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Preface

The work described herein was conducted under Delivery Order DO12 of Task Order Contract DACW39-92-D-0003 by FTN Associates, Ltd. (FTN), Little Rock, AR, for the U.S. Army Engineer Waterways Experiment Station (WES), Vicksburg, MS. Funding for this work was provided by several specific WES work units in the Common High Performance Computing Software Support Initiative; the Zebra Mussel Control Research Program, Dr. Edwin A. Theriot, Program Manager; and the Ecosystem Management and Restoration Research Program, Dr. Russell F. Theriot, Program Manager. The coordinated effort was managed through the WES Ecosystem Modeling Institute (EMI). Dr. Robert H. Kennedy, Environmental Processes and Effects Division (EPED), Environmental Laboratory (EL), WES, served as lead Technical Contact for this work in his capacity as Director of EMI.

This report was prepared by Mr. Jack B. Waide and Dr. Lisa M. Gandy, FTN. The materials contained in this report resulted from a workshop held at the WinRock International Conference Center located on Petit Jean Mountain, Morrilton, AR, during the period of June 30 to July 3, 1997. Mr. Waide and Dr. Gandy planned and facilitated the workshop and recorded workshop discussions in collaboration with Dr. Kennedy. Others who contributed directly to planning for the workshop included Drs. Todd S. Bridges, Mark S. Dortch, John M. Nestler, and Richard E. Price, and Mr. Thomas M. Cole, EPED; Dr. Andrew C. Miller, Ecological Research Division, EL; and Dr. L. Jean O'Neil, Natural Resources Division, EL. Ms. Bernadette L. Frank and Ms. Tanas N. Schmidt, FTN, provided word processing support for both this report and all other workshop materials. Mr. Benny D. Baker, Manager, WinRock International Conference Center, provided onsite logistical support for the workshop.

This work was performed under the general supervision of Dr. Kennedy, Director, EMI, and Acting Chief, Ecosystem Processes and Effects Branch, EPED; Dr. Dortch, Chief, Water Quality and Contaminants Modeling Branch, EPED; Dr. Price, Chief, EPED; and Dr. John Harrison, Director, EL.

At the time of the publication of this report, Director of WES was Dr. Robert W. Whalin. Commander was COL Robin R. Cababa, EN.

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Overview of the Workshop on Aquatic Ecosystem Modeling and Assessment Techniques for Application within the U.S. Army Corps of Engineers

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Workshop Rationale and Purpose

Interest is increasing within the U.S. Army Corps of Engineers (USACE) in developing approaches appropriate to the management and restoration of aquatic and terrestrial ecosystems under the jurisdiction of Corps Districts and Divisions and located on Department of Defense (DoD) lands. Development and application of ecosystem management and restoration initiatives will require the USACE to develop improved ecological modeling capabilities, and associated assessment tools and approaches, that go beyond current capabilities in water quality and contaminant modeling. New modeling skills and specific models will be required in order to project and assess impacts of Corps activities and functions and related human actions on aquatic and terrestrial ecosystems, and their constituent biota and ecological processes, at multiple organizational levels and scales of space and time.

To further the development of expanded ecological modeling capabilities relevant to the Corps' ecosystem management and environmental stewardship missions, a workshop was organized and convened to identify and discuss promising and appropriate approaches to ecosystem modeling and assessment for application within the USACE. The workshop brought together scientists from the Waterways Experiment Station (WES) involved in ecological assessment and modeling projects, with scientists having extensive experience with diverse approaches to ecological modeling from universities, other federal agencies and national laboratories, and private consulting firms. The workshop was designed to be highly interactive, with short, focused presentations on specific topics by both WES and outside speakers, followed by extended time for discussing issues raised pertinent to the proposed new modeling initiative.

While the eventual goal of the work that will follow from this workshop is to develop broad ecosystem modeling and assessment capabilities useful in many potential applications, this work will be initiated by a "test case application" focused on evaluating aquatic ecosystem level impacts of zebra mussels at Corps projects. Zebra mussel impacts on water quality conditions, aquatic food webs and trophic dynamics, and other biotic species (*e.g.*, native unionid mussels, phyto- and zooplankton, fish) are of interest in this work, and provide the organizing conceptual basis for the proposed initial modeling activities. The desired modeling approaches that emerge from the workshop should go beyond current water quality and contaminant modeling capabilities; should be capable of being run in some applications coupled to existing water quality/contaminant models; and should include capabilities for modeling zebra mussel and other invertebrate (*e.g.*, filter feeding zooplankton species) and fish populations (both planktivorous and piscivorous species) at broader spatial scales and levels of

ecological organization than are captured in current models. To provide background for proposed modeling activities, workshop presentations were designed to review information on existing approaches to ecosystem modeling and assessment for aquatic and terrestrial environments, along with information on the biology and ecology of zebra mussels and their impacts (water quality, trophic dynamics, biotic composition) on aquatic ecosystems at Corps projects, and on possible linkages to existing capabilities in hydrodynamic and water quality modeling.

This new ecosystem modeling initiative is being conducted as a joint effort among several specific WES work units in the Common High Performance Computing Software Support Initiative (CHSSI), the Zebra Mussel Control Research Program (ZMRP), and the Ecosystem Management and Restoration Research Program (EMRRP). The coordinated effort is managed through the WES Ecosystem Modeling Institute (EMI).

Prior to the workshop, each participant and speaker received a packet of background materials that clearly explained the organization, rationale, purpose, and expected outcomes of the workshop; the sequence of topics included in the workshop agenda; and the expected outcomes and topics of the focused discussion sessions held during the course of the workshop. Each workshop speaker also received detailed guidance on their “assigned” topic and its relation to the overall workshop objectives.

Proceedings Volume Organization

Following this introductory paper discussing the broad purpose and rationale for this workshop, the proceedings volume contains 14 papers summarizing the ideas presented during the six distinct workshop sessions. These papers are followed by a summary and discussion of the main ideas and conclusions that emerged during the workshop discussions following the oral presentations. Appendix A contains the workshop agenda, while Appendix B presents a listing of the names and addresses of the workshop speakers and other participants.

Session 1 - The Institutional and Resource Management Context

Session Purpose

This initial workshop session was designed to provide background information to all workshop participants on the broad organizational context for the workshop, and on the resource management issues and challenges within the U.S. Army Corps of Engineers that motivate the proposed modeling activities and initiative. Discussions of session presentations focused on the USACE resource management challenge to manage and restore aquatic (and terrestrial) ecosystems; the contribution of models and related assessment tools to this process; and desirable characteristics and capabilities of models to be useful for this purpose.

The Challenge to Manage and Restore Ecosystems within the U.S. Army Corps of Engineers: a Corps-Wide Perspective

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The U.S. Army Corps of Engineers (Corps) takes its environmental mission very seriously. Over many years specific environmental programs and capabilities as well as an overall environmental ethic have been evolving within the Corps work force. The Corps now is a leader in many areas of environmental science. Wetlands, aquatic plants, constructive use of dredged materials, water quality, habitat restoration, land management, recreation, lake dynamics, and endangered species are just some of the environmental areas in which the Corps has been and is currently heavily involved. On a daily basis we have had to deal with conflicting uses of limited resources (primarily water). We have developed habitat-based approaches to protect and promote the restoration of populations of endangered birds, plants, mammals, insects, reptiles, and fish. We can successfully model much of the physical, some of the chemical, and a small part of the biological dynamics of lakes, reservoirs, rivers, major estuaries, and large segments of the near-shore ocean. These increases in environmental awareness, understanding, and capabilities within the Corps have been both incremental and measurable, and have created expectations for even larger accomplishments for the future.

In part as a direct consequence of past successes and accomplishments, the Corps is now being challenged to work on a larger scale, in both space and time, and in new environmental dimensions. Today's special challenge is to work and manage resources at the watershed scale and to consider not just individual species but especially entire ecosystems. This is a daunting task for a federal agency such as the Corps, especially considering that it along with most other federal agencies is in a downsizing mode.

In order to meet this new environmental and resource management challenge, Corps staff having environmental management responsibilities need new tools both to evaluate the condition and responses of existing ecosystems and also to design new ecosystems to meet specific management objectives. These tools must provide information on the value of the natural resources which the Corps is challenged to manage, and at the same time provide information on the value of the ecosystem management effort. Forecasting tools that provide some indication of the short- and long-term consequences of alternative management actions on an ecosystem scale are in great demand. We do not need additional micro-scale models such as those which already exist and are useful for managing a certain species rather than an ecosystem. Ecosystems are quite likely the most complex systems on this planet. Attempts to model systems of this complexity in great detail are not practical. Data needs are prohibitive and computational complexity and the information base necessary to develop highly detailed ecosystem models are currently beyond our present capabilities.

There are, however, alternate approaches to ecosystem modeling that should prove useful in relation to the current challenges faced by the Corps. Models that forecast overall ecosystem responses to various stresses or human actions on a fine scale are achievable today. The problem is that we (society) usually don't ask for information on ecosystem response. Rather, we want information concerning the response of (our favorite) species to some planned or existing stress. I suspect that if models were available that could predict the responses of entire ecosystems in terms of how species distribution and diversity might change in relation to various stressors, they would be quite valuable to our environmental decision makers.

At one geographical scale of analysis, there are 2,149 major watersheds in this country. A management tool that could give watershed managers a good sense of the consequences of any actions (stresses) taken within a watershed or an ecosystem would be of great value. I believe that it is possible to develop a modeling capability that will answer, in a defensible and quantifiable way, many of the basic ecosystem/environment questions faced by resource managers in the Corps and other agencies. The challenge is not simply to be able to manage Corps project lands and waters, but to manage Corps project lands and waters with a scientifically derived watershed scale perspective that balances project purposes against sustainable ecosystem functions. Development of a suite of tools that can meet this challenge will move the Corps to the forefront of environmental engineering and should generate a significant demand for Corps expertise and talent to model and assess the condition and dynamics of watershed scale ecosystems.

It is essential for the Corps to maintain a work force that is environmentally knowledgeable so that our models do not lead us or others astray. In responding to the challenges summarized above, we should remember that the stated mission of the Corps Civil Works Program is:

> "the mission of the Civil Works Program of the U.S. Army Corps of Engineers is to promote prosperity and democracy and to strengthen national security through the development, management, protection and enhancement of the Nation's water and related resources for flood damage reduction, commercial navigation, environmental restoration, and allied purposes. This program is accomplished by applying the Corps planning, engineering, scientific, and management skills, in cooperation with non-Federal sponsors, Federal, state, and local agencies, and other interested stakeholders, to achieve productive, efficient, responsible solutions to water resources problems. The Program provides for responsible stewardship of its water resources infrastructure including the associated natural resources and provides emergency services the Nation for disaster relief. The Civil Works Program also provides planning, engineering, environmental, recreation, research, and real estate services to other Federal agencies and non-Federal customers, provides support to the Army in both peacetime pursuits and during national emergencies, and stands ready to adapt to evolving national needs and priorities. The Corps, moreover, plays a major role in the protection of the waters of the United States, including wetlands, by regulating the discharge of dredge and fill material into the Nation's waters."

The Challenge to Manage and Restore Ecosystems within the U.S. Army Corps of Engineers: a Research Scientist's Perspective

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Introduction

The primary mission of a research scientist or engineer at the U.S. Army Engineer Waterways Experiment Station (WES) is to conduct research and development (R&D) of technologies which assist the U.S. Army Corps of Engineers (USACE), the Army, and the Department of Defense (DoD) with execution of their respective missions in the nation. The perspective of the individual scientist or engineer is guided not only by the technical discipline and current state of development, but also by the organization, structure, and management of the research organization itself. This paper provides an overview of the major factors influencing research scientists and engineers in the execution of R&D for environmental quality technology, and examines the research environment from an individual scientist's or engineer's perspective, as well as in relation to R&D strategies and to challenges for scientists and engineers in the execution of R&D projects.

Research Environment

The research environment affecting scientists and engineers at WES is defined by a number of factors, including the type of research (basic versus applied), the specific research problems or needs of R&D sponsors, the method of funding, and the organizational structure of the agency. Each of these factors in turn is related to the research environment in which the individual scientist or engineer must function. These factors are not listed in any priority order, although each is important to the R&D mission.

The type of research conducted at WES is best defined as applied, with some problems requiring basic research prior to development of a product. Within the context of this paper, basic research is defined as that research which leads to new knowledge about a particular phenomenon, not necessarily resulting in a tangible product a sponsor can use directly. Applied research is defined as that which utilizes existing knowledge for a new or different application and results in a specific product for a defined user.

Within the Army Civil Works program, R&D is conducted to develop tools and products that effectively address planning, construction, operation, and maintenance of civil works projects. In the Environmental Quality area, there are needs for R&D for modeling, simulation, and assessment tools for water quality, control of aquatic plants, wetland restoration, and assessment of the effects of watershed activities on project operations. Within the Army

Cleanup and Conservation Pillars, there are needs for modeling and simulation tools for threatened and endangered species, land carrying capacity, land rehabilitation and erosion control, training area management, and contaminant fate and transport. Army environmental managers need specific tools which provide them with the means to model, simulate, or in some other way assess impacts of some activity or change in operations on the natural environment. In terms of the research conducted, the Army manager is not as concerned with how the modeling, simulation, or assessment tool functions as they are with making sure the product addresses their situation and can be delivered in a time frame that fits within the defined project schedule.

Research at WES is focused on problems that are inherently governmental. This precludes competition with academic and private sector organizations engaged in both basic and applied research. Problems that are inherently governmental include those which relate to the specific mission of the Army, such as the cleanup of contaminants at Army installations or the assessment of environmental impacts associated with a change in operation of a flood control project. Although there may be similar R&D efforts underway in academia or the private sector, the unique nature of some of the contaminants, such as explosives, or the operation of large, complex flood control projects are unique to the agency and the federal government.

Funding for R&D is typically referred to as “soft” funding, due the fact that salaries for individual scientists and engineers, travel, and other research costs are not line items in the federal budget. Some R&D needs that are national in scope, such as control of nuisance aquatic vegetation, are funded as a line item in the federal budget. These programs are typically broken down into individual work units, which are assigned to individual scientists and engineers for execution. Problems that are regional or local are usually defined as “reimbursable” and are funded by an individual USACE District or DoD military installation. Products from these projects are applied to a specific problem or need which is closely tied to a specific project function or operation.

One final factor that influences the research environment is the stability of the research organization. As a federal agency, the Army has a long history within this nation, and continues to support the nation through its stewardship of sustainable resources. The WES, as one research laboratory within the Army, was established over 60 years ago and continues to support the Army with innovative R&D products. In this era of downsizing and reducing federal expenditures, the WES will continue to adapt to changing needs for environmental quality R&D.

R&D Strategies

The broad R&D strategy for the Army is derived from the “Statement on the Posture of the United States Army” developed by the Honorable Togo D. West and General Dennis J. Reimer. Within their strategy, the WES performs R&D in two major arenas, military and civil works. In the military arena, the primary focus is on tools that assist environmental managers in the management of sustainable resources. This stems from an earlier strategy entitled “The

Environmental Quality Strategy for the 21st Century," which provided a structure for environmental management that is supported by four "pillars": cleanup, conservation, pollution prevention, and compliance. The R&D component for each of these pillars contains needs for modeling, simulation, forecasting, and assessment tools. A procedure has been developed that links users of R&D technology with scientists and engineers from both Army laboratories and headquarters level management to ensure that R&D is directed at high priority military needs. In this process, the perspective of the individual scientist and engineer is molded by the user not only to understand the R&D need but also to appreciate how the specific product is to be used.

In the civil works arena, an "Environmental Quality Research Area Strategic Plan" has been developed by WES that links environmental focus areas into a common framework. This plan was developed around an ecosystem approach to watershed management, and supports research related to water quality, environmental restoration, natural resource management, and regulatory needs. This strategy emphasized technology application using risk-based approaches for development of decision support tools and models. It is also operations- and maintenance-oriented.

Challenges for the Individual Scientist and Engineer

The challenges that face the individual scientist and engineer in the conduct of their respective R&D programs are not necessarily unique to Army laboratories. In some respects, such as the clarity of the research need, timeliness of the product, and technology transfer, similar challenges are faced by scientists and engineers in academia and industry as in the federal sector. There are other challenges in the federal sector as well, such as the need to distinguish between R&D and policy, the fact that some problems require multidisciplinary approaches to product development, and the need to show a return on R&D investment.

The clarity of the defined research need is probably the most difficult task for the scientist and engineer. In some cases, the user may not be able to define the problem clearly, or may define it in such broad terms that extensive resources and time would be required to accomplish the task. For example, a resource manager may need an ecosystem model to address the likely effects of project operation on the environment. Although this is a real concern, the manager must clearly define the target ecosystem, project boundaries, operational alternatives, and the impacted environment. If the manager can identify specific parameters and endpoints, a the scientist or engineer can usually provide a specific scope of work that addresses his needs. The more clearly the user can specify the problem and controlling parameters, the better the scientist or engineer can define the R&D needed to produce a product for the user.

