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Chapter 6

ECOSYSTEM MODELING AND ENERGY ANALYSIS OF SUBMERGED AQUATIC VEGETATION IN CHESAPEAKE BAY*

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Abstract. This chapter describes ecosystem models and energy analyses associated with a large research program investigating the declining abundance of submerged aquatic vegetation (SAV) in Chesapeake Bay and the effects of this decline on ecological and socioeconomic processes. As a part of this volume, our primary purpose here is to illustrate the deep and manifold influence that H. T. Odum has had on this kind of environmental research. In this study, hierarchically organized models and submodels have facilitated the simplification needed for numerical tractability while maintaining sufficient detail to examine mechanisms of ecological interaction. Two models of SAV ecological subsystems are presented. First, the *Autotroph Model* was used to investigate the consequences of shifting competition for light and nutrients among four groups of primary producers (SAV, phytoplankton, epiphytes, and benthic microalgae). This model, which has been calibrated and verified against independent data sets, was used to extrapolate from controlled experiments to consider effects of nutrient enrichment at the level of the bay itself. The second of these, the *Nekton Model*, was developed to test possible effects of declining SAV on the trophic structure and relative abundance of three fish groups. The model's design utilizes certain elements of traditional fish population models within the functional structure of an ecosystem process model. At a higher level of organization, a resource management model was developed that included the aggregated details of these and other ecological submodels. This SAV management model is linked to a suite of regional models that relate human activities to estuarine processes and societal values. We also developed a preliminary embodied energy analysis that is used to compare the energy fluxes associated with alternative watershed/SAV management strategies; these results are contrasted with parallel calculations using more traditional resource economics. In conclusion,

we point out that the early work of H. T. Odum provided the basic foundations for both (1) the use of simulation modeling as an integrative tool in ecosystem analysis and (2) the application of ecological principles to economic analyses of environmental problems.

Introduction

Estuaries such as Chesapeake Bay are complex and dynamic ecological systems that interact with human societies in many ways. These coastal ecosystems provide a bountiful production of diverse fisheries and myriad recreational opportunities. Biogeochemical processes of estuaries are also capable of transforming many anthropogenic wastes into useful components of regional and global cycles. In some cases, low levels of waste inputs (such as nutrients and organic carbon) can, in fact, enhance estuarine productivity. However, in many of these environments, waste loading rates are large enough to detract significantly from the estuary's value as a source of fisheries, waste removal, and recreation. Hence, a serious problem evolves wherein legitimate but competing uses of the natural resource are in direct conflict with one another.

Chesapeake Bay is one of the largest estuaries in the world, extending some 314 km along a north-south axis and ranging from 6 to 56 km in width. Although the depth of its central channel varies from 10 to 50 m, the estuary's mean depth is only 8.5 m, and 50% of the estuary is less than 6 m deep. The bay's watershed covers an area of 164,188 km², draining piedmont and coastal plain provinces of five states (New York, Pennsylvania, Maryland, Virginia, and Delaware), and its human inhabitants number approximately 14.5 million. The coastal region of this watershed is characterized by one of the highest growth rates of human population in the country, and as a consequence, inputs of anthropogenic wastes have increased steadily over recent decades. The relatively shallow nature of this estuary offers a large potential habitat for submersed rooted-plants communities. It has been estimated that prior to 1970, these submersed plants contributed

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almost one-third of the total annual production of organic foods that support animal growth in the estuary (Kemp et al. 1984).

One significant well-documented change in the structure and function of Chesapeake Bay ecosystems is the general decline (over the past 3 decades) of submerged aquatic vegetation (SAV), which once dominated shallow regions of the estuary (Orth and Moore 1983; Kemp et al. 1983b). Coincident with this loss of aquatic plants, there have been significant changes in water quality, including increased levels of turbidity, nutrients, and agricultural herbicides, as well as declines and shifts in several key fisheries (Boynton et al. 1979). Stevenson and Confer (1978) postulated that these alterations in water quality, which were associated primarily with diffuse waste sources, have been the primary causes of the loss of submerged plants. Subsequent empirical research has corroborated this hypothesis, pointing particularly to the significance of nutrient enrichment in this estuary (Kemp et al. 1983a; Twilley et al. 1985). Moreover, it has been shown that the decline of SAV has contributed to detrimental changes in fisheries abundance and production, as well as significant changes in bay-wide budgets and fates of organic carbon, suspended sediments, and inorganic nutrients (Kemp et al. 1984; Lubbers et al. 1990).

A large and ultimately successful research program investigating the causes and consequences of the SAV decline in the upper reaches of Chesapeake Bay was initiated in 1979 and continued through 1984. Ecosystem simulation modeling and energy analysis played central roles in the design, coordination, and interpretation of this research program. In this chapter we provide a summary description of the modeling framework and energy analyses employed in this study. This chapter is adapted from an article that was included in an unpublished NOAA report (Kemp et al. 1983a); detailed descriptions are available elsewhere for our simulation models (Kemp et al. 1981; Kemp et al. 1994) and for our energy and economic analyses (Boynton et al. 1981; Kahn and Kemp 1985). In keeping with the spirit of this book, we use this chapter to serve as an example of the deep and diverse impact that H. T. Odum has had on our thinking and on our general approach to science.

Background and Research Design

Personal and Conceptual Background

The seeds for this chapter were sown at a meeting of the American Society of Limnology and Oceanography in Tallahassee, Florida, during the summer of 1971, when two of us (WMK and WRB) first met while in energetic pursuit of Professor H. T. Odum, who was co-chairing an important session. Both of us were investigating our respective potentials for initiating Ph.D. programs with HTO in Gainesville. As it turned out, the two of us were able to matriculate at

the University of Florida in the fall of 1972, thus beginning a long-standing collaborative relationship. The foundations for this relationship were (still are) based on an energy systems worldview and an excitable joy of science, both of which were assimilated from HTO. These intellectual foundations, which have been central to our approach to science since 1972, have been somehow enhanced by a shared symbiotic sense of absurd humor, the origins of which are unknown. This chapter provides us with an ideal forum to illustrate a small sampling of how the concepts of H. T. Odum have influenced our research. The third co-author of this chapter (AJH) gained his initial interest in the Odum systems approach while an undergraduate with Charlie Hall at Cornell. AJH obtained an M.S. degree under the joint tutelage of HTO and Suzanne Bayley, after which he joined the University of Maryland research group as an ecosystem modeler in 1980. A natural "simpatico" evolved rapidly among the three of us, helping to catalyze the research described herein.

One of the most important systems ideas underlying the design of this research project is the principle of *hierarchical structure*, which calls for conceptualization at a scale just larger than that of the primary scientific focus. This approach ensures that the research will be cast in an appropriate context that includes all important interactions (Odum 1971). Thus, to understand causes and consequences of SAV loss from Chesapeake Bay waters, it was essential that we consider not only the estuarine ecosystem but also the entire watershed system including its human activities. A related concept considered here is that a hierarchically organized model will provide a means for applying detailed understanding of controlling mechanisms identified at smaller scales to address problems defined at the larger scales (Odum 1983). The role of *simulation modeling as an organizational tool* has been central in this research project, where models served as a format for focusing the collective knowledge of an interdisciplinary group of scientists (botanists, zoologists, microbiologists, chemists, sedimentologists) on a complex problem. Moreover, we have followed the prescription of Odum (1983) by integrating the modeling process itself with the empirical components of our research rather than as a separate activity.

