

In the conceptualization stages of developing the autotroph model, we were forced to recognize that one very basic aspect of macrophyte physiology, nutrient uptake kinetics, had not been described for whole plants in the scientific literature. Although experimental evidence suggested that, for a

given plant, root and shoot uptake of nitrogen and phosphorus were both important and generally interdependent (e.g., Thursby and Harlin, 1982), a kinetic formulation for whole-plant uptake was lacking. Thus, the demands of model description (to express relationships in precise and explicit terms) identified for us a suite of empirical experiments of fundamental importance for understanding macrophyte ecology and physiology (Kemp et al., 1994). Once this kinetic relationship was defined the simulation model was able to calculate the relative importance of root versus shoot uptake of nitrogen under different environmental conditions.

In considering competitive relations among autotrophic groups, model descriptions include numerous interactions, ranging from nutrient exchange to allelopathy to light attenuation. Experiments with the autotroph model demonstrated the crucial significance of light attenuation in determining the outcome of the competition under various simulated conditions. Modeling experiments also illustrated the relative importance of phytoplankton and epiflora in attenuating light from macrophyte under different degrees of fertilization. Sensitivity analyses with the autotroph model helped to explain the marked differences observed for growth cycles of macrophyte abundance in "exposed" versus "protected" sites. Apparently, reductions in flushing rate associated with protected cover allowed macrophytes to compete more effectively with microalgae for water-column nutrients. This mechanism contributed to extended growing seasons in coves, consistent with historical in situ observations (Orth and Moore, 1983).

Although several recent papers have suggested that variations in grazing pressure on epiflora might strongly affect competition between epiflora and their host macrophytes, empirical evidence had appeared inconsistent (Kemp et al., 1994). Simulation experiments led to the formulation of a testable hypothesis involving interacting effects of grazing and nutrient enrichment. Simulation suggested that under oligotrophic conditions grazing had little effect on epiflora or macrophyte production, but that in eutrophic situations increased grazing resulted in enhanced production of both macrophytes and epiflora.

These examples illustrate how ecological modeling can complement empirical research by identifying poorly understood relationships worthy of empirical study, by aiding in the explanation of field and laboratory results, and by clarifying and formalizing loosely defined ideas into testable scientific hypotheses.

Resource Management Applications

In this study, numerous experiments were conducted to determine the potential importance of different factors (such as sediment loading, herbicide runoff, and nutrient enrichment) as sources of stress for macrophyte growth in the Bay (Kemp et al., 1983a). All these experiments examined one factor in isolation from the others, and the controlled nature of these studies makes simple extrapolation of results to conditions in nature tenuous. The models presented in this paper, however, provided a vehicle for integrating empirical results and extrapolating to nature. The autotroph model allowed results from mesocosm fertilization studies to be extended to actual estuarine situations. This was done by numerically supplementing mesocosm results (reproduced by the model) with natural processes such as tidal exchange and wind mixing, which had been omitted from the empirical experiments because of logistical limitations.

The macrophyte management model was used to compare the relative importance of herbicides, suspended sediments, and nutrients as stressors for macrophyte growth under various scenarios. For conditions at one field site in the early 1980s, nutrient enrichment and sediment loading were shown to have many times greater impact than herbicide inputs on macrophyte abundance, and nutrient enrichment of bay waters was estimated as the single most important factor contributing to the macrophyte decline. These results were influential in the formulation of state and federal agency policies to reduce eutrophication of Chesapeake Bay. The modeling studies also supported a government policy of encouraging minimum-tillage agriculture in the estuary's watershed, since

this approach tends to reduce nutrient and sediment losses from farmlands at the expense of increased application of herbicides for weed control (Kemp et al., 1994).

The macrophyte management model also demonstrated the nature of an interaction between macrophytes and fish at opposite ends of the trophic web. Because of the complexity of relationships, including feedback effects (grazing on epiflora, nutrient regeneration, and the like), such connections would be otherwise difficult to establish. Although field data had shown far greater abundances of fish in vegetated as compared to bare habitats, sensitivity analyses with the model allowed the relative importance of different characteristics of the macrophyte habitat (for example, increased food versus refuge from predators) to be partitioned. Model results were combined with resource economic analyses to estimate the shadow-priced value of macrophytes for commercial and recreational fisheries in Chesapeake Bay to be in excess of \$1 million dollars per year (Kahn and Kemp, 1985). This habitat role of macrophyte beds, as clarified by modeling analyses, has been recognized by government agencies and incorporated into current fisheries management policies. Thus, we conclude that ecological modeling of submersed macrophyte communities in Chesapeake Bay has contributed both to basic understanding of estuarine ecology and to judicious management of the bay's natural resources.

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