The timeliness of product delivery to the user is particularly relevant to declining federal budgets. Although the pace of research may not coincide with the needs of users and resource managers, the role of the scientist or engineer is to identify R&D which can be accomplished within a time frame that will provide the user with a meaningful product. In the past, criteria for prioritizing research needs consisted of factors such as the ability to solve a particular research

problem within a 3 to 5 year time frame. With research programs of national scope, longer term projects are possible. However, with reimbursable projects, the time frame for producing a product may extend from several months to many years. In these cases, direct involvement of the user in the project is key to generating a timely product.

The transfer of technology to the user is a critical process in validating R&D projects. In the case of direct allotted research programs, technology is transferred to a broad audience, usually national in scope. In some cases, the individual scientist or engineer may not know or interact with the ultimate end user of the product. Technology is disseminated through a variety of media, such as written reports, models, and databases. However, reimbursable projects usually have a clearly identified user who monitors R&D progress and ultimately uses the product in his decision making process. In these cases, the transfer of the product is most effective because of ongoing interaction between the project scientist or engineer and the end user.

Some R&D needs as stated by users are controlled more by policy than technology. For example, the management of water levels in a flood control project is driven by many concerns, including the need for hydrologic storage, environmental concerns, riparian rights, and others. How to blend all of these concerns into a decision making tool is a valid R&D need; however, the setting of priorities among the various concerns becomes a policy issue which is outside the mission of the R&D community. In another example, the use of risk assessment procedures is an accepted method for environmental impact assessment. The communication of the risk assessment to the public is a critical part of the assessment; however, at present, public communication of risk is not a defined R&D need.

Many of the problems and research needs address issues that require multidisciplinary approaches for their solution. As the complexity of the research need increases, the number of disciplines required to address the problem also increases. In the example of the flood control project used above, the concerns with water level management would involve hydrology, hydraulic engineers, ecologists, wetland scientists, and other environmental scientists to develop an assessment tool to evaluate various project alternatives. As the number of concerns associated with ecosystem and watershed level impacts increases, the need to involve multiple disciplines in the R&D becomes more critical.

In recent years, the funding for R&D efforts has become tighter. In addition, sponsors are requesting information from scientists and engineers that demonstrates the economic return on the R&D investment. In some areas where the costs of a particular environmental concern can be readily and reliably quantified, this analysis of return on investment is possible. For example, costs associated with mitigation projects can usually be determined. In fish impingement studies, the cost of a fishery can be determined by a resource agency. R&D to determine more efficient project designs which minimize fish impingement can be compared directly to the cost of the fishery for a return on investment analysis. In the case of regulatory requirements, such as maintaining a minimum dissolved oxygen concentration in reservoirs, the

cost for not achieving the desired concentration can not be easily determined. Without this, a rigorous return on investment analysis is not possible.

Conclusions

The mission of individual scientists and engineers at WES is to conduct R&D to develop technologies that support the agency (*i.e.*, USACE, Army, DoD). In relation to the execution of this mission, a number of factors affect the research environment, including type of research, agency mission, funding source, and stability of the organization. WES scientists and engineers must also conduct R&D in the context of broad strategies developed by Headquarters elements of the organization, while facing challenges such as unclear definition of research needs, producing timely products, ensuring adequate technology transfer, distinguishing between policy and research issues, incorporating multiple disciplines in R&D projects, and demonstrating a good return on the R&D investment. The magnitude of these challenges is only increased as the scale of environmental management is enlarged to deal with concerns regarding the management and restoration of ecosystems under the jurisdiction of USACE Districts and Divisions and DoD installations.

Need for an Expanded Ecosystem Modeling and Assessment Capability in the U.S. Army Corps of Engineers: An Ecologist's Perspective

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Introduction

The U.S. Army Corps of Engineers (USACE) has traditionally performed engineering-related tasks in a variety of civil works activities and in support of the military. Civil works activities have historically involved water resource development, including the design, construction, and operation of dams and waterway features. Since most operational projects (and the lands that border them) are now authorized as multiple use environmental resources, recent civil works activities have included a growing role for the USACE in environmental restoration and management. This often raises difficult management issues related to regulatory compliance and environmental policy. For example, the Marine Protection, Research and Sanctuaries Act of 1972 requires that dredging activities in coastal shelf regions be designed and conducted in ways that minimize the effects on "... marine life, including ... changes in marine ecosystem diversity, productivity and stability; and species and community population changes." Similar statutory requirements were established for near-shore coastal areas by the Clean Water Act of 1977 (minimize effects on "potential changes in marine ecosystem diversity, productivity and stability; and ... species and community population dynamics").

Similar environmental management challenges are faced by those responsible for using and managing military lands. For instance, military commanders are concerned about maintaining training realism (*i.e.*, characteristic vegetative cover, topographic features, etc.). The central question for military training commanders is - at what point will training impair or compromise the training landscape? A related suite of questions must be addressed by the natural resource manager. How can the training landscape be maintained to prevent unacceptable degradation or be restored after it has been degraded? What costs will be associated with maintenance or restoration? Will training activities result in regulatory violations? Will threatened or endangered species be impacted?

Ecosystem Modeling and Assessment

The challenges of addressing the above questions are not trivial nor are many established or well-accepted methods for doing so available to managers. While the USACE has developed and successfully applied state-of-the-science numerical tools for describing and predicting hydrodynamic phenomena, material transport, and water quality in reservoirs, rivers, and estuaries, similar tools for other environmental settings are less well developed. In addition,

currently employed tools for assessing aquatic ecosystems (*i.e.*, 'water quality' models) lack appropriate portrayals of important biological (*e.g.*, reproduction, recruitment, etc.) and ecological processes (habitat preference, successional change, etc.) relevant to many current environmental issues.

Thus, sound management will require development of tools that provide defendable assessments and simulations of biological and ecological outcomes for a variety of environmental settings (terrestrial, aquatic, and mixed landscapes), and across a range of spatial and temporal scales. In general, assessment and modeling tools should allow the linkage of spatial descriptions of landscapes, developed from field data or models, and models describing biological and ecological events (Figure 1). Linkages must resolve significant differences in our understanding of ecological events and the physical processes which influence the spatially complex environmental setting in which they occur. Also to be resolved are equally important differences in modeling approach (*e.g.*, deterministic versus stochastic).

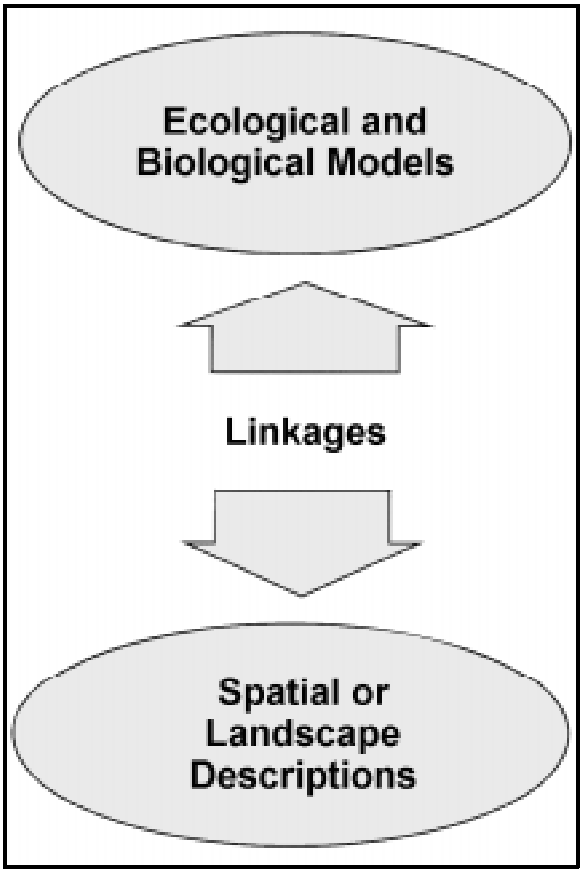

Figure 1. Generalized model linking ecological events with spatial complexity.

Developing a Modeling Approach

The relatively recent invasion of North American inland waters by the zebra mussel (*Dreissena polymorpha*) raises a number of difficult management issues relevant to water resource projects operated by the USACE. Physical obstruction of water intakes and withdrawal structures, and accretion of large masses of zebra mussels on structural surfaces (*e.g.*, gates, lock walls, trash racks, etc.), can severely impact project operation and increase maintenance costs. The introduction of zebra mussels to lakes and reservoirs can also alter their ecological structure and function. For instance, zebra mussels modify nutrient cycling in the overlying water column by filtration and excretion, impact dissolved oxygen concentrations through respiration, increase water clarity by particle filtration, and accumulate contaminants. Zebra mussels can also influence pelagic trophic dynamics by consuming reduced carbon, in the form of algal cells and filterable organic detritus, or by shunting it to the sediments as pseudofeces.

The USACE's ongoing efforts to better understand factors influencing zebra mussel demographics, to assess impacts on water quality, and to design and implement effective control strategies, provide an opportunity to develop and evaluate numerical methods for simulating or predicting zebra mussels and their ecological interactions. Current hydrodynamic and water quality models provide the capability to simulate physicochemical and selected biological (*e.g.*, changes in total phytoplankton biomass) events. Coupling water quality models, which provide a spatially and temporally explicit description of environmental conditions, and models describing selected aspects of zebra mussel biology and ecology events (Figure 2), provides a realistic means to describe both water quality impacts and trophic interactions. This approach also provides, in a general sense, a robust template for addressing a variety of ecological issues requiring an understanding of the interplay between biological events and spatial complexity of the environment.

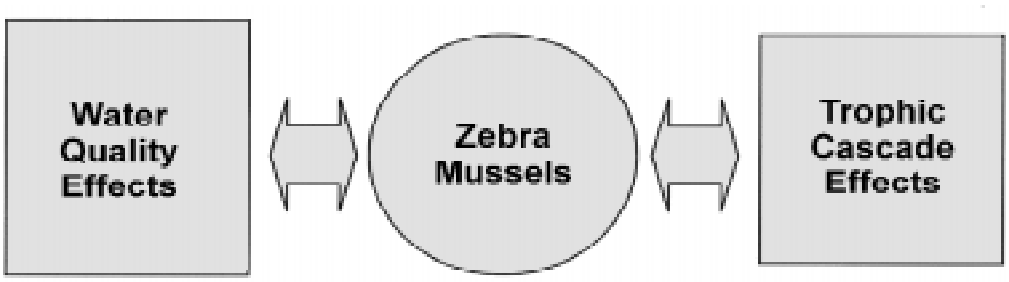

Figure 2. Generalized model of the environmental impacts of zebra mussels.

Going Beyond Current Water Quality Modeling Practices to Assess Ecosystem Impacts - A Modelers's Perspective

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Overview of Current Water Quality Modeling Approaches

The current state of water quality modeling is briefly reviewed as background for a discussion of future directions in the modification of these models for addressing ecosystem impacts. Current mechanistic water quality models are based on the principle of mass balance. For aquatic systems, the mass balance principle is developed within the Reynolds transport theorem which relates changes in solute mass or concentration with respect to time and space, to the movement of water, *i.e.*, to advection and diffusion. Reaction terms are included in the transport equations to account for changes in mass due to chemical transformations and transfers involving biological components. In most cases, an Eulerian reference frame is used whereby concentrations of constituents of interest can be observed at any specific location as the water passes by the viewer. The dimensionality of water quality models varies from simple zero dimensional screening-level models to comprehensive three dimensional (3D) models. Models may be time-varying or steady-state.

Water quality transport requires knowledge of the water currents and circulation. This information is usually generated with a hydrodynamic model. The hydrodynamics may be simulated within the same computational code as the water quality model, or they may be computed externally with another code and supplied as input to the water quality model.

Water quality models require boundary conditions for tributaries, point and non-point source loadings, and other potential inputs of mass, such as atmospheric loadings. Other boundary interactions must be accounted for, such as exchanges across the air-water interface for heat, solar radiation, and gas exchange, and across the benthic sediment-water interface for nutrients, dissolved oxygen, and contaminant fluxes. Modeling has progressed to the state that these boundary interactions are now simulated rather than being specified as boundary conditions.

Water quality models require observations with which to compare model results during calibration. The mechanistic relations of water quality models are not fully closed, meaning that modeled processes are not described well enough to allow accurate simulation of observations without adjustment of specified model parameters. Thus, most water quality models still contain some degree of empiricism. In contrast, 3D hydrodynamic models with turbulence closure routines contain very little, if any, empiricism. Thus, these models leave little room for parameter adjustment and generally provide accurate results if the system geometry and boundary conditions are properly specified.

The U.S. Army Engineer Waterways Experiment Station (WES) provides technical capabilities to the U.S. Army Corps of Engineers for water quality and contaminant modeling. This mission has required the development, maintenance, and application of a wide variety of models. Models are available for the study of contaminants (*e.g.*, toxic organics and trace metals), as well as for conventional pollutants and eutrophication. Both long-term fate and transport and short-term accidental spill models have been developed and utilized. All types of water bodies have been modeled, including reservoirs, streams, estuaries, waterways, harbors, coastal zones, wetlands, and watersheds. Additionally, groundwater models are being developed and used to assess remediation strategies.

WES has developed a series of water quality models for surface waterbodies that range from one dimensional models of rivers and reservoirs to 3D estuarine models. Models for conventional pollutants generally include physical variables, such as temperature, salinity, and suspended solids, multiple phytoplankton groups, dissolved oxygen (DO), various forms of carbon, nitrogen, and phosphorus, silica, light climate, pH-alkalinity-inorganic carbon equilibria, and detritus. In recent years, several of the models have been enhanced to include simulation of benthic sediment diagenesis and DO and nutrient fluxes across the sediment-water interface. Additionally, several living resource compartments have been added as discussed below.

Existing WES water quality and contaminant models provide a solid basis for simulating hydrodynamics, transport, and physical variables, such as temperature and salinity. In most cases the models also do a good job of simulating DO. Available models do a fair job of simulating phytoplankton dynamics and nutrient concentrations, although these variables are not computed nearly as accurately as are physical variables and DO. Future developments in water quality models should provide less parameterization and more mechanistic closure. For example, the nitrification rate constant is generally specified as an input parameter in current models and is adjusted to bring the model into agreement with observations. The preferred approach would be to simulate the nitrification rate as a function of spatially and time-varying environmental conditions that affect nitrification. However, the latter approach requires a more complete understanding of the various processes affecting nitrification and the associated closure equations.

Most existing water quality models tend to under-predict carbon fixation in aquatic ecosystems, possibly due to nutrient recycling rates being too low. This problem may also stem from the choice of mathematical relations used to describe phytoplankton production, which are based on Monod (*i.e.*, saturation uptake) kinetics, or perhaps from an inadequate understanding of phytoplankton nutrient recycling processes. It appears that this problem must be resolved before water quality models can be advanced significantly to assess many types of aquatic ecosystem impacts.

Future Model Developments Required to Assess Ecosystem Impacts

The major problem with water quality models, the primary topic that stimulated this paper, is the general lack of linkages in current models to higher trophic levels. Traditionally, results from water quality models have been used indirectly to infer impacts on living resources. The assessment of ecosystem impacts could be improved substantially if water quality state variables and state variables describing living resources were to be dynamically coupled.

A primary issue for debate in regards to future model developments concerns what types of living resource models to link with water quality models and how to link them. There is a wide range in types of ecological models, including models of habitat relations, bioenergetics, population dynamics, individual responses, ecosystem trophic networks, ecosystem processes, and mixtures of model types. The WES experience in ecological modeling is mostly aquatic and mechanistic, based on mass balance considerations. WES also has experience in habitat modeling (*e.g.*, IFIM and HSI). Higher trophic levels have been included directly within WES water quality models using the mass balance principle and mechanistic process descriptions. A prime example is the WES model of Chesapeake Bay. Initial modeling of Chesapeake Bay involved 22 state variables, including various forms of carbon and nutrients and three phytoplankton groups. This model was initially developed to assess the effectiveness of watershed nutrient reduction strategies for reducing anoxia and phytoplankton blooms in the Bay. The model was later extended to include 31 state variables in order to assess the effects of nutrient reductions on living resources, including submerged aquatic vegetation (SAV), benthos (deposit and filter feeders), and zooplankton (micro- and meso-zooplankton). These living resource compartments are biomass based and include relations for production, metabolism, and predation. However, this model does not include processes related to reproduction or succession.

Simple mass balance models of living resources are not sufficient to address complex ecosystem impacts. Perhaps a combination of modeling approaches, such as mass balance models linked to population or individual models, would offer the best hope of simulating the interactions among water quality conditions, habitat, and living resources. Such linkages will require development of common currency for exchanges of information among the different model and state variable types.