We would like to think that our training as "environmental generalists" has facilitated our role as scientific integrators in the sense of Odum (1971). By recognizing the *energy basis for all ecological interactions*, our models readily combine flows and transformations of nutrients, carbon, oxygen, and hydrodynamic energy into the same system of equations, producing a powerful tool for examining ecological processes and relations (Odum 1983). We tackled the difficult problem of simulating fish population dynamics (e.g., reproduction and recruitment) within an ecosystem context by embedding a simple representation of fish life cycles (including both biomass and numerical

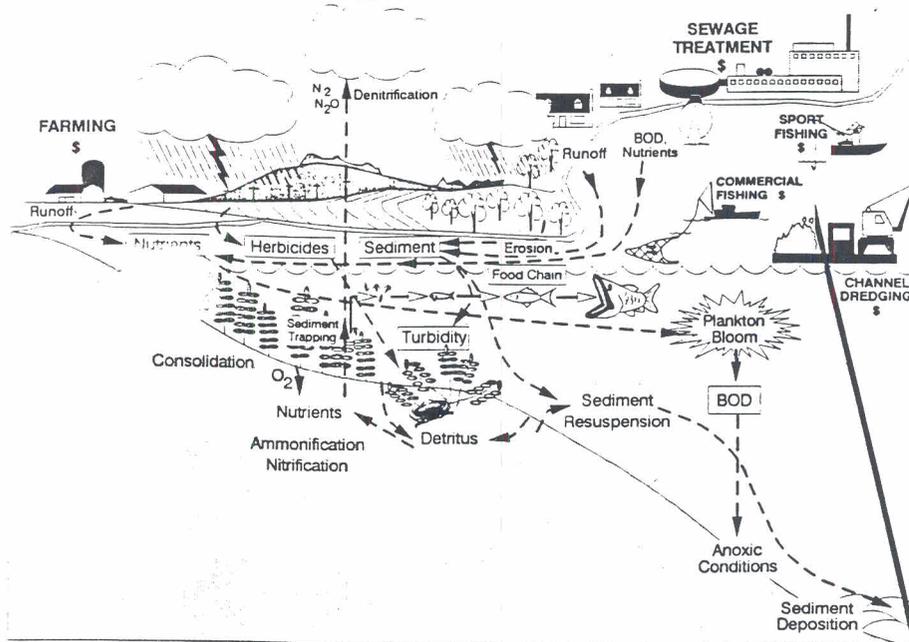


Figure 6.1 Conceptual schematic depicting submerged aquatic vegetation in relation to human activities and ecological production along with other resource values in the Chesapeake Bay region. N_2 = nitrogen; N_2O = nitrous oxide; O_2 = oxygen; BOD = biochemical oxygen demand.

abundance) into our ecological process model (Odum 1983). Finally, we employed a preliminary analysis of *embodied energy* to develop an objective comparison of cost and benefits associated with SAV in relation to alternative management scenarios (Odum and Odum 1976). In principle, these energy-value calculations would provide an assessment of the problem, which is unbiased by the short-term perceptions associated with consumers in a market economy. We compared these embodied energy calculations of societal costs associated with SAV losses with a partial analysis by traditional techniques of resource economics.

Perception of Problem

The problem of understanding the SAV decline in Chesapeake Bay can be represented by three research questions (Boynton et al. 1981): (1) What are the factors contributing to the decline? (2) What are the ecological consequences of the decline? (3) What are the socioeconomic ramifications? In a conceptual cartoon (Figure 6.1), we illustrate SAV acting as natural nutrient sinks and sediment traps, both processes having economic functions as equivalent costs for sewage treatment and channel dredging operations, respectively. Furthermore, SAV communities are thought to be important sources of food and habitat promoting growth of fish, shellfish, and waterfowl populations that are harvested in commercial and recreational endeavors. In this diagram, various watershed activities are

also shown to influence estuarine water quality (nutrient, sediment, and herbicide additions) via point discharges, runoff, and groundwater flow that are, in turn, regulated by rainfall and other factors. Throughout this cycle, some economic enterprises (e.g., agriculture) may have detrimental influence on SAV, while conversely others (e.g., fishing and dredging) are affected by plant losses. While this presentation may be useful as an overview of the basic relationships involved in the problem, it does not indicate the nature of such relationships. Hence, we need a more explicit framework within which mechanistic connections are explicit (Odum 1983).

We recognized in this research project a rare opportunity to address several scientific hypotheses of theoretical and empirical interest within a broad context of resource management questions. However, to do so effectively, we had to use a scheme whereby the complexity of this problem could be dealt with in an organized, piecemeal, simplified fashion. Therefore, we developed a hierarchical approach for the overall research program that enabled us to integrate highly controlled experiments (testing mechanistic hypotheses) together with descriptive field measurements (characterizing the structure and function of these SAV ecosystems). This allowed us to combine a spectrum of research methods and scales of interest into a unified effort. The relative merits and philosophical underpinning

of this scheme (e.g., Odum 1971) are discussed elsewhere at length (Kemp et al. 1980).

A variety of conceptual and simulation models were utilized to integrate this research program. We reasoned that models could facilitate the coupling of experimental findings on "causality" (i.e., influence) with the inherently holistic perspective of descriptive in situ observations. Furthermore, simulation models could be used to confer generality upon specific results at either end of the controllability–realism spectrum (Kemp et al. 1980). This would be done by constructing, calibrating, and verifying models with data from a variety of systems. Thus, we concluded that simulation models could be used to examine the possibility that altered water quality conditions contributed to the decline of SAV for various plant species, occurring in widely differing environments throughout Chesapeake Bay. Such models would help to interpolate and extrapolate the results of experimentally inferred relations for any combination of water quality factors observed (past or present) in nature.

Simulation Modeling Structure

We employed two distinctly different approaches to simulation modeling within this SAV research program. One approach was directed primarily toward understanding the dynamic behavior of the seagrass ecosystem including energy flux, predator–prey interactions, nutrient cycling, and trophic structure. Here we utilized a hierarchical perception to decompose a detailed SAV ecosystem model into a cluster of subsystem models. This allowed us to maintain sufficient ecological detail within the limits of conceptual and computational tractability (Odum 1983). The other approach in our modeling program emphasized the role of these plant communities in a larger context of the entire estuarine system including socioeconomic considerations. Here we developed an aggregated version of the SAV ecosystem model (i.e., combined submodels) and placed it into a sequence of cascading connections of influence, which lead from human uses of the estuary for waste disposal, through the SAV ecosystems, to human uses of the estuary as a source of fisheries harvest and other recreational activities. In this chapter we describe the structure and the logic behind this dual modeling framework, and we provide a few selected results from these models to indicate briefly the breadth of research questions that were addressed.

SAV Ecosystem Model

Ecosystem Modeling Framework

The initial step in developing a simulation model of the SAV ecosystem involved identification of the level of aggregation and essential state variables (Mar 1974; Schaffer 1981; Gardner et al. 1982; Figure 6.1). In this model, we aggregated organisms into state variables according to

functional groups and also considered other ecological characteristics such as metabolic time constants (Goodall 1974), life histories, and habitats (Boling et al. 1975). We have reduced the number of chemical variables (e.g., plant nutrients) by recognizing basic principles of chemical kinetics whereby biochemical rates are determined by a single rate-limiting step or substrate (Brezonik 1972). In all we defined thirty-seven state variables to be included in this model.