Conceptual Issues Underlying Development of New Approaches to Modeling and Assessing Human Impacts to Aquatic and Terrestrial Ecosystems for Application within the U.S. Army Corps of Engineers

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Précis

The primary issues discussed at this workshop essentially pertain to the use, within the U.S. Army Corps of Engineers (USACE), of mechanistic or process-based models to predict and assess human impacts to aquatic and terrestrial ecosystems, and their constituent biota and ecological processes, across a range of organizational levels and scales of space and time. This paper develops and discusses a set of issues that will, in part, provide the conceptual foundation and motivation for the development of new, ecologically based models and modeling approaches that contribute to and support ecosystem management and restoration initiatives within the USACE.

Context for Current Discussion

The ability to predict and assess the responses of ecological systems of interest to natural (*e.g.*, major storm events) and human (*e.g.*, air and water pollution, habitat alteration, species introductions) disturbances, and indeed the ability to manage natural resources and ecosystems successfully, rests on a sound understanding of the dynamics and organization of the ecological systems of interest at appropriate organizational levels and scales of space and time. It also depends critically on a fundamental understanding of the physical and biological processes that determine or regulate observable ecosystem dynamics and responses, of interactions among these processes, and of the spatial and temporal scales and organizational levels at which these processes operate to regulate ecosystem dynamics.

Attempts to understand linkages between underlying physical processes and factors, and biological or ecological patterns and processes, at specific scales of space and time, are at the foundation of ecology and the environmental sciences. Individual organisms, populations, and entire assemblages of interacting species populations respond to and in turn influence their physical, non-living environment. Interactions between physical and biological processes and components of ecological systems lead to recognizable and repeatable patterns of ecological organization at definable spatiotemporal scales (Waide 1995). Sound management of ecological

systems, and the natural resources embedded within them, requires both understanding and, to some degree of accuracy, prediction of interactions among key system processes, and of system dynamics and responses to disturbance, both natural and man-induced. This joint task of understanding and prediction is made difficult by the fact that ecosystem dynamics and responses to disturbance are governed by numerous biological and physical processes, some of which are only poorly understood, that span multiple organizational levels and multiple scales of space and time.

Over the past quarter century, mechanistic or process-based models have become useful and regularly applied tools for managing ecosystems and evaluating their likely responses to diverse human actions. The utility of such models is fundamentally defined by the specific process formulations incorporated into model structure, and by the degree of resolution and understanding reflected in model formulations of relevant processes. The predictive ability and management utility of current management- or assessment-oriented models is limited by the lack of detailed understanding and resolution of many key processes important to the prediction of relevant system dynamics. While many environmental processes of interest (*e.g.*, physicochemical transport and transformation processes) are relatively well-described by available mechanistic models based on extensive underlying theory and knowledge, significant limitations exist in developing and implementing appropriate formulations for many other processes, particularly many biological or ecological processes that operate over long time frames and across large spatial domains. Improved understandings and formulations, for example, of select demographic processes, competitive and prey/predator interactions, trophic dynamics, energy capture and storage, biogeochemical cycling, and other ecological interactions are required for effective management and simulation of ecological systems and resources. These model shortcomings are exacerbated by the understanding that many resource and ecosystem management issues require descriptions or predictions of system attributes and responses across multiple levels of ecological organization (*e.g.*, local population, metapopulation, local multi-species assemblage, ecological landscape) and across multiple scales of space and time. These problems represent significant sources of uncertainty in current ecological models and process formulations. However, most existing models lack the ability to evaluate significant sources of uncertainty and their consequences for resulting model predictions and management decisions.

The essence of the issues which the present workshop was designed to address concern the development of new models and modeling approaches, that are richer in biological/ecological detail and based on the formulation of a broader array of biological and ecological processes, and that are specifically designed to be useful for predicting and assessing human impacts to aquatic (and terrestrial) ecosystems and biota, across an array of organizational levels and space-time scales. The USACE, through work funded at its research laboratories such as the U.S. Army Engineer Waterways Experiment Station (WES), has invested significant resources in development, testing, and application of an array of models useful for addressing water quality and contaminant problems in diverse surface water environments (*e.g.*, see Dortch this volume). These models have proved to be extremely useful tools relative to the specific purposes for which they were developed. But, these models generally do not contain sufficient details and resolution of key biological and ecological processes to be useful for assessing

human impacts to aquatic ecosystems, biota, and processes at appropriate scales and organizational levels, and for responding to new ecosystem management challenges faced by the USACE.

Thus, new models and modeling approaches are required for managing ecological systems and resources, and for assessing human impacts to aquatic and terrestrial ecosystems, within the USACE. Such models and modeling approaches should: (1) incorporate and provide detailed resolution of relevant biological and ecological processes, and their couplings to pertinent physicochemical processes; (2) facilitate analyses of ecosystem dynamics and responses to human actions across a range of appropriate spatial and temporal scales; and (3) include specific methods (*e.g.*, Monte Carlo simulation capabilities) for evaluating major sources of uncertainty in model predictions, and their consequences for resource/ecosystem management and impact assessment. While initially developed and implemented for a specific suite of ecosystem management/impact assessment issues and for a specific ecological system, the selected modeling approach should be adaptable or generalizable across the range of natural resource/ecosystem management and impact assessment issues, as well as the array of ecological settings, of relevance to USACE and Department of Defense (DoD) missions regarding environmental stewardship and ecosystem management and restoration.

Purpose and Approach for Current Discussion

Our purpose in this contribution is to present and discuss a set of issues that will, in part, provide the conceptual foundation and motivation for ecologically enhanced approaches to modeling and assessing human impacts to aquatic ecosystems within the USACE. We do so by first reviewing a series of "case study" examples, that typify the sorts of large scale resource/ecosystem management challenges currently being faced by the USACE as this agency deals with the management and restoration of aquatic and terrestrial ecosystems under its jurisdiction. Each ecosystem management case study is discussed in terms of (1) the goal or objective of the project under review, (2) the key ecosystem or resource management challenges involved in the project, and (3) the modeling issues and requirements that pertain to the project. Based on this analysis of a limited set of pertinent ecosystem management case studies, we then synthesize a set of conceptual issues that will, in part, motivate development of the enhanced modeling skills and initiatives required to assess human impacts to aquatic ecosystems, biota, and processes, at multiple levels of ecological organization and scales of space and time.

The five specific ecosystem management case study examples discussed here with reference to the USACE are:

- assessing (non-contaminant) human impacts to eelgrass beds and associated faunal communities in the San Diego Bay Ecosystem;
- Upper Mississippi River-Illinois Waterway System (UMR-IWWS) Navigation Study;
- ecological restoration of the Kissimmee River, Florida;
- restoration of salmonid fishes to the Columbia-Snake River Basins in the Pacific Northwest; and
- assessing zebra mussel impacts to aquatic ecosystems at USACE projects.

Discussion of Ecosystem Management Case Study Examples

Case Study 1: Assessing (Non-Contaminant) Human Impacts to Eelgrass Beds and Associated Faunal Communities in the San Diego Bay Ecosystem

The specific goal or objective of this project is to evaluate (non-contaminant) human impacts on the growth, location, and habitat quality of eelgrass beds, and on associated faunal communities (fish, Least Terns, lobsters, mussels), in the San Diego Bay Ecosystem (Monitoring Subcommittee 1993, Waide 1996). This project was originally envisioned as providing the initial test case for the development of the new, ecologically enhanced modeling approaches under discussion at this workshop, with funding from the DoD Common High Performance Computing Software Support Initiative. Changes in available funding under this and other WES programs led to the decision to re-focus initial model development activities on zebra mussel impacts at USACE projects.

This project poses a number of specific resource/ecosystem management challenges and issues relevant to the present discussion, including:

- There is broad multi-agency interest and involvement in this project, including significant contributions from the DoD/Navy (specifically, NRaD Environmental Sciences Division, a key USACE partner and sponsor for related work), WES, the National Marine Fisheries Service (NMFS), numerous local agencies (*e.g.*, County of San Diego), and several universities (University of California-San Diego, San Diego State University).

- Within the San Diego Bay ecosystem, major ecological concerns are focused on impacts of specific stressors and habitat variables on eelgrass beds and associated faunal communities; primary stressors of interest within the bay ecosystem include algal and non-algal turbidity, suspended sediments, salinity, wind/wave/current action, light, space, depth, and nutrients, as influenced by diverse human activities in the bay, particularly activities at the Navy shipyard and non-point source pollution (NPS) inputs to the bay from its surrounding watershed.

- At local and intermediate spatial scales, major ecological concerns focus on the spatial distribution and local dynamics of eelgrass beds, specifically their location, extent, spatial distribution, productivity, growth form, and habitat quality for associated faunal communities.

- At larger spatial scales, concern exists in respect to factors regulating landscape patterns of eelgrass beds in relation to habitat features within the bay ecosystem; these concerns motivate a metapopulation context for understanding eelgrass dynamics.

- Competition for space (propagule establishment and development) between eelgrass and several mussel species is a concern at finer spatial scales.

- At larger spatial scales within the bay ecosystem, management concerns focus on ecological couplings between eelgrass dynamics and the dynamics of select faunal populations and communities, including a nesting population of Least Terns, lobster, numerous species of fish, and mussels (both native and introduced).

This array of resource and ecosystem management issues and concerns defines a series of specific requirements and needs for a suite of models useful for assessing human impacts to and managing ecological resources within the bay ecosystem, including:

- Such models should reflect a strong coupling, at fine spatial scales, of eelgrass dynamics to transport processes and morphometry within the bay ecosystem.

- Models useful for this effort should contain explicit formulations of demographic and bioenergetic processes within individual eelgrass beds, with specific focus on processes regulating eelgrass productivity and decay, biomass, growth form, and stem density.

- Eelgrass dynamics within the large-scale bay ecosystem should be formulated in a broad metapopulation context, with explicit attention to eelgrass reproduction, propagule dispersal, establishment, competition for space, and landscape patterns.

- Useful models should formulate relevant processes in a spatially explicit manner.

- Relevant models should reflect the coupling of eelgrass dynamics, at large spatial scales, to the productivity and dynamics of various faunal populations and communities of interest, including mussels, lobster, Least terns, and fishes.

- The suite of models useful for evaluating human impacts to eelgrass-based systems within the bay ecosystem should involve the explicit formulation and coupling of models across distinct space/time scales and organizational levels: At a fine scale, eelgrass dynamics should be coupled to transport processes and water quality variables. Models formulated at intermediate spatial scales should focus on the local dynamics of eelgrass beds. At larger spatial scales, models should formulate eelgrass dynamics in a metapopulation context as well as couplings to specific faunal species. Thus, the modeling system designed for this project should be capable of simulating the dynamics of the bay ecosystem across overlapping spatial scales, from fine scale transport and water quality processes, to the dynamics of local eelgrass beds at intermediate scales, to large-scale “landscape” processes operating over the entire bay ecosystem.

Case Study 2: Upper Mississippi River - Illinois Waterway System (UMR-IWWS) Navigation Study

The specific goal or objective of this second example project is to evaluate ecological impacts of increased navigation traffic in the UMR-IWWS, with results of on-going analyses to serve as input to an Environmental Impact Statement being prepared by the USACE for

Congress. The resource/ecosystem management challenges posed by this project of relevance to the present discussion include the following issues and concerns:

- As was true for the project discussed above, this project is characterized by broad multi-agency interest and involvement, including several USACE Districts (St. Paul, Rock Island, St. Louis), WES, U.S. Fish and Wildlife Service (USFWS), USDI-GS Biological Resources Division (USDI-GS/BRD), and resource management agencies in several states.

- Major analyses are under way to evaluate impacts of increased barge traffic on mortality and survivorship of both larval and adult fish, including both direct mortality and mortality mediated through the aquatic food chain, as well as impacts on fish reproduction and recruitment, particularly those impacts that are largely habitat mediated.

- Other analyses are attempting to evaluate impacts, largely due to altered hydrodynamics and sediment resuspension/transport, on the physiology, growth, and survivorship of mussels, as well as on the spatial location, distribution, and establishment of mussel beds within the waterway system.

- A final set of analyses is focusing on evaluating impacts of increased navigation traffic on demographic (fragmentation, uprooting, and mortality resulting from wave action) and bioenergetic (growth and physiology, as impacted by sediment resuspension and transport) processes in aquatic vegetation, as well as on the spatial location, distribution, and establishment of aquatic vegetation beds throughout the waterway system.

The suite of models useful for addressing this array of resource and ecosystem management challenges in the UMR-IWSS should be structured in response to the following modeling issues and needs:

- Models should reflect a strong coupling of pertinent biological processes to transport and water quality variables and processes at fine spatial scales.

- Models should include explicit formulations of both demographic and bioenergetic processes for specific populations of fish, mussels, and aquatic vegetation.

- The suite of models developed for this project should reflect an overall metapopulation context for evaluating landscape scale dynamics of mussel and aquatic vegetation beds.

- Models should include the formulation of relevant biological processes in a spatially explicit manner.

- The suite of models assembled for this effort should be formulated across multiple spatial scales, including both local and landscape scale dynamics of mussel and vegetation beds,

and should develop procedures for translating model results or coupling models across several pertinent spatial scales.

Case Study 3: Ecological Restoration of the Kissimmee River Ecosystem, Florida

The specific goal or objective of this large-scale ecosystem restoration project is to restore the Kissimmee River from its current state as a channelized river to a state approximating its historical condition as a flowing, meandering, river-floodplain-wetland ecosystem, through reestablishment both of the historical channel configuration and morphometry and of the historical hydroperiod (Loftin *et al*. 1990, USACE Jacksonville District 1991). The broad ecosystem and resource management challenges and issues associated with this project that are relevant to the present discussion include the following:

- This project is again characterized by extensive multi-agency interest and involvement, including several USACE Districts (especially Jacksonville), the South Florida Water Management District (SFWMD), USFWS, USDI-GS/BRD, and several state agencies including the Florida Game and Fresh Water Fish Commission.

- Environmental concerns with the restoration of the Kissimmee River ecosystem are confounded with agricultural NPS management problems in the Kissimmee River basin, and associated water quality problems within the Kissimmee River, both of which increase in severity down river.

- Major resource management concerns are presently focused on the impacts of river restoration on dissolved oxygen (DO) levels in the restored river, and on the impacts of DO levels on the growth, survivorship, and distribution of important fish species.

- Related concerns are focused on the impacts of river restoration and interim construction activities on sediment transport and resuspension, and on select in-river processes including light penetration and primary productivity.

- A major factor motivating river restoration plans concerns the re-establishment, location, and functional dynamics of the expected extensive wetland complex in the restored river ecosystem, particularly in relation to the dynamics of nutrients and dissolved organic carbon (DOC) within restored wetlands and their couplings to in-river processes during the flow recession period following major storm events.

- At larger spatial scales, river restoration plans are focused on restoring biological couplings of the restored river-floodplain-wetland complex to populations and communities of wading birds in the larger Kissimmee River ecosystem.

To be useful for addressing the river restoration and management concerns listed above, the suite of ecological models developed for the Kissimmee River project should be responsive to the following model requirements and issues:

- Existing water quality models are quite adequate to handle some of above concerns, particularly those related to DO levels and select in-river processes (*e.g.*, light penetration, algal productivity).

- At finer spatial scales, modeled biological processes should be coupled to and driven by hydrodynamic transport processes.

- Useful models should contain detailed formulations of bioenergetic and demographic processes for fish species of concern.

- The overall suite of management-driven models should incorporate the spatially explicit formulation of wetland dynamics in an overall landscape context, including wetland location and extent, specific functional processes, and couplings to in-river processes (*e.g.*, couplings of nutrient and DOC dynamics in wetlands to in-river water quality dynamics including DO and biological productivity).

- At larger spatial scales, models should explicitly include biological couplings of wetland process formulations to the dynamics of wading bird populations and communities within the Kissimmee River ecosystem.

- As in the case examples above, models developed in support of the Kissimmee River restoration effort should be formulated and coupled across several relevant spatial scales.

Case Study 4: Restoration of Salmonid Fishes to the Columbia-Snake River Ecosystem in the Pacific Northwest

The broad goal or objective of this very large-scale ecosystem management and restoration effort in the Pacific Northwest is to restore portions of the Columbia-Snake River ecosystem to a free-flowing river ecosystem, and to restore historical populations of several salmon species to that river, through removal/permanent drawdown and bypass of select existing dams, and through reestablishment of the historical river hydroperiod (Independent Scientific Group 1996, USACE Walla Walla District 1997). Among the large number of ecosystem management and restoration concerns associated with this project, the following are pertinent to this discussion:

- This is again a very large-scale, multi-agency project, involving collaboration among several USACE Districts (Walla Walla, Portland), WES, NMFS, USFWS, USDI-GS/BRD, the Northwest Power Planning Council (NWPPC), Battelle National Laboratory, Indian tribes, the USDA Forest Service, and other state and federal agencies.