There are several published examples of analytical or simulation models for seagrasses or other submerged macrophytes (Titus et al. 1975; Adams et al. 1979; Short 1980; Weber et al. 1981; Verhagen and Nienhuis 1983; Wetzel and Neckles 1986; Zimmerman et al. 1987). Most of these models, however, have dealt with plant production only, and none contained more than eight state variables. It was decided that this many (thirty-seven) variables in one model would produce a virtually unmanageable system of equations, particularly given the necessary high degree of connectivity. Consequently, a hierarchical scheme of six subsystem models (each with 6 or 7 state variables) was used to define the SAV ecosystem (Figure 6.2). Other modelers have similarly utilized hierarchical approaches (Goodall 1974; Overton 1975; McIntire and Colby 1978), and various methods have been suggested for interconnecting subsystem models. Initially, subsystem models were simulated independently, where outputs of each served as inputs to the others. Because of bidirectional connections among submodels, this procedure was necessarily iterative. Respective inputs and outputs were matched between subsystem models, whereby the modeler served as an interfacing mechanism. The degree to which simulations were compatible among subsystem models was directly related to the quality of the calibrations for each submodel. Once each subsystem model was well calibrated, the input/output connections between submodels were consistent. While this process can be a tedious, it has the flexibility to allow the modeler's intuition to function freely.

Although there are no clear hierarchical boundaries within ecosystems (e.g., Kemp et al. 1980), we defined subsystems so as to maximize internal interactions and minimize connections with external variables (Simon 1973). In this way, the numerical simulations dealt directly with the most important (strongest) interactions among ecological variables. The resulting subsystems (Figure 6.2) are: (1) the *Autotrophs*, which compete for light and nutrients; (2) the *Epibiota*, which inhabit leaf surfaces of the dominant autotroph (SAV); (3) the *Water Column*, with its suspended and dissolved substances; (4) the *Benthos* and the sediments supporting them; (5) the *Large Mobile Invertebrates*; and (6) the *Nekton*, which feed on production from other subsystems. While the definition of submodels is somewhat arbitrary, it is clear that each submodel focuses on a different functional (also taxonomic) group of organisms and/or a different habitat. The sum of the

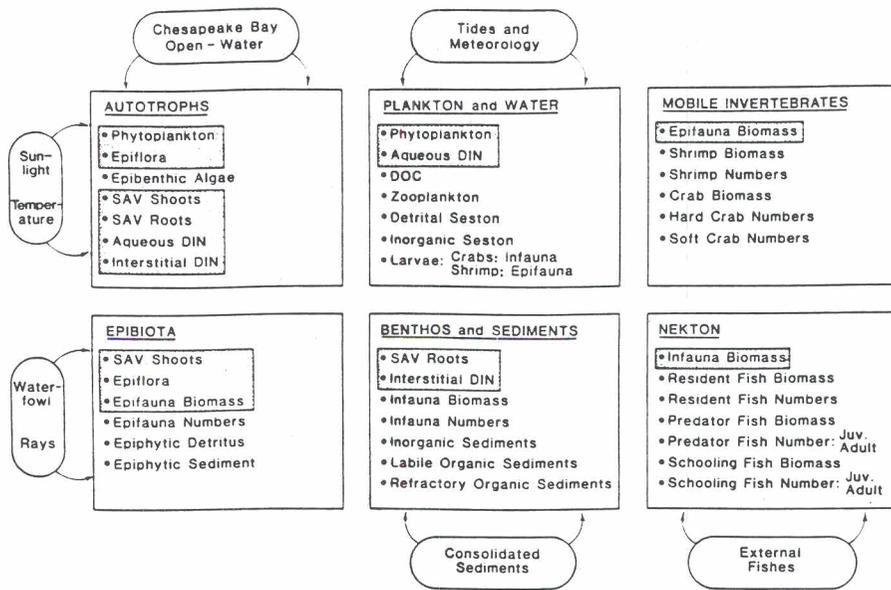


Figure 6.2 Definition of six ecosystem submodels in terms of state variables used in each, and external forces acting on them. Variables listed in shaded boxes reappear in one or more other submodels. DIN = dissolved inorganic nitrogen; DOC = dissolved organic carbon; SAV = submerged aquatic vegetation.

state variables contained in all six subsystem models is forty-five; however, eight of these occur in more than one subsystem. This redundancy of variables ensures consistency in the overall behavior of the SAV ecosystem model and its subsystem simulations. The number of common variables (in shaded boxes) decreases away from the Autotrophs, suggesting a reduction in the number of direct interactions among variables at higher trophic levels (Figure 6.2).

These models were designed to represent a unit area of water and sediment in an SAV ecosystem, thus averaging spatial variability. Both carbon (C) and nitrogen (N) are modeled in this scheme, where N is conserved within the model during all transactions and C is transformed (with carbon dioxide making the difference) as needed according to prescribed C:N ratios for all biological state variables. Flows of both C (and associated free energy) and N are crucial to the behavior of this ecosystem. To include both C and N with completely conserved materials would have, however, required substantially increased computation time with little improvement in understanding of processes relevant to the goals of this study. Other chemical factors such as oxygen and phosphorus are assumed to be nonlimiting to the ecosystem's behavior and are omitted. Several previous modeling studies have considered both C and N explicitly (e.g., Walsh 1975a; Walsh 1975b; Kremer and Nixon 1978; Hopkinson and Day 1977; Najarian and Taft 1981; Scavia et al. 1988; Fasham et al. 1990). However, most ecosystem models have been confined to

tracing the flows of either C (energy or nutrients but not both (Najarian and Harleman 1977; Wetzel and Wiegert 1983).

The mathematical structure of the 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. Detailed development of equations can be found in Kemp et al. (1994). In the following two sections of this chapter, we report some salient aspects of two of these subsystem models, the Autotrophs and the Nekton. These subsystems are at opposite ends of the ecological trophic chain, one (autotrophs) being more externally regulated (to sunlight, temperature, nutrient inputs, and so forth), while nekton dynamics result more directly from production at lower trophic levels.

The Autotroph Subsystem Model

A major objective in developing the Autotroph subsystem model was to examine the consequence of changing patterns of turbidity, nutrients, and grazing on the competitive balance among the primary producers in an SAV community. In this model, phytoplankton, epiflora, SAV, and benthic microalgae all utilize common and limited pools (or fluxes) of light and nutrients (Figure 6.3). Competition for light is direct via shading; for example, light absorbed by phytoplankton pigments is attenuated and unavailable for SAV. Competition occurs for two sources of dissolved nutrients (water column pools and sediment porewaters) through periodic depletion of supplies, and only SAV have direct access to both nutrient sources. The seven state variables here are connected to numerous external factors, both those in another subsystem (e.g., benthic infauna) and those entirely external to the SAV community (e.g., external, open-water phytoplankton communities).