- A fundamental management concern that is driving much of the effort to restore historical hydrologic and ecological conditions in the Columbia-Snake River ecosystem is focused on the differential survivorship of salmon smolts during their passage through the riverine ecosystem (*i.e.*, differential survivorship in reservoir pools vs in free-flowing river segments vs during passage through dams).

- There is a strong need for detailed understanding and modeling of smolt bioenergetics during system passage under different possible management scenarios.

- The recent NWPPC Independent Scientific Group report, *Return to the River*, provides extensive support for viewing and modeling the dynamics and productivity of salmon populations in the overall context of metapopulation dynamics, with explicitly identified core and satellite populations (Independent Scientific Group 1996).

- This report also develops strong support for modeling spatially explicit dynamics of salmon productivity, focused on the historical importance of large alluvial mainstem river reaches with well-developed gravel bars and floodplains and high habitat complexity.

- Significant management concerns are focused on the post-restoration transport of large amounts of sediment currently stored in the dammed river system, and on the impacts of these "rolling sand dunes" on biological processes within the restored river.

- Significant management concerns are also focused on evaluating the impacts of river management and restoration alternatives on primary and secondary productivity in the river ecosystem, based on the expected fundamental shift in the productivity base associated with restoration, from largely pelagic productivity dominated by phytoplankton, zooplankton, and reservoir fishes, to largely benthic/epipelic productivity dominated by benthic algae, benthic invertebrates, and riverine fishes, and on the ability of the modified riverine food web to support desired levels of smolt production.

- Other agency concerns include the post-restoration dynamics of macrophyte populations, perhaps confounded by increased agricultural NPS inputs to the large-scale river ecosystem through the Palouse River and other major tributaries.

The array of models that would contribute to resolution of these management concerns pertinent to the restoration of the Columbia-Snake River ecosystem should have the following attributes:

- As in previous case studies, models formulated for the Columbia River effort should include strong couplings of relevant biological processes to hydrodynamic transport processes and to the geomorphic structure of the river ecosystem. Such couplings should occur at both finer (*e.g.*, phytoplankton-nutrient cycling processes) and larger (*e.g.*, passage of juvenile salmonids through the system) spatial scales.

- Models should include enhanced formulations of salmon demographic and bioenergetic processes in order to simulate responses to management alternatives for the juvenile salmon passage problem.

- Models should be based on the formulation of a spatially explicit metapopulation framework in order to model the dynamics of salmonid populations and productivity within the entire Columbia-Snake River basin ecosystem.

- Modeled processes should include enhanced resolution of food web dynamics and trophic relations that control primary and secondary productivity in the restored and current riverine ecosystem, as well as food available to salmonids at various life stages.

- Detailed process models of macrophyte dynamics will be required for the restored system.

- Specific scale couplings or translations will be required among various models formulated at several discrete spatial and temporal scales.

Case Study 5: Assessing Zebra Mussel Impacts to Aquatic Ecosystems at USACE Projects

The broad goal or objective for this project, which will serve as the initial test case for the ecologically enhanced models under discussion in this workshop, is to assess the impacts of zebra mussel populations on aquatic ecosystems at USACE projects. This case study is presented only briefly here; additional details may be found in the papers by Miller (this volume). The specific ecosystem and resource management challenges and issues associated with this fifth case study include the following:

- Some management concerns with the establishment of zebra mussel populations in aquatic ecosystems managed by the USACE focus on the transport and fate of toxic contaminants in relation to the water filtering activities of zebra mussels.

- One of the most significant potential impacts of zebra mussels involves alterations to food web processes and structure (*i.e.*, impacts on abundances and biomass of phyto- and zooplankton, other filter feeders, juvenile fishes) through zebra mussel filtering of particulate organic carbon (POC), including both algal cells and detritus.

- Zebra mussels may have significant direct impacts on biotic composition of aquatic ecosystems (*e.g.*, on native unionid species, through interference with feeding, growth, locomotion, respiration, and reproduction).

- Through their filtering activities, zebra mussels may impact water clarity and light regimes, and thus the occurrence and distribution of macrophytes.

Specific attributes of models that would be useful for assessing and managing zebra mussel impacts at USACE projects include the following:

- Some impacts of zebra mussel populations are handled quite well by existing water quality models that contain zebra mussels as a state variable (*e.g.*, based on specific formulations of water, particulate, and chemical filtering and transport, and of factors

regulating water clarity and light regimes). The paper by Bierman *et al*. (this volume) is a good example of such an "enhanced" water quality model.

- In order to accurately simulate mussel impacts on trophic dynamics, models will require enhanced resolution of specific food web processes, especially those related to the filtering or processing of POC and the couplings of such processes to other species, functional groups, and trophic transfers.

- For some applications, where it is important to model zebra mussel population dynamics directly rather than by simply specifying their densities or population sizes as some sort of model parameter or initial condition, models should include detailed formulation of population demographic processes (*e.g.*, reproduction, dispersal, establishment/early growth, competition for space, species interactions) of zebra mussels. It is not clear whether it would be appropriate to model such processes in a metapopulation or other spatially explicit modeling context.

Synopsis: Conceptual Issues Underlying Development of New Modeling Approaches in Support of Ecosystem Management and Restoration Initiatives within the USACE

The case study examples reviewed briefly above typify the sorts of complex, large scale ecosystem management and restoration challenges the USACE is currently facing in different regions of the U.S., often in collaboration with other federal and state agency partners. From these case studies, it is possible to distill a series of fundamental issues that will, in part, provide the conceptual foundation and motivation for new, ecologically oriented models and modeling approaches to be developed and applied in support of ecosystem management and restoration initiatives within the USACE.

Commonness of Large Scale Ecosystem Management and Restoration Projects. Large-scale, multi-agency, place-based ecosystem management and restoration projects are becoming increasingly common in all regions of the U.S. Such projects call for the development of new, ecologically motivated approaches to modeling human impacts to aquatic ecosystems, biota, and processes. Models useful for these purposes must be based on detailed formulation of a much greater array of biological and ecological processes than are contained in current water quality and contaminant models developed and applied by the USACE.

Assessment Focus of Aquatic Ecosystem Models. While considerable research may be required to develop these models initially, the models themselves will not be primarily used for research purposes. Rather, these must be management- or assessment-oriented models useful for assessing impacts of diverse human actions and management alternatives to aquatic ecosystems, biota, and processes as part of the overall process of adaptive ecosystem management (in the sense of Walters 1986, Walters and Holling 1990).

Generalizable Modeling Approach. Although models must be tailored to the specific ecosystem management/impact assessment issues and ecological system under consideration in a given project or study, the intent is to develop a portable modeling approach that is generalizable to the array of similar ecosystem management and impact assessment issues, and the array of ecological settings, relevant to USACE and DoD missions regarding environmental stewardship and ecosystem management and restoration. The fundamental approach underlying these new models should be generalizable in the same sense that a common framework and conceptual foundation underpins the suite of water quality and contaminant models developed by WES.

Couplings to Transport Processes. In that biological processes in aquatic ecosystems operate in the overall context of transport and flow, it is critical that methods be developed to couple new models and process formulations to current formulations of hydrodynamic transport processes and to system geomorphology. In this sense, new modeling approaches will be broadly similar to current water quality models. Such couplings will be most common at fine spatial scales, but may also be critical at larger scales (*e.g.*, coupling juvenile salmon passage to flow and transport regimes in the Columbia-Snake River system).

Enhanced Ecological Process Detail. The key requirement of new models and modeling approaches is that they must incorporate substantially richer details of biological and ecological processes -- demographic, bioenergetic/trophic dynamic, biogeochemical, and other -- than are contained in current water quality and contaminant models. Existing models do not contain either the breadth or the depth of ecological process formulations required to assess impacts of diverse human actions and management alternatives to aquatic ecosystems, biota, and processes.

Spatially Explicit Process Formulations. In many cases the processes contained in new, ecologically motivated models must be formulated in a spatially explicit manner, to take account of specific couplings of select ecological processes to important spatial features or structure. A broad metapopulation approach may be an appropriate context for dealing with many spatially explicit biotic processes at larger landscape scales. It may also be useful to formulate such spatially explicit models in an overall Geographic Information System (GIS) computing environment, or at least to couple such models to a GIS for display and analysis of model projections.

Organizational Level and Spatiotemporal Scale. New, ecologically motivated models must deal more explicitly with issues of organizational level and spatial/temporal scale than has been the case with other models developed and applied by USACE and WES. In the case of most large scale ecosystem management and restoration efforts, a suite of models, formulated across overlapping organizational levels and scales of space and time, will be required to deal with the array of resource and ecosystem management issues and challenges posed by the project. In such cases it will be important to develop specific means to couple or interface models formulated at inherently different scales and organizational levels, and to translate output from models at one scale or level for use by models at adjacent scales or levels.

Uncertainty Analysis Capabilities. In that the new models under discussion here are intended to contribute to ecosystem management and restoration efforts within the USACE, it is important to incorporate into these new modeling approaches the ability to evaluate sources and magnitudes of uncertainty present in model projections, and the consequences of such uncertainty for resulting management decisions. Such uncertainty analysis capabilities might span the range from simple qualitative or ranking procedures to detailed Monte Carlo analyses.

A Final Caution Regarding Model Complexity. It is important to end this discussion with a concluding caution about dangers inherent in model complexity. In that the scale and complexity of the ecosystem management problems that models are being used to resolve are continually increasing, the clear tendency is to build ever more complex models that simulate an ever growing number of interacting processes. However, at some level of model complexity, models lose some of their power to contribute to ecosystem management and impact assessment projects, and prediction accuracy and ease of use are overwhelmed by the propagation of error and uncertainty and by the unwieldy nature of the models themselves. Models that address environmental problems at larger spatial scales or organizational levels do not need to do so in a brute force manner, by adding an ever greater number of parameters and interacting processes - models should be reformulated at these larger scales and levels to include only those key processes critical to understanding and predicting system responses at these scales and levels. This point corresponds to an argument recently provided by Clark (1996). In a review of usable environmental assessments (defined as those that made a difference in the resolution of the problem) of global climate change and similar environmental problems, Clark pointed out that the most usable assessments have been those that respond to questions posed by managers and decision makers in plausible, transparent ways, and that user-friendly, open models capable of rapid iteration, complemented by qualitative assessment approaches, constitute an essential component of usable assessments. Thus, new models useful for assessing human impacts to aquatic ecosystems, biota, and processes should be sensitive to this caution in respect to problems inherent in continued increases in model complexity. They should also contain various sorts of communications interfaces useful for communicating model results to ecosystem managers and policy analysts clearly and in a form that is both understandable and directly related to the decision making process.

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Session 2 - Test Application: Assessing & Managing Zebra Mussel Impacts at Corps Projects

Session Purpose

This session was designed to provide background information on the extent and nature of zebra mussel impacts -- on water quality conditions, on trophic dynamics and food web processes, and on biotic composition and species interactions -- to aquatic ecosystems and biota at Corps projects, and on current understandings of the biology and ecology of zebra mussels as prerequisite to understanding and managing such impacts. Discussions of session presentations focused on the zebra mussel "problem" as an organizing focus for initial development of an assessment-oriented aquatic ecosystem modeling approach and capability; linkages of zebra mussel biology to other ecosystem components and processes (specifically, linkages to water quality processes, to trophic dynamic/food web processes, and to biotic composition/species interactions); and development of a conceptual model of biotic components, processes, and linkages to serve as the conceptual underpinnings of the proposed modeling framework.

Current Understandings of the Physiological Ecology and Life History of Zebra Mussels (*Dreissena polymorpha*)

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Zebra mussels (*Dreissena polymorpha*) are small, bivalve molluscs that were accidentally brought to this country from Europe in the ballast water of an ocean vessel. They are reproductive within the first year of life, attach tenaciously to virtually any surface with hundreds of proteinaceous byssal threads, and can tolerate extreme crowding. Infestations up to 5 cm thick have been reported on concrete walls, screens, the interior of pipes, and gravel/cobble substratum in large rivers. Although there appears to be some selection for warm-water tolerant individuals in the south, this is basically a cold-tolerant species that exhibits good growth in water between 13 and 24° C and an upper incipient lethal temperature of 29° C (Claudi and Mackie 1994). The biofouling nature of this species has required increased maintenance at hydropower and water supply facilities in the north central United States and Canada (Nelepa and Schloesser 1993). Although many control methods can be used for this species (McMahon 1990), the most widely used strategies include: antifoulant coatings, oxidizing and nonoxidizing biocides, physical cleaning, as well as heat, desiccation, and freezing.

The first report of *D. polymorpha* in North America was from Lake St. Clair in June 1988 (Hebert *et al*. 1989). By late summer 1989, *D. polymorpha* had spread downstream into the Detroit River, Lake Erie, Niagara River, and western Lake Ontario (Griffiths *et al*. 1989). By late September 1990, mussels had spread through Lake Ontario and down the St. Lawrence River to Mesenna, NY. They were also collected in Lake Huron, Lake Superior at Duluth, MN, and in western Lake Michigan at Gary, IN (O'Neill 1990). These latter sites are close to the source of the Illinois River, which connects Lake Michigan to the inland waterway system.

In June 1991, biologists from the Illinois Natural History Survey found adult *D. polymorpha* at Illinois River miles 50, 60, and 110 (Moore 1991, Sparks and Marsden 1991). In 1993 *D. polymorpha* had been found in the lower Mississippi River as far south as New Orleans, in the upper Mississippi River near St. Paul, MN, and in the Arkansas River in eastern Oklahoma. Mussels were probably carried up rivers on the hulls of commercial vessels (Keevin *et al*. 1992) and down rivers on currents. As of February 1997, zebra mussels have been found throughout much of the Ohio River system including the lower Cumberland River, most of the Tennessee River, and the lower reach of the Allegheny and Monongahela Rivers east of Pittsburgh, PA. They have been found in the Arkansas River, but reproducing populations have not been found west of the Rocky Mountains (O'Neill 1996).

In response to the Nonindigenous Aquatic Nuisance Prevention and Control Act of 1990, Public Law 101-646, the U.S. Army Corps of Engineers (USACE) initiated a program to develop methods and strategies to control zebra mussels at public facilities. "Public facilities"

includes locks, dams, reservoirs, commercial dredges and vessels, as well as non-Corps structures such as intakes for power generation, potable water, and sewage treatment. Research conducted under this program has focused on three objectives: 1) to evaluate existing control methods, 2) to develop strategies for dealing with infestations, and 3) to monitor effects of infestations and control methods on native biota.

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Potential Impacts of Zebra Mussels (*Dreissena polymorpha*) on Aquatic Ecosystems

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In 1992 six individual zebra mussels (*Dreissena polymorpha*), all attached to native mussels, were collected at the mussel bed in the lower Ohio River located between river miles (RM) 966 and 969.2. In 1993 the maximum density of zebra mussels sampled on natural substratum, which included gravel, cobble, live mussels, and shells, was approximately 200/m^2. In 1994 and early 1995 maximum zebra mussel densities reached more than 100,000 individuals/m^2 at some sites. Approximately 95% of native unionids greater than 50 mm total shell length were covered with 100 or more zebra mussels. Less than 5% of native species were recently dead, characterized by the presence of some tissue attached to the valves.

Total shell length of zebra mussels collected in 1995 was between 11 and 27 mm, revealing that most were probably the result of reproduction in 1993. During much of that year water depths were 2-3 times normal and pooled over the bed. This was the result of backwater flooding from the extreme high water in the nearby Mississippi River. This provided opportunity for veligers from the Illinois River to be carried up the Ohio River and to settle on the mussel bed.

Between August and October, 1995, virtually all *D. polymorpha* of this cohort died, most certainly of natural causes. In late October the remaining population consisted of individuals less than 10 mm long, with a total density of less than 100/m^2. Virtually every native unionid collected was covered by byssal threads but no live zebra mussels. By August 1996, the majority of these 1995 recruits were 10-16 mm long. There was some evidence of recruitment from late 1995 or early 1996; this cohort was 2-6 mm long and comprised approximately 50% of the population (Figure 1). Zebra mussel density, based upon collections made in August and October 1996, was less than 1,000 individuals/m^2.

Each year an index of recruitment for native mussels was estimated by determining the percentage of individuals and species that had at least one individual present less than 30 mm total shell length. Organisms less than this size were spawned within the last 2-3 years. This index reflects conditions 1-2 years in the past when young were being produced, as well as present conditions when immature individuals must survive existing disturbances.

These indices were calculated for native mussels for 1987, 1988, 1990, 1995, and 1996. For comparison, recruitment information from a mussel bed in the upper Mississippi River (UMR) with similar unionid density and species richness (Miller and Payne 1996) is included (Table 1). At the bed in the UMR adult zebra mussels were first found in 1993. Densities on rock surfaces increased from 10 individuals/m^2 of rock surface in 1993, to greater than 50/m^2 in

1994 (Beckett *et al*. 1997). In 1995 and 1996, zebra mussel density was at least 100 times greater than in 1994.

At both sites there was no relationship between native mussel recruitment rate, expressed as percentage of young individuals or species, and the introduction and spread of zebra mussels. In the lower Ohio River only 1.5% of the individuals were new recruits in 1990 and 22.6% were new recruits in 1987, two years when zebra mussels were not present. During the years of heavy infestation, 1995 and 1996, 46.6 and 18.2% of the native mussels were new recruits. Lack of a relationship between native mussel recruitment and presence of zebra mussels was also observed in the UMR (Table 1). The two best years for recruitment were 1987 before zebra mussels were present, and in 1996 when the infestation may have been at its peak.

Table 1. Percentage of Native Mussel Species and Individuals Less than 30 mm Total Shell Length at a Site in the Lower Ohio and Upper Mississippi Rivers.

Year	Lower Ohio River		Upper Mississippi River	
	Individuals	Species	Individuals	Species
1987	22.6	61.1	34.4	75.0
1988	2.5	14.3	24.5	52
1990	1.5	25.0	14.8	42.1
1995	46.6	26.7	11.3	54.2
1996	18.2	28.6	32.5	66.7

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Session 3 - From Water Quality and Contaminant Models to Aquatic Ecosystem Models

Session Purpose

This session was intended to stimulate discussion both of extensions of current WES water quality and contaminant modeling capabilities and approaches required to deal with the resource management challenges identified in the initial workshop session, and of potential linkages of new modeling approaches to existing water quality and transport models and modeling approaches. Discussion of the single session presentation focused on processes and characteristics to include in the desired new modeling framework/approach, that are not included in existing water quality and contaminant models, in order to develop capabilities to model and assess human impacts to biotic components and processes in aquatic ecosystems at multiple spatial scales and organizational levels, and on possible linkages of the new modeling framework to, and compatibilities with, existing water quality/contaminant models.

Coupled Phytoplankton - Zebra Mussel Model for Saginaw Bay, Lake Huron

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Introduction

Saginaw Bay is a broad, shallow extension of the western shore of Lake Huron (Figure 1). The bay is 82 km long, varies in width between 21 and 42 km, and has a surface area of 2,960 km^2. The bay has been severely impacted by anthropogenic inputs and has been identified by the International Joint Commission as one of 42 Great Lakes Areas of Concern.

The principal consequences of cultural eutrophication in the bay were adverse taste and odor, and filter-clogging problems in municipal water treatment plants. In the Saginaw-Midland water supply system, 42 percent of daily threshold odor values in 1974 were equal to or greater than the U.S. Public Health Service standard (Chartrand 1974). Threshold odor was strongly correlated with blue-green cell number concentration in the raw water intake at Whitestone Point (Bierman *et al*. 1980).

Between 1972 and 1988 over $500 million was spent on municipal wastewater treatment plant improvements in the Saginaw Bay watershed (Great Lakes Water Quality Board 1989). Combined with a ban by the State of Michigan on the use of high phosphate detergents, these improvements resulted in a 79 percent decrease in phosphorus loadings from these sources over this 16-year period. In response, blue-green algal populations and taste and odor problems in municipal water supplies declined substantially.

Between 1990 and 1993 Saginaw Bay experienced an invasion by the zebra mussel, *Dreissena polymorpha* (Nalepa *et al*. 1995). Nuisance blooms of the blue-green alga *Microcystis* have occurred in the bay every summer since 1994 (Vanderploeg 1996). These blooms were thought to be related to zebra mussel dynamics and possible changes in external phosphorus loads. Variability in observed zebra mussel densities and external phosphorus loads during the period 1991 to 1995 confounded interpretation of the underlying cause-effect mechanisms.

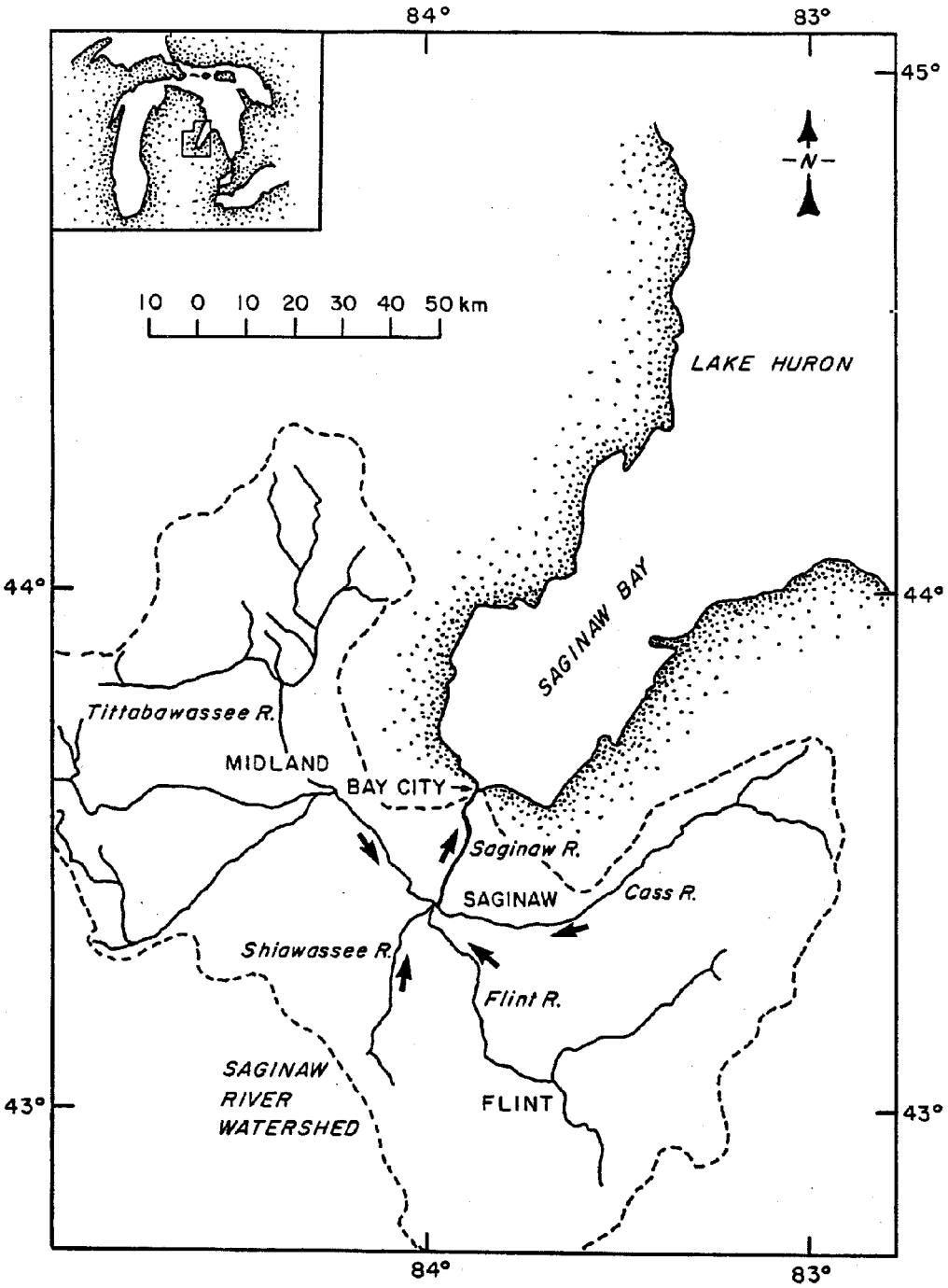


Figure 1. Saginaw Bay site map.

As part of an overall ecosystem study of Saginaw Bay, a coupled phytoplankton-zebra mussel mass balance model was developed. Limno-Tech, Inc. (1995) contains complete descriptions of water quality issues on Saginaw Bay, available data sources, and development of the coupled phytoplankton-zebra mussel model. Limno-Tech, Inc. (1997) contains results for model calibration and use of the calibrated model for various predictive scenarios. The present paper contains a summary of results from predictive simulations designed to estimate responses of the bay to changes in external phosphorus loads and zebra mussel densities, and to investigate different hypotheses on zebra mussel, phytoplankton, and phosphorus dynamics.

Phytoplankton-Zebra Mussel Model

Conceptual Approach

The overall modeling approach (Figure 2) included three separate models: (1) a multi-class phytoplankton model; (2) a zebra mussel bioenergetics model; and (3) a coupled phytoplankton-zebra mussel mass balance model. The phytoplankton model (Figure 3) was a modified version of the original model developed for Saginaw Bay by Bierman and Dolan (1981, 1986a, 1986b). The zebra mussel bioenergetics model (Figure 4) was developed and tested as a stand-alone model and then linked with the multi-class phytoplankton model (Limno-Tech, Inc. 1995). The coupled phytoplankton-zebra mussel model was then calibrated to a comprehensive set of field data for 1991 on Saginaw Bay (Limno-Tech, Inc. 1997).

Approach to Predictive Simulations

External phosphorus loads and zebra mussel densities were varied over ranges that represented reasonable perturbations about actual conditions for the period 1991 to 1995. The model was not used to investigate differences between or among individual years during the period 1991 to 1995 because actual time-series forcing functions were developed for only the 1991 calibration year. Phosphorus loading changes were imposed on the model in the form of simple scale factors on the 1991 loading time series. For all of the predictive simulations all other forcing functions remained the same as in the base calibration to the 1991 field data.

Phosphorus Loads

The Saginaw River is the principal source of external phosphorus loads to Saginaw Bay. In 1991 the Saginaw River accounted for 74 percent of total phosphorus load and 71 percent of available phosphorus load to Saginaw Bay (Limno-Tech, Inc. 1995). Figure 5 depicts annual Saginaw River phosphorus loads from 1991 to 1995 and, for comparison with earlier historical conditions, average phosphorus loads for the period 1981 to 1990.

Although there is inter-annual variability in both total and soluble reactive phosphorus loads, there do not appear to be significant temporal trends. Three different phosphorus loading conditions were used in the predictive simulations: (1) actual 1991 phosphorus loads; (2) actual 1991 loads plus 30 percent; and (3) actual 1991 loads minus 30 percent. Loading increases and decreases were imposed as simple scale factors on the actual Saginaw River loading time series in the calibrated model.

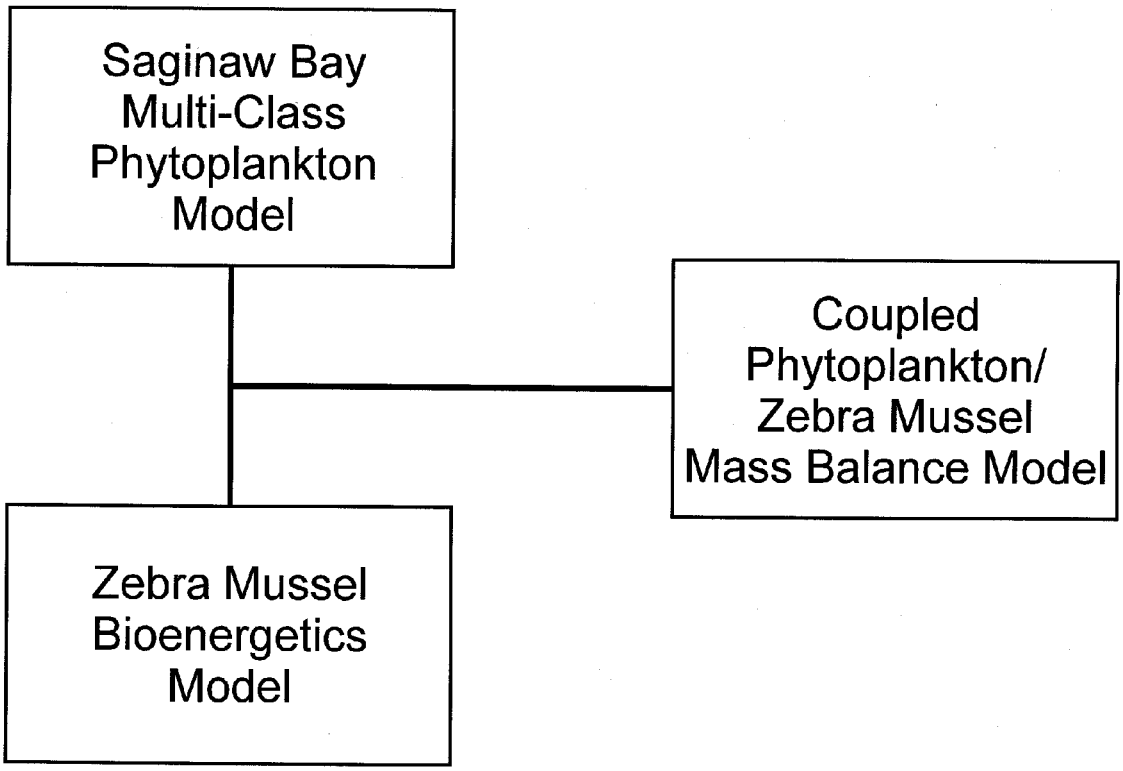


Figure 2. Conceptual approach for Saginaw Bay model.

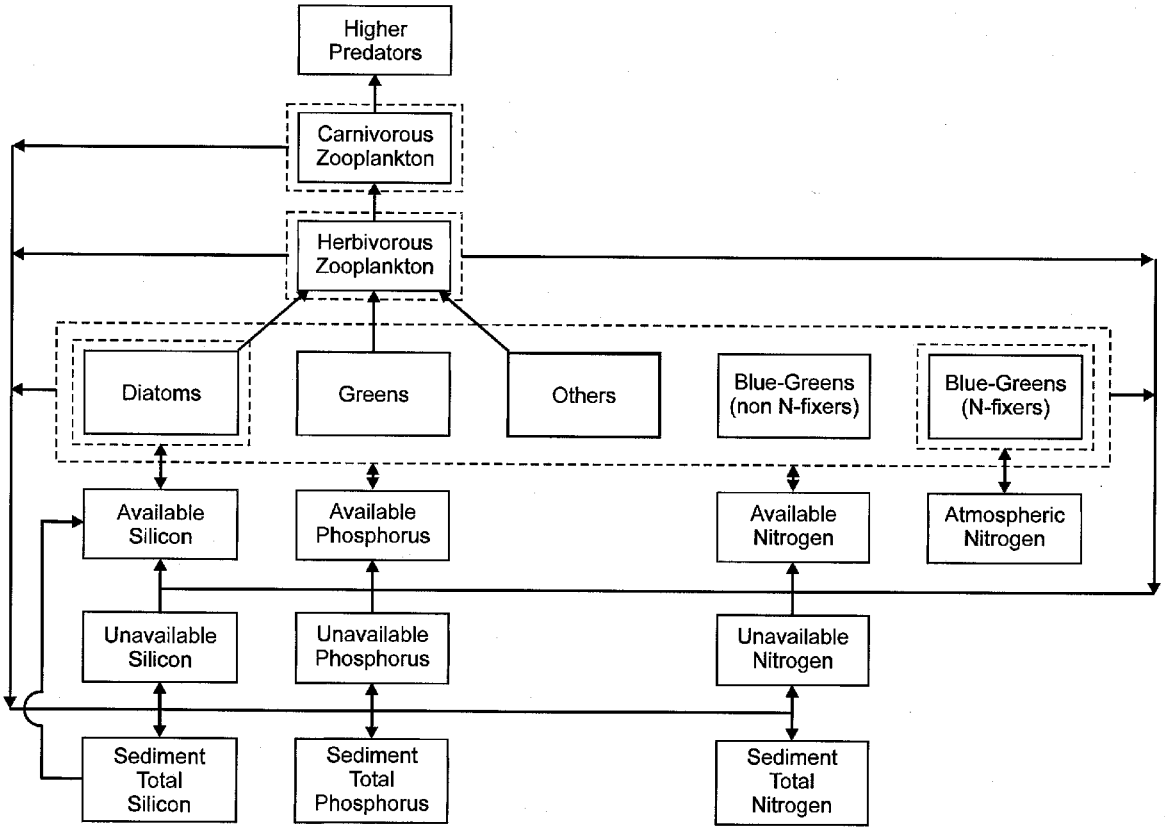


Figure 3. Saginaw Bay multi-class phytoplankton model.