The nature of mathematical formulations used can be illustrated with the primary production term (PROD) in the SAV growth equation:

$$\text{PROD} = [\text{C/N}][\text{ATTEN}][\text{LKIN}][\text{TEMP}][\text{NKIN}][\text{LAJ}] \quad (6)$$

Here, SAV production (PROD) 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

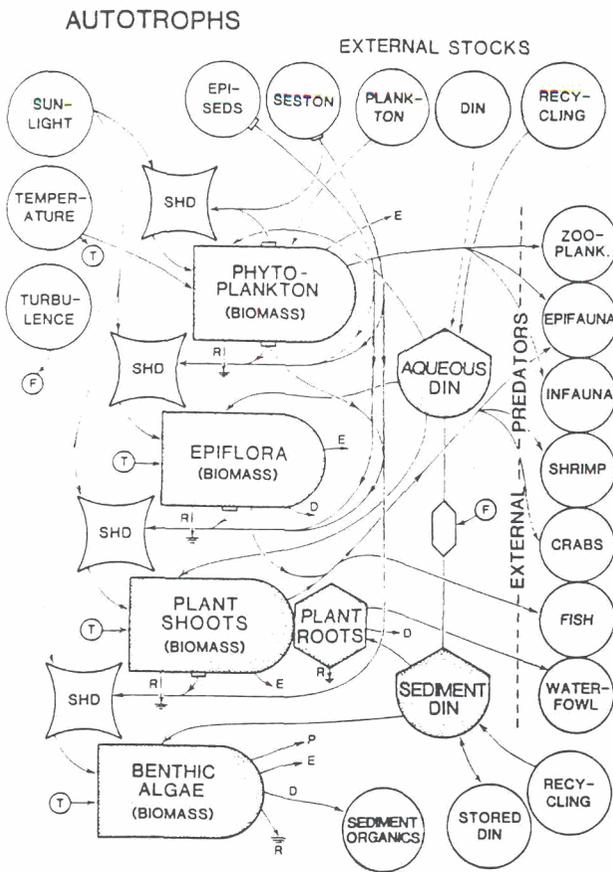


Figure 6.3 Autotroph ecosystem submodel presented in terms of state variables (shaded symbols) and interactions (lines with arrows) among variables and with external forcing functions (circles). Symbols are based on Odum 1971. DIN = dissolved inorganic nitrogen. From Kemp et al. 1994. Reprinted with permission of Prentice Hall Publishers, Englewood Cliffs, NJ.

[TEMP], the temperature kinetic relation; [NKIN], the nitrogen uptake relation; and [LAI], an index of leaf area representing the ability of the plant to absorb photons. Light attenuation follows a simple Beers–Lambert relation with various materials contributing to the effect (e.g., Parsons et al. 1979):

$$\text{ATTEN} = I_z/I_0 = e^{-k(Z)}, \quad (2)$$

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, epiphytic material, and SAV leaves, where each k is a linear function of the amount of material (expressed as g C) per m^2 , 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. 1979):

$$\text{LKIN} = P_m [(I_z)/(K_L + I_z)], \quad (3)$$

where P_m is the maximum photosynthesis possible, and K_L is the light level at $0.5 P_m$. Data for all of the light relations were obtained from experiments in our laboratory (Goldsbrough and Kemp 1988). The temperature (T) function used is a simple Arrhenius relation,

$$\text{TEMP} = e^{-(K_t/T)}. \quad (4)$$

Values for K_t were obtained from the literature for related species (Titus and Adams 1979; Barko and Smart 1981). A higher-order equation (Johnson et al. 1974) that accounts for temperature stress via protein denaturation at elevated T was used in some versions of the model.

There is little information in the literature concerning the appropriate kinetic relations for describing integrated nitrogen uptake (NKIN) for SAV, where uptake can occur from two sources, water column and sediment pore water (Zimmerman et al. 1987). We derived a formulation analogous to the Michaelis–Menten relation, and assuming a single maximum uptake rate ($V_m = f(P_m)$) but differing half-saturation constants,

$$\text{NKIN} = V_m \{(N_a + k' N_b) / [K_s + (N_a + k' N_b)]\}, \quad (5)$$

where N_a and N_b are water column and sediment concentrations of dissolved inorganic nitrogen (mostly NH_4^+), K_s is the half-saturation constant for uptake of N_a , and (K_s/k') is the half-saturation for N_b . Again, these coefficients were calculated from our own experimental data, primarily for the SAV species, *Potamogeton perfoliatus* (Kemp et al. 1994). Similar expressions were used to describe light, nutrient and temperature interactions in primary production of other autotrophic groups.

The basic behavior of this model is illustrated in the calibration output (Figure 6.4). The close correspondence between model and field data is also apparent here. For clarity the variances associated with these data are not given. However, the model trace is generally well within the 95% confidence interval for field observations. Subsequently, the veracity of this model was compared to a second independent data set, and again good agreement was obtained between model and measurements (Kemp et al. 1983b). The effects of nutrient additions to this model system were also very similar to those observed in large experimental ponds (Twilley et al. 1985), and the model was used to extrapolate results from these systems to actual estuarine conditions (Kemp et al. 1983a). It is interesting to note the slight asynchrony of peak summer abundance for these four components, indicating that the annual variations in production (or biomass) of each autotrophic group was greater than the variability in total autotrophy (Lewis 1980).

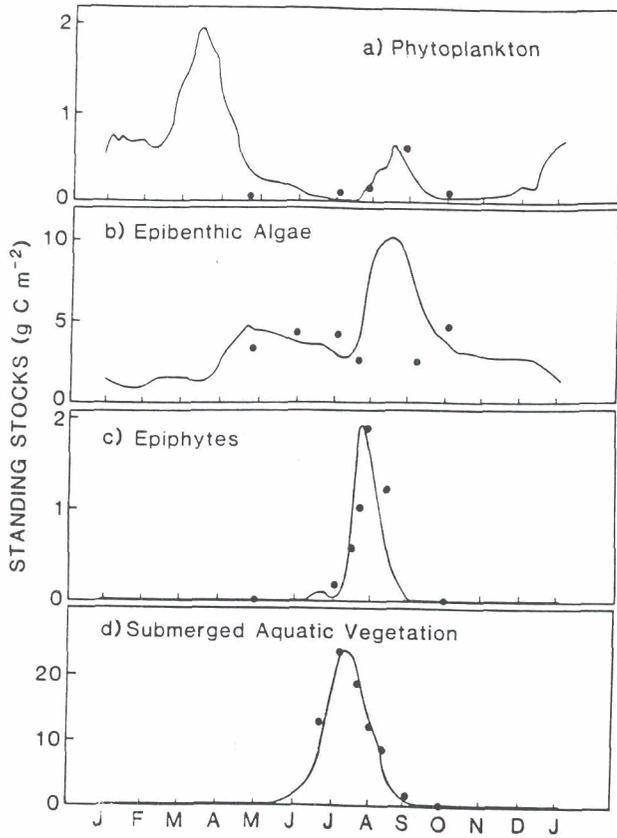


Figure 6.4 Calibration comparison of model simulations (solid lines) with field data (points) from autotroph ecosystem submodel (Figure 6.3) for standing stocks of a) phytoplankton, b) epibenthic algae, c) epiphytes, and d) submerged aquatic vegetation. Not reflected in calibration data are the simulated late winter phytoplankton bloom, which is driven by external inputs, and the summer epibenthic algal peak, which results from phytoplankton deposition. Details are given in Kemp et al. 1981; Kemp et al. 1984; and Kemp et al. 1995.

The Nekton Subsystem Model

The hypothesis to be investigated with the Nekton model was that changes in SAV abundance would influence total fish abundance and would shift the balance among various trophic and habitat fish groups. This model is important in the overall simulation framework because nekton provide a crucial feedback control for the other ecosystem submodels (Figure 6.2) and because its output provides a principal linkage to management concerns.