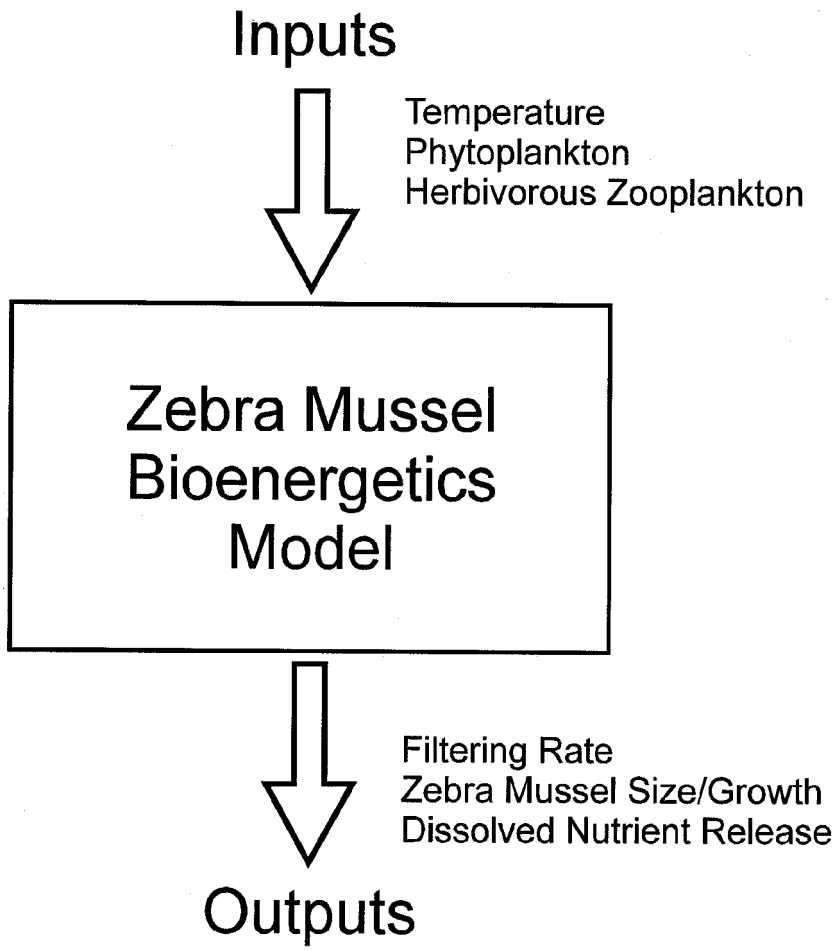


Figure 4. Schematic representation of zebra mussel bioenergetics model.

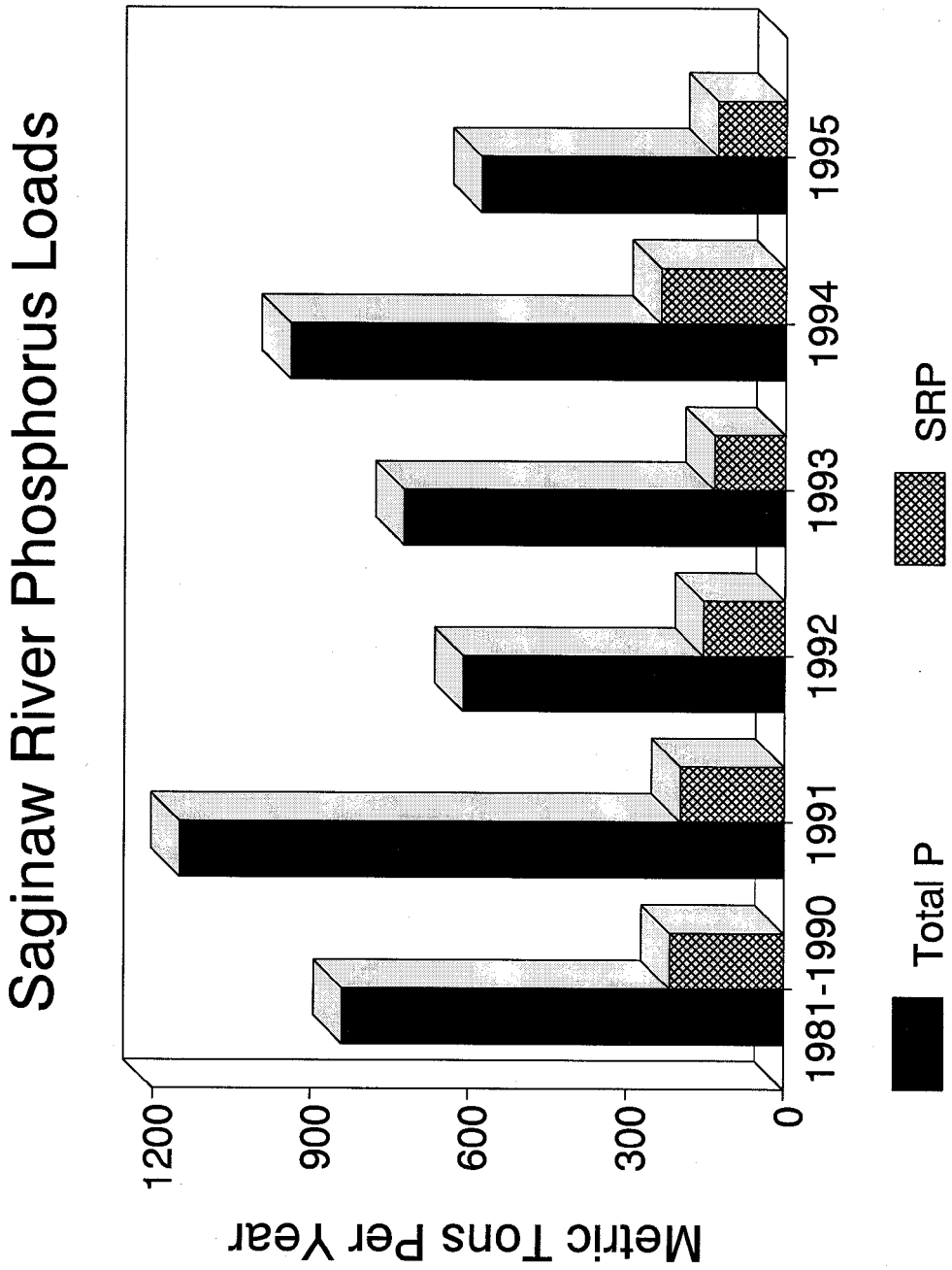


Figure 5. Annual Saginaw River phosphorus loads, 1991 to 1995.

Zebra Mussel Densities

Zebra mussel densities were estimated using data reported by Nalepa *et al*. (1995) and additional data provided by the National Oceanic and Atmospheric Administration, Great Lakes Environmental Research Laboratory (T. Nalepa, personal communication). The primary data consisted of size frequency distributions, density estimates on hard and soft substrates, and biomass estimates. Zebra mussel numbers were assigned to three year classes based upon reported size-frequency distributions. There are large uncertainties in the estimated segment-specific densities due a limited number of sampling stations (15), large variations in zebra mussel number densities among individual sampling stations, and large uncertainties in relative proportions and areal extent of substrate types.

Figure 6 depicts estimated inner bay average zebra mussel densities from 1991 to 1995. There are large spatial-temporal differences in total zebra mussel densities and in distributions of zebra mussel numbers among different cohort groups. Four different zebra mussel density conditions were used in the predictive simulations: (1) zero zebra mussels; (2) 1991-1995 average zebra mussel densities; (3) 1991-1995 average zebra mussel densities plus 50 percent; and (4) 1991-1995 average zebra mussel densities minus 50 percent.

The range of zebra mussel densities in the predictive simulations was not centered about 1991 conditions because these conditions were not fully representative of zebra mussel densities over the period 1991 to 1995. Zebra mussels in 1991 consisted primarily of large numbers of young-of-year (YOY), with the first large recruitment not occurring until late summer (Nalepa *et al*. 1995). Zebra mussels in other years consisted of much larger numbers of adults that were present during the entire growing season.

Results of Predictive Simulations

Results from the predictive simulations are provided for the open water zone in the inner portion of the bay and an adjacent near shore zone in the southeast portion of the bay. There are substantial differences in water quality responses between these two zones due to differences in zebra mussel number densities, water column depth, and the relative influence of Saginaw River inflow. The open water zone contains 71 percent of the total inner bay water volume and is 8.0 meters deep. The near shore zone contains 11 percent of the total inner bay water volume and is 3.8 meters deep. As a broad generalization, water quality responses in the open water zone are more strongly influenced by chemical-biological processes in the water column, and responses in the near shore zone are more strongly influenced by Saginaw River inflow and constituent fluxes across the sediment-water interface due to particulate settling and resuspension.

Results from the predictive simulations are provided for four water quality response parameters: annual average total phosphorus and total suspended solids concentrations, annual total phytoplankton production and annual blue-green phytoplankton production. These parameters represent the principal physical, chemical, and biological impacts of changes in

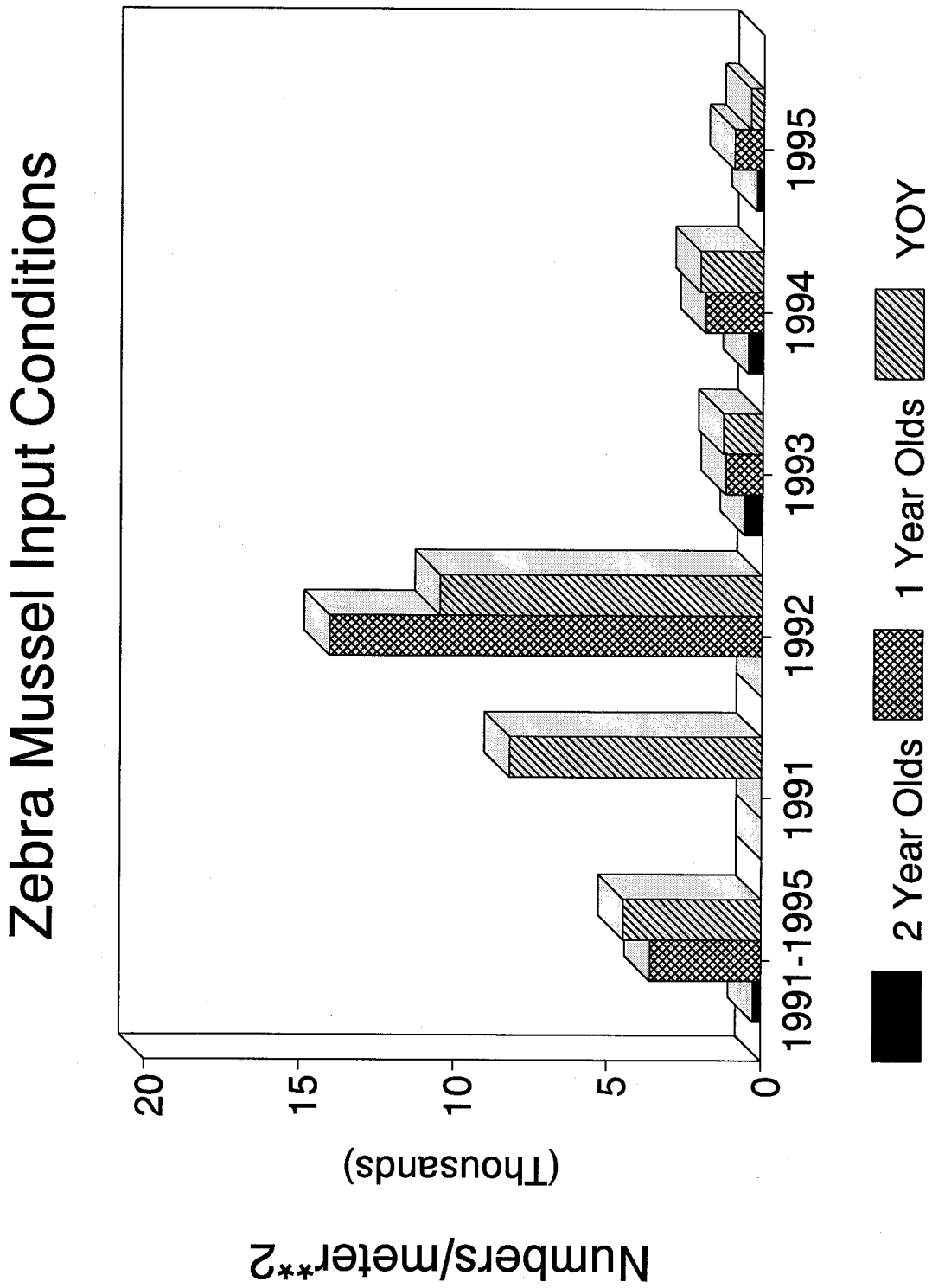


Figure 6. Inner bay average zebra mussel input conditions, 1991 to 1995.

external phosphorus loads and zebra mussel densities. They also represent differences in responses between the open water and near shore zones.

Figure 7 contains results for responses of average annual total phosphorus concentrations in the open water and near shore zones. In general, total phosphorus concentrations increase with increasing external loads and decrease with increasing zebra mussel densities. Responses in the near shore zone are greater than responses in the open water zone. For both zones, differences between absence and presence of zebra mussels are greater than differences due to plus and minus 50 percent variations about 1991-1995 average zebra mussel densities.

Figure 8 contains results for responses of average annual total suspended solids concentrations in the open water and near shore zones. In general, total solids concentrations are not strongly dependent on external phosphorus loads but they decrease substantially in the presence of zebra mussels, especially in the near shore zone. Differences between absence and presence of zebra mussels are much greater than differences due to plus and minus 50 percent variations about 1991-1995 average zebra mussel densities, especially in the near shore zone.

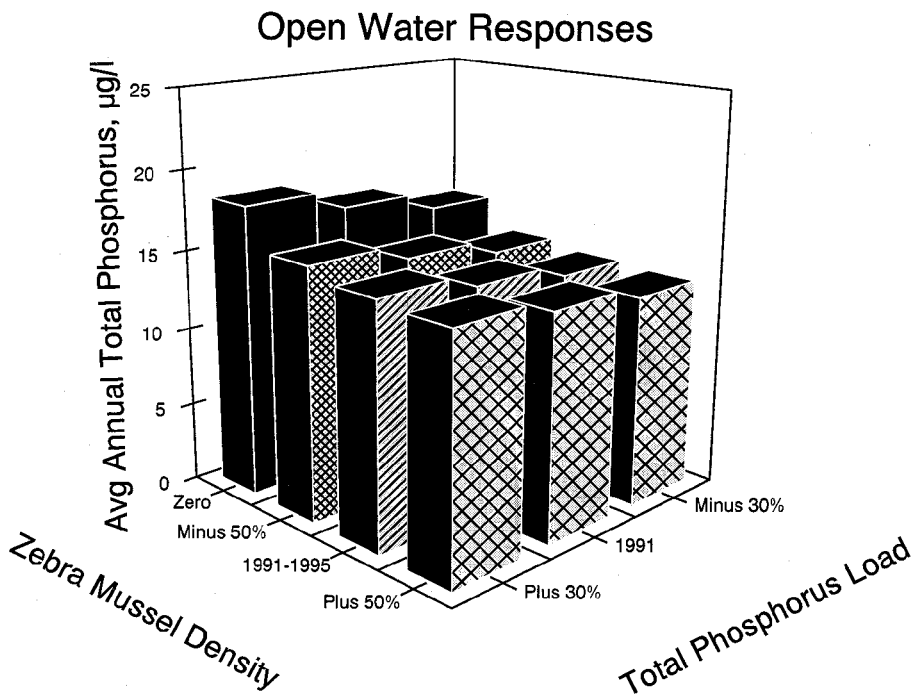
Figure 9 contains results for responses of annual total phytoplankton production in the open water and near shore zones. In general, total phytoplankton production increases with increasing external phosphorus loads and decreases with increasing zebra mussel densities. There is a large “step reduction” in the near shore zone between the absence and presence of zebra mussels, similar to responses for total suspended solids (Figure 8). There are smaller responses due to plus and minus 50 percent variations about 1991-1995 average zebra mussel densities.

Figure 10 contains results for responses of annual blue-green phytoplankton production in the open water and near shore zones. In general, blue-green production increases strongly with increasing external phosphorus loads especially in the near shore zone. In contrast to responses for all of the previous water quality parameters, blue-green production increases very strongly with increases in zebra mussel densities. In addition, there are large “step increases” in both the open water and near shore zones between the absence and presence of zebra mussels.

Sensitivity Analysis and Hypothesis Testing

A separate series of sensitivity analyses was conducted with the calibrated model to investigate different hypotheses on zebra mussel, phytoplankton, and phosphorus dynamics. The purpose of these analyses was to gain a better understanding of the possible role of zebra mussels in promoting blue-green phytoplankton blooms in the bay.

All sensitivity analyses were conducted with the calibrated model using 1991 phosphorus loads and average zebra mussel densities for the period 1991 to 1995 as base conditions. The following scenarios were investigated:



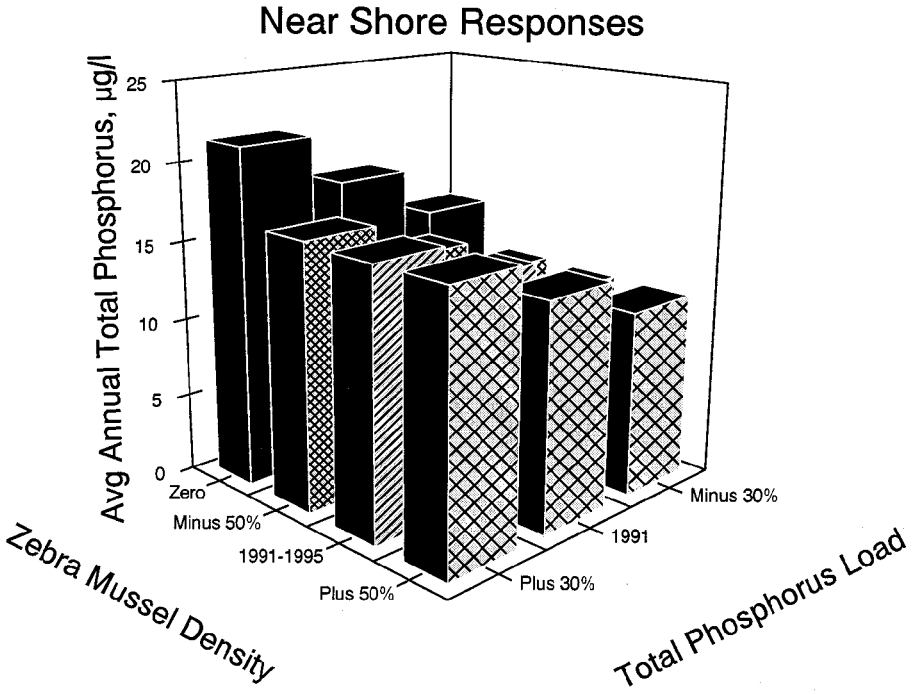


Figure 7. Responses of average annual total phosphorus concentrations in open qater (top plate) and near shore (bottom plate) to changes in zebra mussel densities and total phosphorus loads.

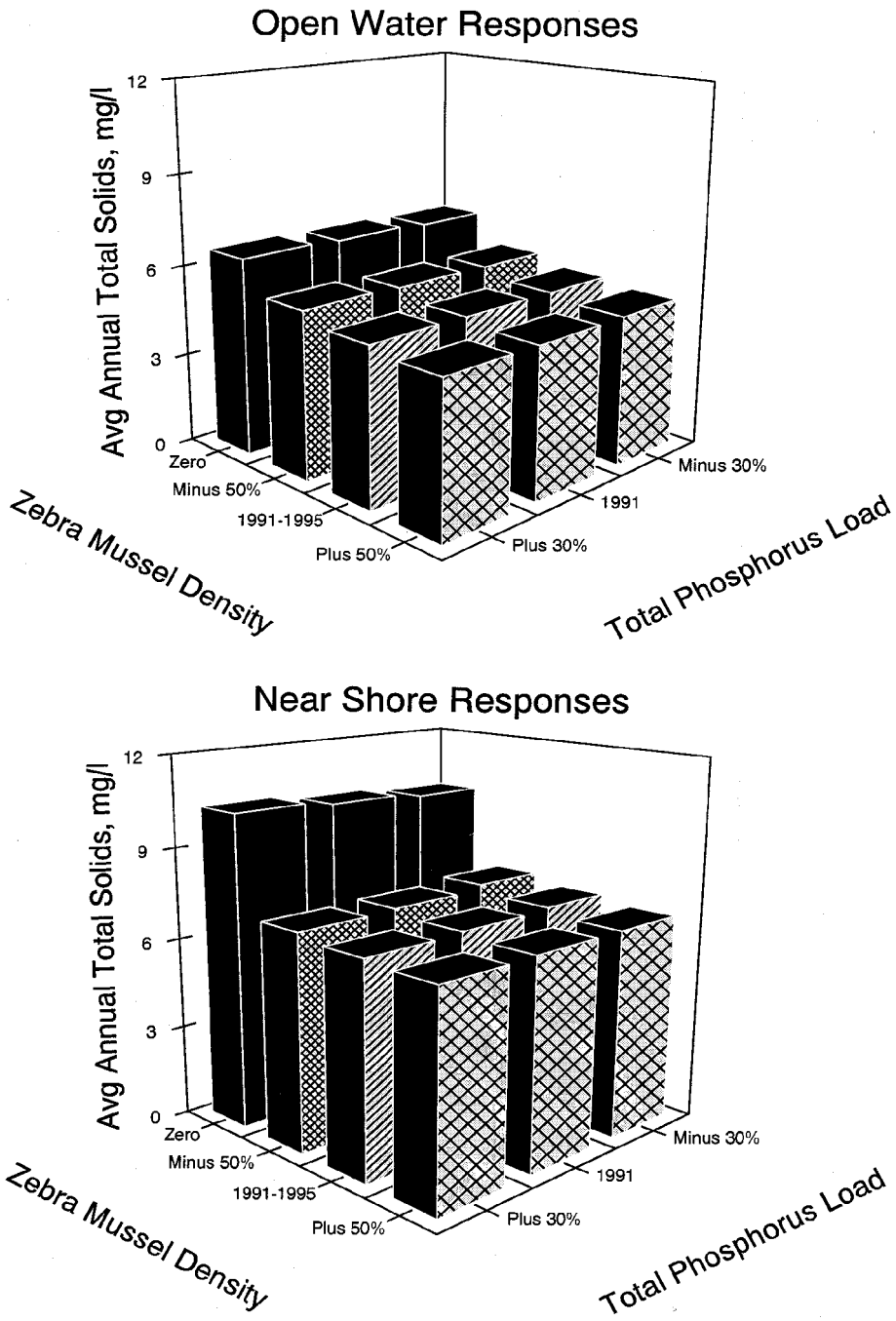


Figure 8. Responses of average annual total suspended solids concentrations in open water (top plate) and near shore (bottom plate) to changes in zebra mussel densities and total phosphorus loads.

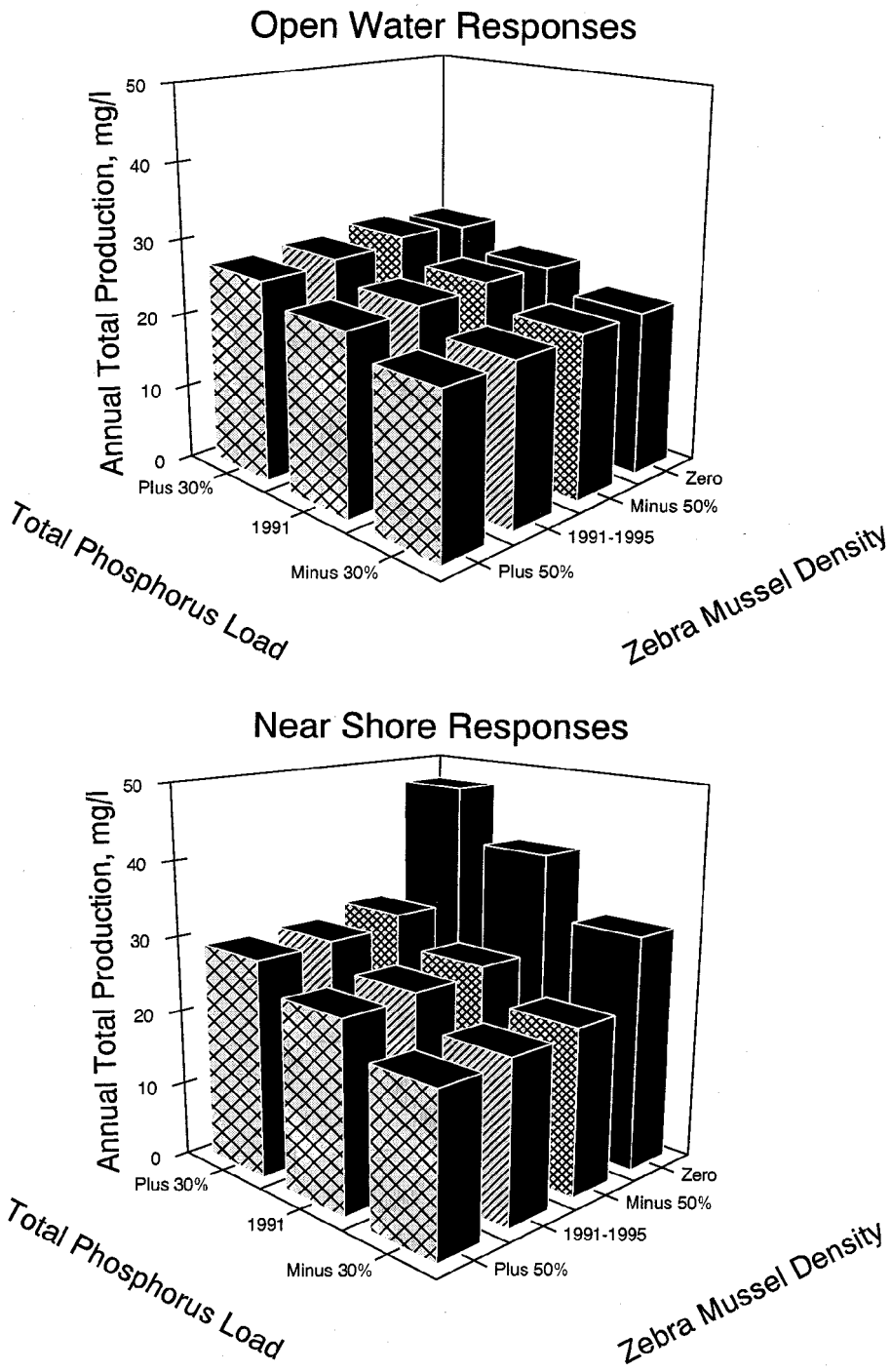
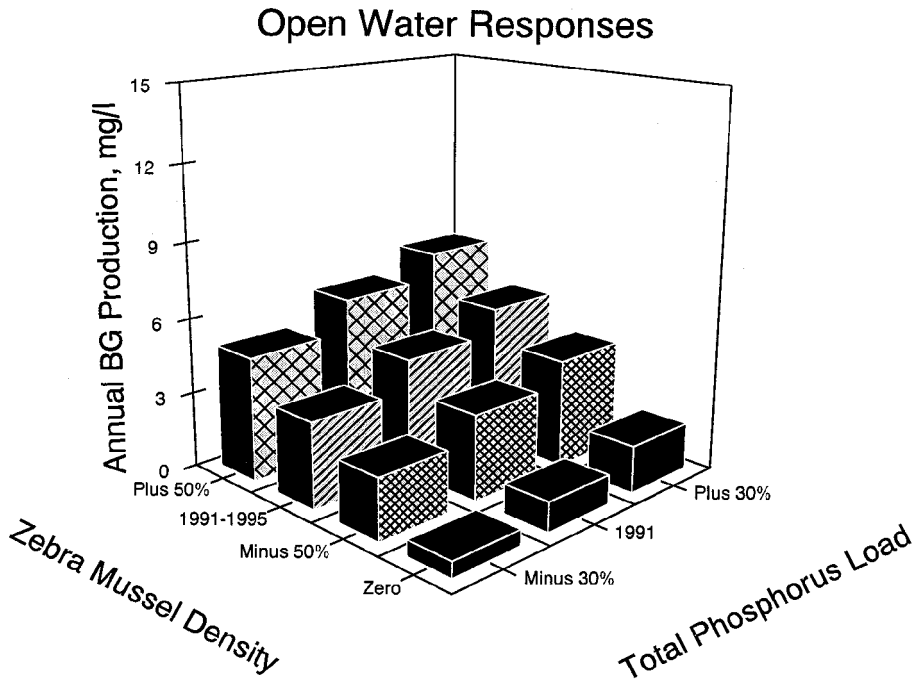


Figure 9. Responses of annual total phytoplankton production in open water (top plate) and near shore (bottom plate) to changes in zebra mussel densities and total phosphorus loads.



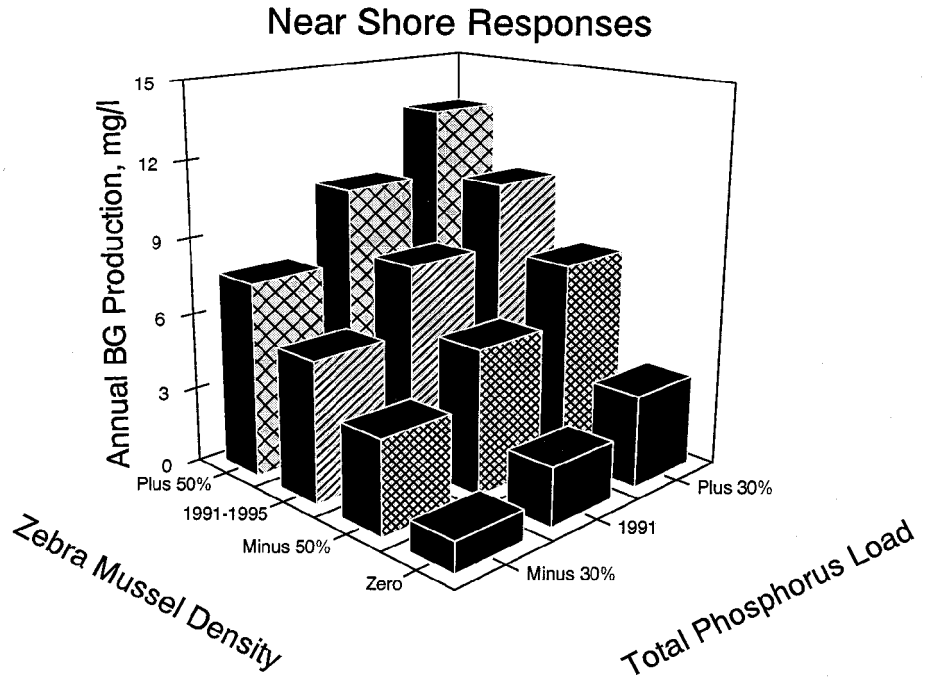


Figure 10. Responses of annual blue-green phytoplankton production in open water (top plate) and near shore (bottom plate) to changes in zebra mussel densities and total phosphorus loads.

a. zebra mussel filtration of blue-green phytoplankton;
b. factor of two increase in sediment-water phosphorus flux;
c. scenarios (a) and (b) simultaneously;
d. factor of two increase in initial zebra mussel densities; and
e. equal zebra mussel numbers in each cohort group.

Zebra mussel filtration of blue-green phytoplankton was investigated to determine the importance of selective rejection of blue-green phytoplankton as a competitive mechanism. Increased sediment-water phosphorus flux was investigated because it has been reported that sediment-water nutrient fluxes are higher in the presence of zebra mussels than in their absence (Johengen and Cotner 1995). Increased zebra mussel densities were investigated because of the above model results showing increases in blue-green phytoplankton with increases in zebra mussel densities, and because there are large uncertainties in specification of initial zebra mussel densities in Saginaw Bay. Equalization of zebra mussel numbers among the three cohort groups was investigated because older, larger zebra mussels have greater water quality impacts than younger, smaller zebra mussels, and because there are large uncertainties in assignments of total zebra mussel numbers to individual cohort groups.

Results are presented for annual average total phosphorus concentration and annual production of total and blue-green phytoplankton for both the open water and near shore zones. All results are presented in terms of percent changes relative to base conditions.

Figure 11 contains results for the case in which zebra mussels are hypothesized to filter all five phytoplankton groups in the model, including blue-greens. With the removal of selective rejection by zebra mussels as a competitive advantage, blue-green phytoplankton production decreases by almost 100 percent in both the open water and near shore zones. Changes in total phosphorus concentration and total phytoplankton production are small.

Figure 12 contains results for the case in which sediment-water flux of available phosphorus is increased by a factor of two, relative to the base value specified in the calibrated model. Although changes in total phosphorus concentrations are small, phytoplankton production increases in both the open water and near shore zones. Furthermore, there is selective enhancement of blue-green phytoplankton groups in both zones.

Figure 13 contains results for the simultaneous imposition of zebra mussel filtration on blue-green phytoplankton and a factor of two increase in sediment-water flux of available phosphorus. Results are similar to the case in which zebra mussels filter blue-greens (Figure 11) in that blue-green production again decreases by almost 100 percent in both the open water and near shore zone. Taken together, results in Figures 11-13 indicate that although increased sediment-water flux of available phosphorus can be important in promoting enhancement of blue-green production, such enhancement can only occur if blue-greens are not filtered by zebra mussels.