The general organization of the Nekton submodel is described in Figure 6.5, where three functional groups of fish (including total biomass and adult or juvenile numerical abundance for each) compete for various food items; benthic infauna, which are one of the most important sources of food for fish, are explicitly included in this model. Other food items are simulated as external forcing

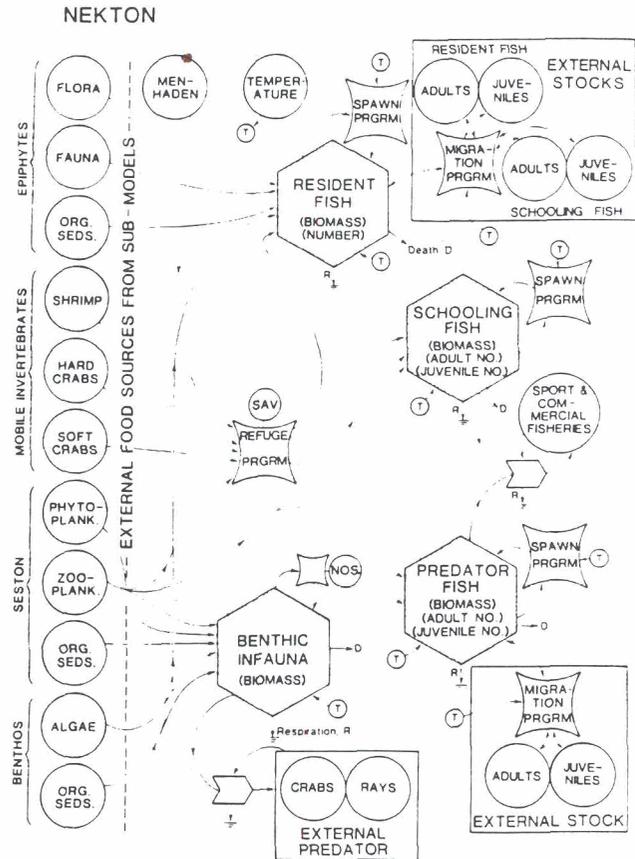


Figure 6.5 Nekton ecosystem submodel presented in terms of state variables (shaded symbols) and interaction (lines with arrows) among variables and with external forcing functions (circles). Symbols are based on Odum 1971. NOS = nonorganic sediments; SAV = submerged aquatic vegetation

functions, where it is assumed that top-down control from fish predation is relatively unimportant. The nekton system here is defined by nine state variables in four categories. There are three variables within two fish groups and two within the third, "Resident Fish." There is some direct predator-prey interaction among the three fish groups however, competition of limited foods also represents an indirect mechanism of interaction. Model fish groups are connected to external fish populations, with immigration and emigration controlled by temperature cues and life-history factors.

The three categories of fish are functional classifications defined on the basis of similar habitat, trophic relations, and life histories. The ecological units were developed as a compromise allowing aggregation by retaining some of the mechanistic relationships that characterize populations in nature (namely, where they live, what they eat, and how and when they reproduce). The condensation process is a necessary abstraction of ecological modeling, representing an attempt to balance among

criteria of realism, precision, and generality (Levins 1966). These fish groups are what Boling et al. (1975) referred to as "para-species," defined consistent with modeling objectives. It is fortunate that the fish assemblages in Chesapeake Bay's brackish SAV ecosystems are of relatively low species diversity. In fact, 80–95% of the fish biomass in each of the three categories (defined previously) is composed of three or fewer principal species (Lubbers et al. 1990) with similar functional characteristics. The major "Resident Fish" are *Fundulus* spp., *Lucania parva*, and *Apeltes quadracus*; the most important "Schooling Fish" are *Anchoa mitchilli* and *Menidia* spp.; "Predatory Fish" are dominated by *Pomatomis saltatrix* and *Morone americana*.

The elements of nekton life cycles are included in the model by utilizing special subroutines for spawning, recruitment, and migration. Recruitment from juvenile to adult age (size) classes is also represented in the model structure for Schooling Fish and Predatory Fish in terms of juvenile and adult numerical abundance. Thus, issues of stock recruitment and density dependence can be treated in the model, albeit at a coarse-grained level. The use of fish numbers and biomass as distinct, but coupled, state variables allows considerable flexibility and structural condensation while maintaining realistic model behavior. This approach, which was used by Steele (1974) for zooplankton in his model of the North Sea pelagic ecosystem, provides a means for tracking both energy flow (as biomass) and population information (as numbers). Predator-prey relations are often best described in terms of numerical abundance, while metabolic processes are more a function of biomass. Traditional population models consider numbers only (in separate age groups), while most ecosystem models utilize biomass only. This model attempts to combine the strengths of both.

The mathematical form of equations used in the model can be illustrated in terms of Schooling Fish biomass and adult numbers. The temporal rate of change for biomass (dQ_{35}/dt) is

$$\begin{aligned} dQ_{35}/dt = & \text{assimilation} - \text{predation mortality} \\ & - \text{fishing mortality} - \text{spawning effort} \\ & - \text{respiration} + \text{immigration} - \text{emigration}, \end{aligned} \quad (6)$$

while for adult numbers (dQ_{36}/dt) the rate of change is

$$\begin{aligned} dQ_{36}/dt = & \text{recruitment from juveniles} \\ & - \text{predation mortality} - \text{fishing mortality} \\ & + \text{immigration} - \text{emigration}. \end{aligned} \quad (7)$$

Overall, the terms in the biomass equation are a function of both biomass and number, where, for example, assimilation (a fixed fraction of consumption) and mortality involve biomass and numbers of both prey and predator, while the respiration term involves only biomass (Q_{35}). The terms in Equation 7 are (with the exception of recruitment) derived from those in Equation 6, with the

reciprocal of average size used to convert from biomass units to numbers. Although fish bioenergetic balances are best represented by models based on age-specific rates that are a function of temperature and food quality (e.g., Kitchell et al. 1977), our model formulation (with rates a function of mean size) is made robust by the inherent allometric relations associated with all metabolic processes (e.g., Peters 1983).

Predation rates by fish functional groups are a function of food abundance (with feeding thresholds, e.g., Wiegert 1975), with food selectivity coefficients (e.g., Ivlev 1961) and empirical observations from the field (Lubbers et al. 1990). The effects of SAV structure providing refuge from predation are incorporated into the grazing terms, with functional relations based on experimental observations (Heck and Orth 1980). Analyses of field data on feeding rates and food abundance (Lubbers et al. 1981) led to a parameterization of predation as the product of the predator activity (PRED) times prey availability (PREY). In the case of adult Schooling Fish,

$$\text{PRED} = K_1 Q_{35} \{ \log [L_1 + K_2 (Q_{35}/Q_{36})] (e^{k_3 T}) \}, \quad (8)$$

where T is temperature, L_1 is related to minimal feeding rate for small organisms, (Q_{35}/Q_{36}) is average size of predator, and K s are empirical coefficients. Similar expressions are used for predation by juveniles, but different prey items are involved. Thus, both juvenile and adult feeding contribute to biomass (Q_{35}), allowing for ontogenetic changes in diets (e.g., Carr and Adams 1973).

Prey availability is defined as the product of prey biomass (Q_b), an empirical function (Lubbers et al. 1981) of average prey size, $f(Q_b/Q_n)$, and an SAV prey refuge function,

$$\text{PREY} = K_4 Q_b \{ f(Q_b/Q_n) \{ L_2 + \exp[-K_5 (Q_p - L_3)] \} \}, \quad (9)$$

where L_2 is the maximum refuge offered, L_3 is the lower threshold of plant biomass (Q_p) for incipient refuge effect, and the availability function cannot exceed unity. The polynomial function of average prey size exhibits a broad central region (20–180% of mean prey size) with reduced availability when prey become very small or very large. Other details of model formulation are described in Kemp et al. 1983; Kemp et al. 1994).

The general behavior of this model is indicated in the calibration simulation presented in Figure 6.6. Simulated time-course of the benthic infaunal biomass is reasonably similar to field observations, both in magnitude and in timing, although the model shows a slower winter-spring growth in the community than do the data. At this preliminary stage of model development, we can say only that model output is in the right order of magnitude and that certain temporal trends such as abundance of Resident and juvenile Schooling Fish are reasonably consistent with the data. Generally, seasonal patterns of biomass are skewed too far into the autumn, probably due to problems

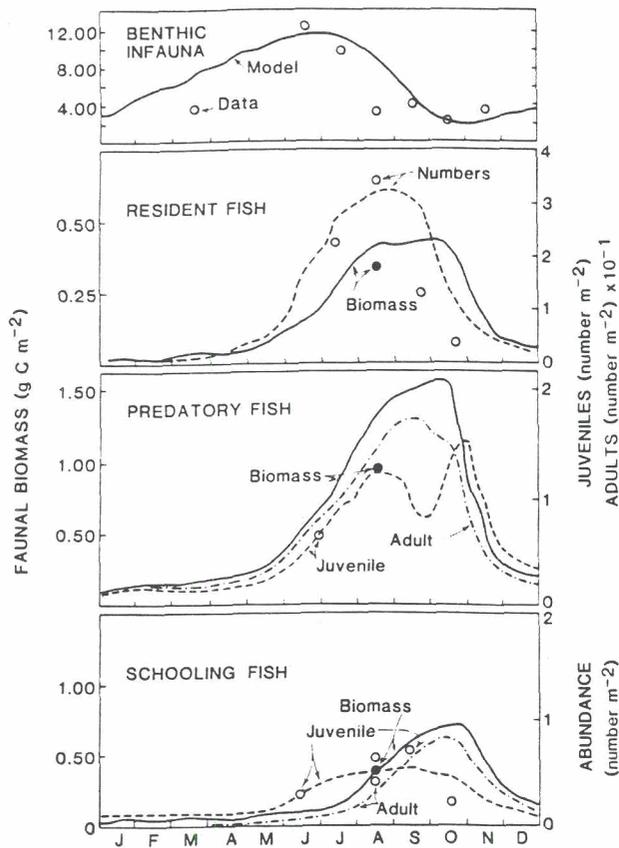


Figure 6.6 Calibration comparison of model simulations (solid lines for biomass, dashed lines for numerical abundance) with field data (filled circles for biomass; open circles for adult and juvenile numbers) from nekton ecosystem submodel (Figure 6.5) for benthic infauna, resident fish, predatory fish, and schooling fish. Data for adult numbers and biomass are from the same date. Empirical observations are taken from Kemp et al. 1981 and Lubbers et al. 1990.

in the emigration subroutines. Ultimately, it is hoped that this model will help us to understand the way in which changes among the autotrophic groups (e.g., reductions in SAV) influence the relative balance in fish abundance among the three groups (Figure 6.5), which are well down the trophic chain from those primary producers. These model simulations suggested that reductions in SAV led to decreases in fish abundance through effects of both habitat loss (e.g., predatory refuge) and food production. This distinction could not easily be made through field experimentation (Lubbers et al. 1981; Lubbers et al. 1990).

Resource Management Modeling

Management Modeling Framework

Parallel to the detailed ecosystem modeling, we developed a system of resource management models for focusing on the multiple interactions of human activities with resource ecosystems. In general, this modeling effort was designed to assist in utilizing scientific knowledge for developing balanced and productive management of Chesapeake Bay resources. In contrast to the detailed ecosystem models, this research was intended to assess both the relative importance of factors contributing to the decline in SAV abundance and the consequences of this decline (in terms of such factors as fish production). The modeling framework explicitly establishes the interactions between SAV ecosystems and human economic systems. Direct and indirect effects of alternative management scenarios were assessed in terms of economic values and ecological processes. Finally, this framework provided a heuristic format for understanding some principles of resource management.

This scheme is illustrated as a cluster of interconnected models representing the influence of human activities and physical forces (e.g., rain, sunlight, tides) on SAV ecosystem dynamics, which in turn affect resources valued by society (Figure 6.7). Briefly, meteorological conditions coupled with agricultural practices are shown as inputs to the Watershed Runoff Model (Holtan and Yaramanglou 1979), which links the Universal Soil Loss Equation to hydrologic and chemical process models, thereby routing water, nutrients, sediments, and herbicides from fields to estuary. The Estuarine Circulation Model is a simplified two-layer (ten-segment) "box model" based largely on continuity at steady state (Officer 1980); it receives agricultural runoff and sewage nutrient wastes and transports water and materials through the estuary, providing an ambient water quality field to which SAV are exposed. These materials, along with direct agricultural runoff, provide inputs to the SAV Ecosystem Management Model (SEMM), the details of which will be discussed in the next section. Outputs from SEMM, including fisheries and recreational activities, are input functions to the Resource Economics Model, which estimates equivalent economic values associated with these features (Boynton et al. 1981; Kahn and Kemp 1985).

Marginal costs and benefits associated with various economic activities, such as Land Development, Agriculture Production, and Sewage Treatment (Figure 6.7, left side) are calculated according to the procedure given in Boynton et al. (1981). Also associated with these economic processes are direct or indirect effects on waste loading to the estuary. Resource values are combined with costs, and benefits of watershed activities are estimated through shadow-pricing and embodied energy analyses. These computations help to establish viable Resource and Waste

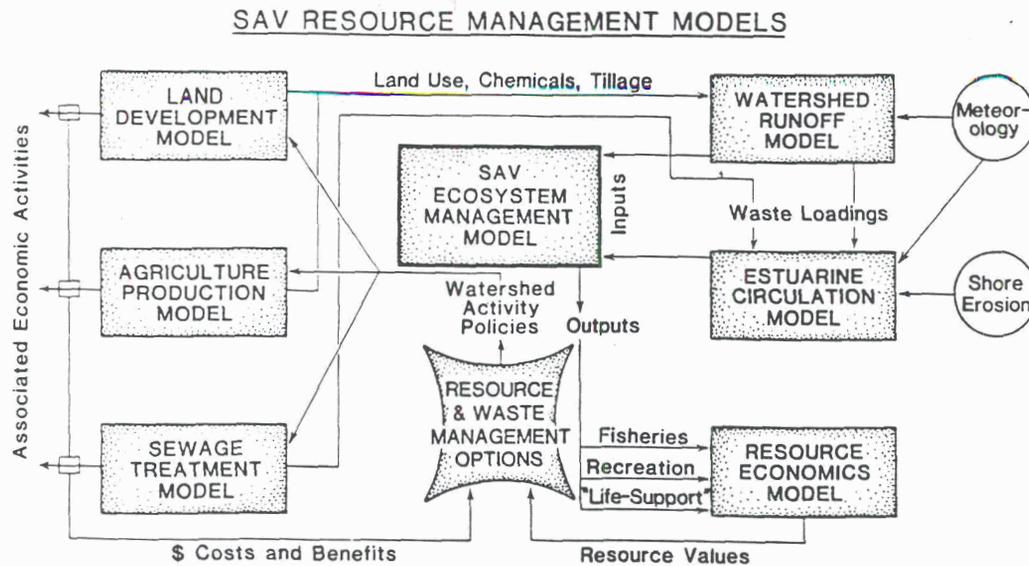


Figure 6.7 Schematic diagram illustrating interrelations among modeling programs organized toward developing overall management strategies for submerged aquatic vegetation in Chesapeake Bay. Other external inputs to land development, agriculture, and sewage treatment are not shown.

Options, which managers and citizens consider toward developing resource policies. In general, connections between submodels are unidirectional, with feedback occurring only indirectly through the management decision process. For example, materials enter the estuary from the watershed, while 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, because direct feedbacks are limited. In other words, the output information from simulations in one submodel used by the modeler to define input conditions for the next submodel in the sequence. The process of interconnecting submodels is necessarily an iterative one.

SAV Ecosystem Management Model

At the focal point of this resource management framework is the SAV Ecosystem Management Model. The SEMM was designed to emphasize interactions between SAV ecosystems and human systems (Figure 6.8), specifically water quality effects on SAV production and abundance, and the habitat and food-chain factors whereby SAV enhances fish production. The structure of SEMM aggregates much of the complexity that had been emphasized in the SAV ecosystem submodels (e.g., Autotroph and Nekton Models in Figure 6.3 and Figure 6.5). Our intention here was to preserve sufficient detail in ecological function so that relevant interactions with socioeconomic activities could also be included, while a relatively

simple model was maintained. Sensitivity analyses performed for the ecosystem submodels provided guidance on strategies of aggregation. All variables and processes were examined with sensitivity analysis, wherein crucial variables and pathways were preserved, and less sensitive factors were either omitted or combined.

The general structure of SEMM (Figure 6.8) is composed of fifteen state variables organized into five groups: (1) the Autotrophs, or photosynthetic organisms, all competing for limited light and nutrient resources; (2) the Sediments and their associated chemistry; (3) the Water with its dissolved nutrients and herbicides, as well as suspended sediments (seston); (4) the Herbivorous Invertebrates at the lower end of the food chain; and (5) the Carnivorous Fish at the top of the food chain. These state variables are driven by eleven seasonally varying external forcing functions. SEMM includes two new state variables (aqueous and adsorbed herbicide, atrazine) not occurring in the ecological submodels but included here because of the potential importance in resource management. The differential equations that formalize this model are essentially similar to those used in the Autotroph, Nekton, and other subsystem models (e.g., Equations 1–9). The mathematical expressions used at this higher level of aggregation are more linear in form, which is consistent with theories of scale and linearity of interaction (e.g., Patten 1975; Odum 1983).

Multiple simulation experiments with SEMM allowed us to consider the relative effects of herbicide, sediment, and nutrient loading on SAV production; these are summarized

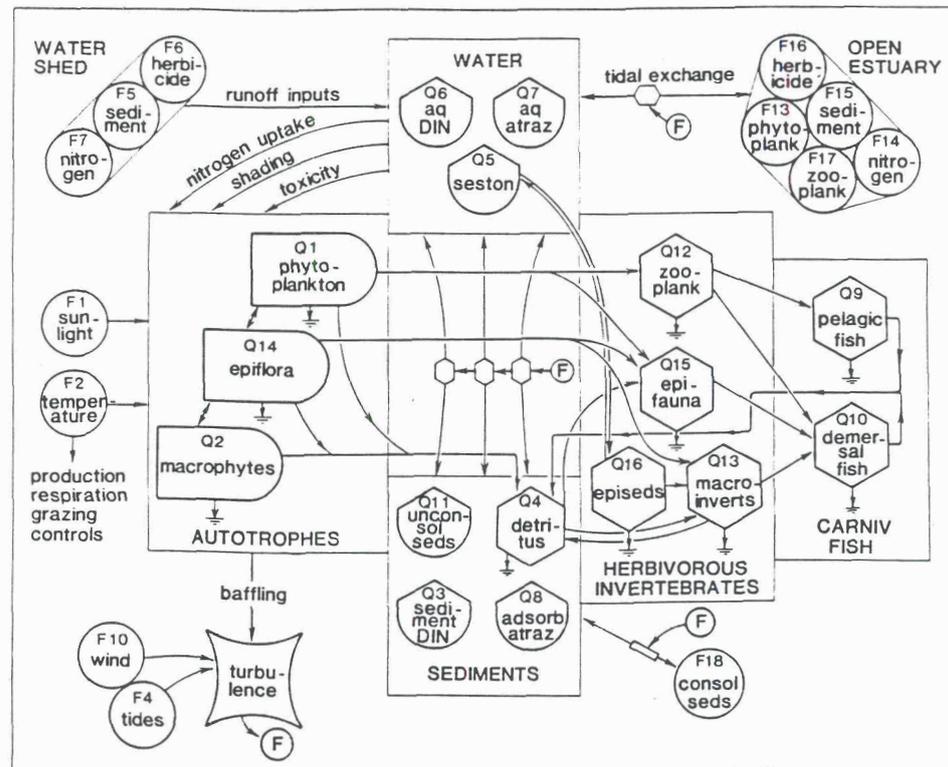


Figure 6.8 Submerged aquatic vegetation Ecosystem Management Model presented in terms of state variables [shaded symbols] and generalized interactions (lines with arrows) among variables and with external forcing functions (circles). Symbols are based on Odum 1971. atraz = atrazine (an herbicide); DIN = dissolved inorganic nitrogen; F = force; Q = stored quantity. From Kemp et al. 1994. Reprinted with permission of Prentice Hall Publishers, Englewood Cliffs, NJ.

here (Figure 6.9). Although phytotoxic responses to herbicide inputs were observed in experimental manipulations, estuarine concentrations were low and declined rapidly with degradation and dilution (Kemp et al. 1985). The simulation model integrated these individual processes to illustrate that growth of SAV exhibited little response to changes in herbicide loading from the watershed. Sediment inputs directly reduce light available to SAV, thereby producing a more dramatic effect on SAV. It appears, however, that much of the total estuarine sediment loading is derived from natural processes such as shore erosion (e.g., Kemp et al. 1984) and is therefore less manageable. Many of the plant species formerly inhabiting the upper portion of the bay are capable of assimilating nutrients directly from the overlying water into leaf tissues, and nutrient availability can limit SAV growth during summer (Kemp et al. 1984). Thus, model simulations indicate that nutrient loading at low levels produces an enhancement of SAV growth. Simulation studies suggest, however, that further increases in nutrient inputs (beyond our simulated 1960 conditions) cause reduction in SAV growth. Evidently, the reduction in SAV photosynthesis at high nitrogen levels

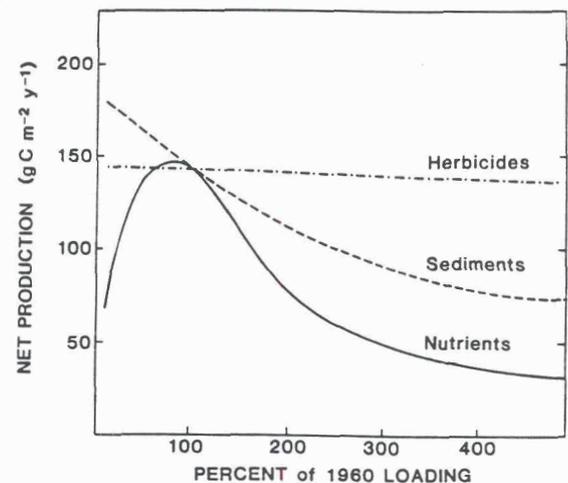


Figure 6.9 Summary of the effects of changing inputs of herbicides, sediments, and nutrients on annual net production of submerged aquatic vegetation (SAV). Lines represent the distillation of several simulation scenarios from SAV Ecosystem Management Model (Figure 6.8). From Kemp et al. 1995. Reprinted with permission of Prentice Hall Publishers, Englewood Cliffs, NJ.

results from enhanced growth of planktonic and epiphytic algae, which effectively reduce light available to SAV. It is clear from these modeling studies that reductions in nutrient loading to the estuary would be most effective in restoring SAV to levels of abundance similar to those extant in the early 1960s.

Management Options and Socioeconomic Trade-offs

Results of SEMM simulations were integrated into a larger analytical framework in which the socioeconomic consequences of several management options were evaluated using the framework presented in Figure 6.7. Preliminary

Table 6.1 Comparison of economic and embodied energy costs and benefits for agricultural and estuarine resource values associated with alternative scenarios of watershed management

Value Measure	Management Scenarios		
	100% Conventional Tillage	25% Reduction of Fertilizer Use	10% Reduction of Agricultural Land
<i>Economic Values*</i>			
Agroecosystem	-\$30,000	-\$900,000	-\$200,000
Relative impact [#]	0.6	18.6	4.1
Estuarine Ecosystem	-\$20,000	+\$100,000	+\$50,000
Relative impact [#]	3.1	15.4	7.7
Benefit:Cost Ratio	NA	0.11	0.28
<i>Embodied Energy Value[†]</i>			
Agroecosystem	-259.0	-16.7	-152.0
Estuarine Ecosystem	-2.7	+4.9	+11.2
Benefit:Cost Ratio	NA	0.29	0.07

Source: Adapted from Boynton et al. 1981. Printed with permission of Elsevier Science Publishing Co., Inc., Amsterdam.

*Economic values for Choptank River estuary given as 1978 U.S. dollars based on consumer surplus (Kahn and Kemp 1985).

[#]Relative impacts on agriculture and fisheries sectors of the regional economy were calculated as fraction of "gross sectorial product" (GSP).

[†]Change in energy throughput for agricultural or estuarine ecosystems given in units of 10⁹ kcal coal equivalents (Boynton et al. 1981).

estimates of economic and ecological trade-offs between agriculture and fisheries were made for selected management scenarios. Agricultural costs and estuarine benefits (compared to the present situation) are summarized (Table 6.1) for three such scenarios: (1) reversion back from 50% conventional/50% minimum tillage to 100%

conventional tillage; (2) 25% reduction in fertilization rates; and (3) 10% reduction of area in cultivation. While each of these scenarios would have some impact on herbicide and sediment loading to the estuary, the SEMM simulation results indicate that reductions in nutrient inputs are the primary effect that would benefit SAV.

We have estimated costs and benefits in economic ("surplus value") terms. Economic benefits and costs to each sector of the economy ranged from \$10,000 to \$900,000, and benefit:cost (B:C) ratios were always substantially less than 1.0 (Table 6.1). The impact on agriculture was at least three times greater than that on the estuarine resources. Given the preliminary nature of these analyses,

a cautious approach would call for management options with ratios approaching 0.3 to be further considered with improved data and analyses.

To place these values in perspective, we also calculated the relative impact of each cost or benefit on agricultural and fisheries sectors of the regional economy. This was done by dividing each cost or benefit value by the "gross sectorial product" for the respective sector (and multiplying by 100 to compute a percentage). It can be seen that, while the gross economic effects are greater for agriculture than for fisheries, the relative impacts on the regional sectorial economy are generally equal or greater for fisheries (Table 6.1). This latter view suggests that, while there might be short-term advantages (because of the benefits accrued to the farmer) in allowing agricultural wastes to diminish the value of estuarine resources, in the long run, it may be considered unfair for the smaller, estuarine-based activities to bear the burden of associated costs. Thus, the impact of agricultural wastes on the fishing industry and related human enterprises would be proportionally greater than the impact of changes in farming practices needed to reduce the losses of SAV from the estuary.

Benefit:cost ratios calculated in both economic and embodied energy terms suggest that the absolute costs to agriculture outweigh benefits to the estuary, although the effects of different scenarios were substantially different between energy and economic analyses. According to the embodied energy analysis, reductions in fertilizer use had three-fold higher B:C ratios than reductions in land used for agriculture. According to the economic analysis, reductions in farm land had a

three-fold higher B:C ratio than reductions in fertilizer use. This is because of the relatively inexpensive pricing of fertilizers. We conclude from this analysis that efficient, low-cost methods should be developed for reducing nutrient inputs to the estuary to levels that approximate conditions in 1960. Obviously, the choice of scenarios treated in

this chapter is limited and somewhat arbitrary; recent research results have identified other agricultural practices that could efficiently decrease nutrient loading to the estuary (e.g., Staver et al. 1989). Future analyses should consider a wider range of management options, and greater emphasis should be given to understanding the essential differences between economic and energy-based techniques.

Results of this study were reported to the U.S. Environmental Protection Agency's (EPA's) Chesapeake Bay Program in 1982, and they have been elaborated on in various papers published in the scientific literature (e.g., Boynton et al. 1981; Caffrey and Kemp 1990; Goldsborough and Kemp 1988; Kahn and Kemp 1985; Kemp et al. 1980; Kemp et al. 1983a; Kemp et al. 1983b; Kemp et al. 1984; Kemp et al. 1985; Kemp et al. 1995; Lubbers et al. 1990; Twilley et al. 1985; Twilley et al. 1986). Although it is impossible to measure the real impact of such research results on management decisions, the goals established in the 1987 Chesapeake Bay Agreement were completely consistent with results of the current study. This agreement, which was sponsored by the EPA and signed by governors of major watershed states, calls for a 40% reduction in nutrient loading to the estuary by the year 2000 (Smith et al. 1992). Such a decrease in nutrient inputs to the bay would create nutrient conditions similar to those in 1960 (cf. Figure 6.9).

Concluding Comments

In this chapter, we illustrate how we have integrated ecological modeling into a large research program to assist in the following scientific objectives (Odum 1983): (1) to organize and structure research activities; (2) to identify missing information or poorly understood relationships; (3) to formalize scientific hypotheses; (4) to interpolate and extrapolate from limited data bases; (5) to test sensitivities of model variables in relation to their real-world counterparts. While the ultimate success in meeting such goals can be judged only a posteriori, several pragmatic benefits have clearly evolved from our modeling effort. For example, the conceptual exercise associated with model development has provided a means for a productive dialogue among diverse research specialists to integrate varied information. As such, our models have served as formats for discussion. Furthermore, models at the conceptual level have helped to bridge the dichotomy between descriptive and experimental research objectives. Within the framework of our ecological models, the linkages between mechanistic processes and overall ecological structure have been made explicit, and these can be tested over time as the need arises. This integral role of ecosystem modeling in environmental research is part of a vision that H. T. Odum laid out for the research community more than 2 decades ago (Odum 1967; Odum 1971).

Others have also contributed significantly to the development of specific ecosystem modeling methods and approaches (e.g., Patten 1975; Watt 1975; Wiegert 1975).

These models have also served as tools for applying scientific understanding developed from field and laboratory research on SAV to address problems of managing the bay's resources. In general, it appears that there has been a reluctance among estuarine researchers to apply their research findings to management problems. Again it is H. T. Odum who has, since the mid-1960s, continued to urge his scientific colleagues to venture into the murky waters at this interface between science and management. Today, methodologies are being formalized for applying ecological concepts and energy analysis techniques to address these environmental management problems, and the seeds for this movement were clearly being sown by HTO 2 decades ago (Odum 1971). One of the many challenges that Odum's colleagues and students face for the coming decades is to contribute to the maturation of this process and to seamlessly integrate ecosystem modeling and energy analysis into the main streams of environmental science.

Acknowledgments

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