Figure 14 contains results for a factor of two increase in initial zebra mussel densities. Total phytoplankton production changes very little; however, blue-green phytoplankton

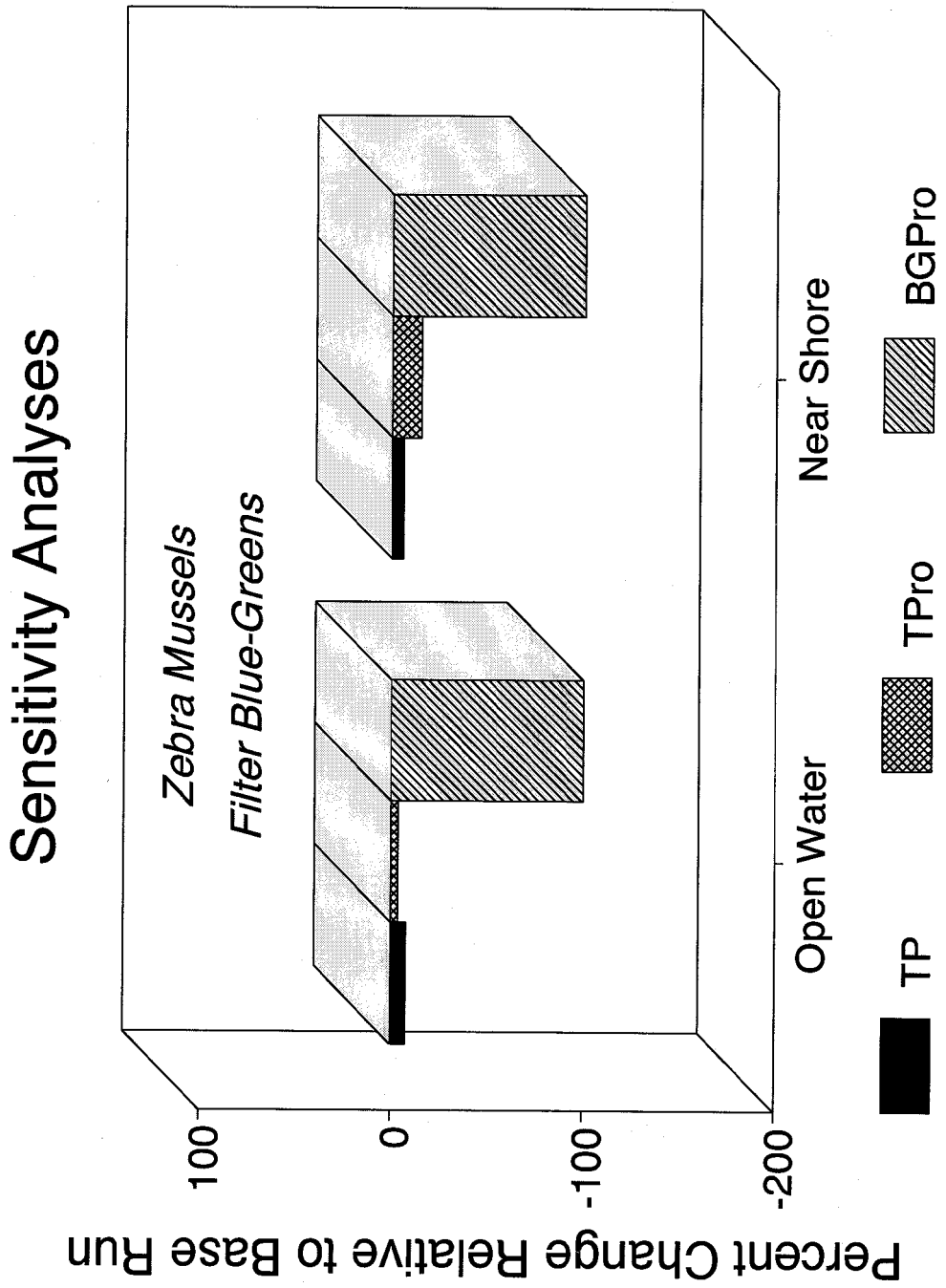


Figure 11. Model responses for sensitivity analysis to zebra mussel filtration of blue-green phytoplankton groups.

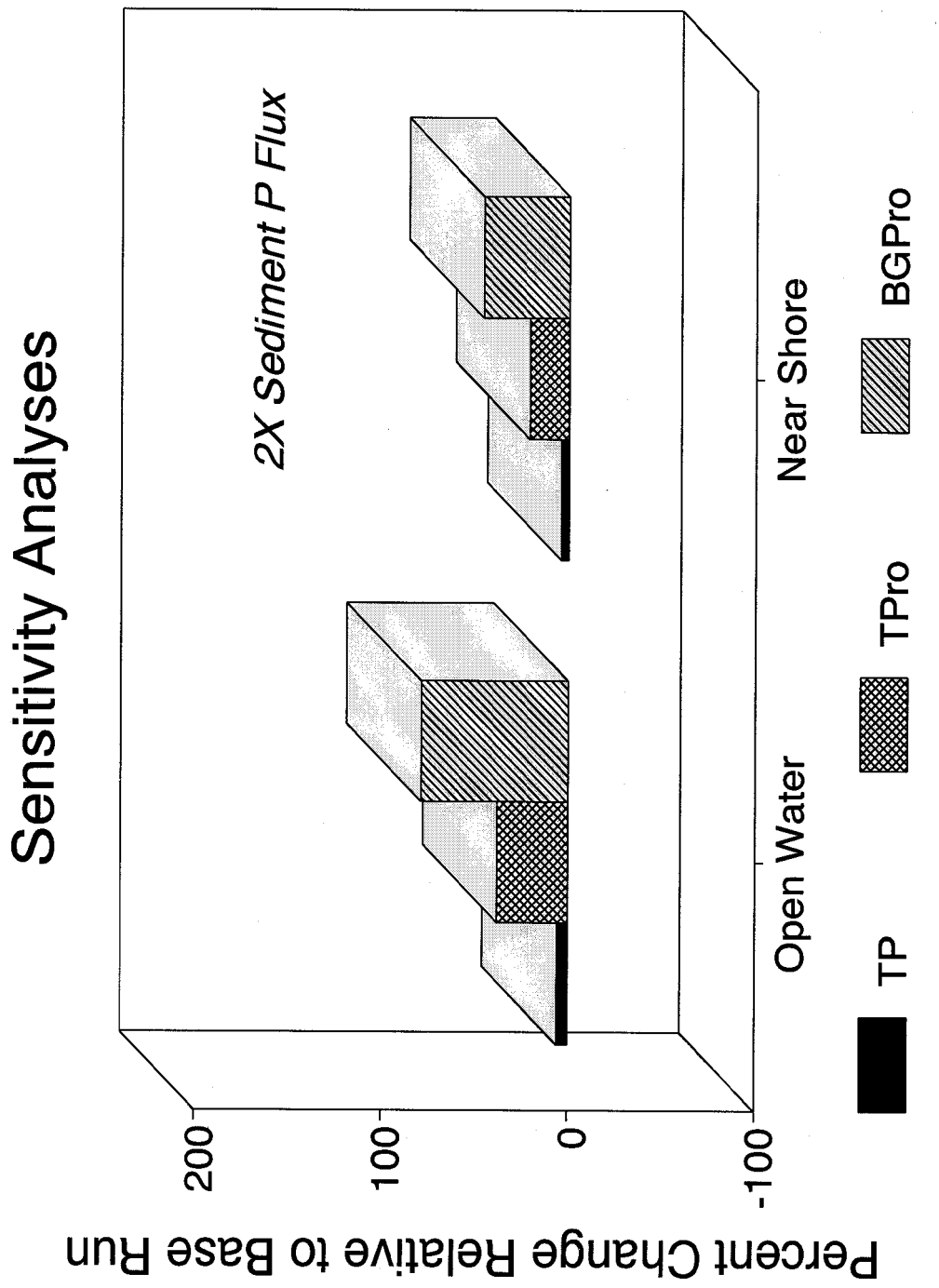


Figure 12. Model responses for sensitivity analysis to doubling of sediment phosphorus flux relative to base value in model calibration.

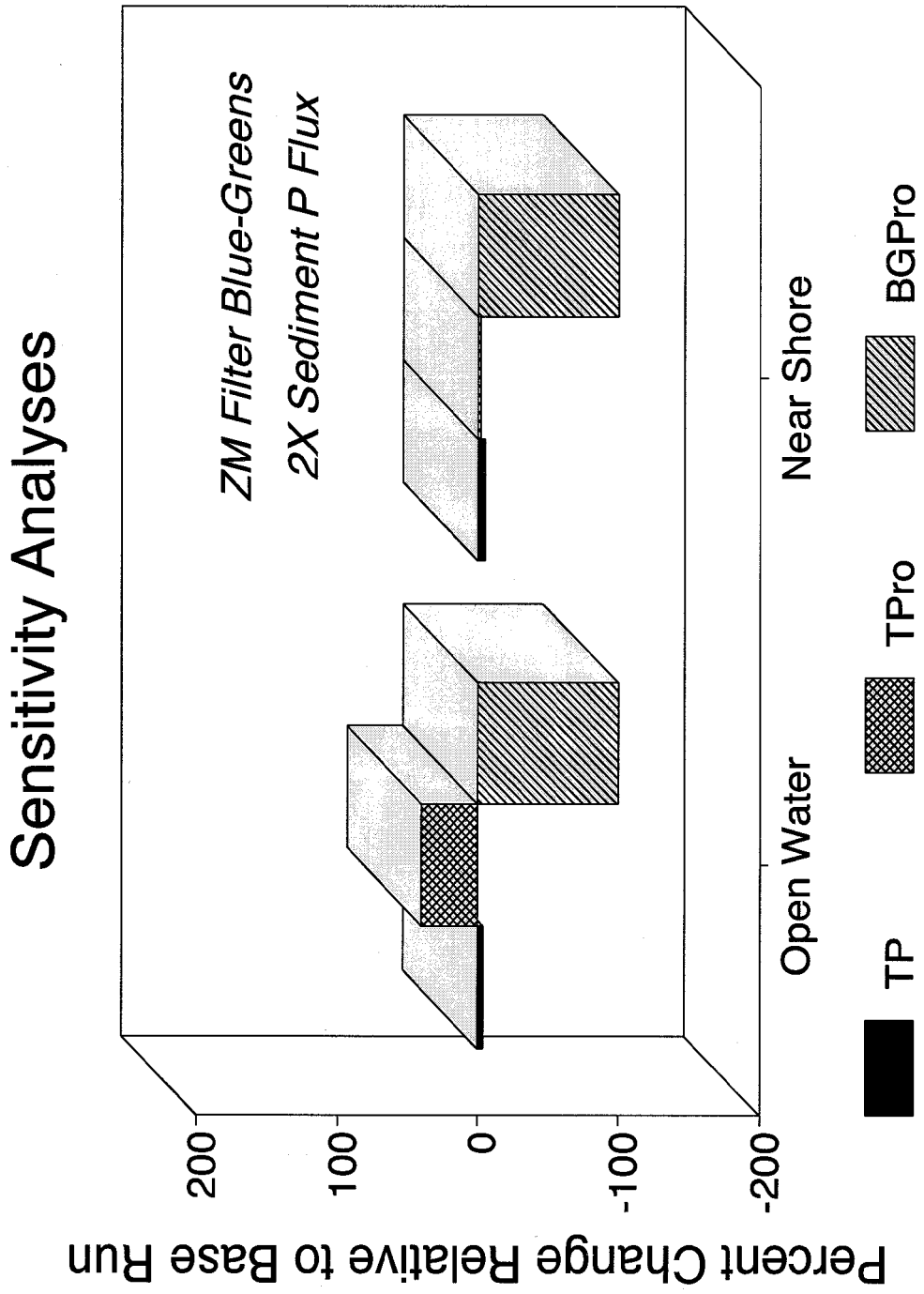


Figure 13. Model responses for sensitivity analysis to zebra mussel filtration of blue-green phytoplankton and doubling of sediment phosphorus flux relative to model calibration.

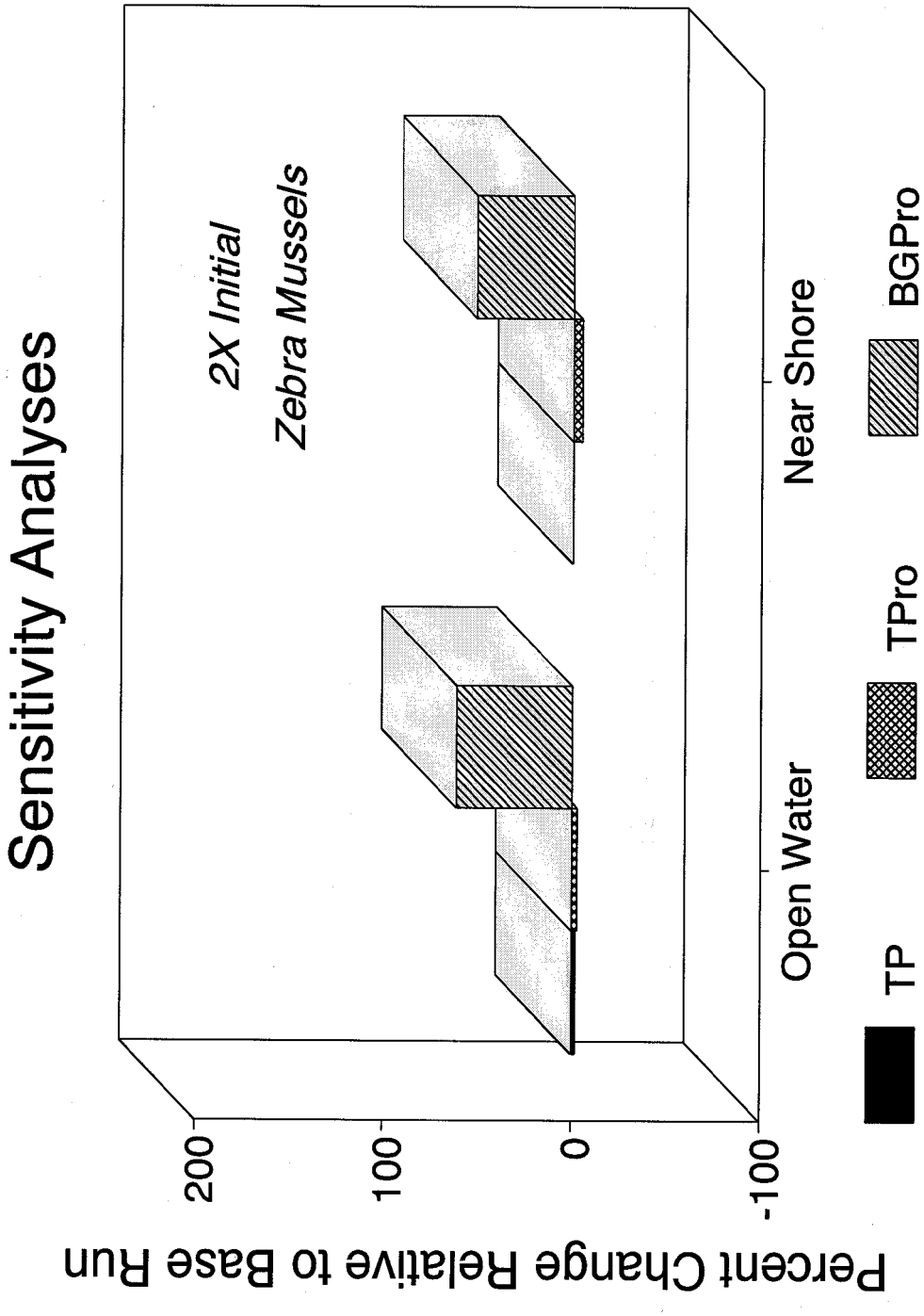


Figure 14. Model responses for sensitivity analysis to doubling of initial zebra mussel densities relative to model calibration.

production increases substantially in both the open water and near shore zones. These responses are consistent with increased filtration of diatoms, greens, and "other" phytoplankton, thus strengthening the competitive advantage enjoyed by the blue-greens.

Figure 15 contains results for assigning equal numbers of zebra mussels to each of the three cohort groups (2 Year Olds, 1 Year Olds, YOY). Total zebra mussel densities were not changed from base conditions; however, this re-assignment of total zebra mussel numbers generally resulted in larger numbers of adults and smaller numbers of YOY for a given model spatial segment. Although total phytoplankton production changes very little, blue-green production increases substantially in both the open water and near shore zones. These responses are consistent with increased filtration of diatoms, greens, and "other" phytoplankton due to the fact that older, larger zebra mussels have higher filtering rates than younger, smaller zebra mussels.

Discussion

Model responses to changes in zebra mussel densities were qualitatively similar to observed water quality responses in Saginaw Bay that took place during the period of the initial zebra mussel invasion (1990-1993). Model results for total phosphorus and total suspended solids concentrations, and total phytoplankton production, generally showed step decreases between the absence and presence of zebra mussels, especially in the near shore zone. Fahnenstiel *et al*. (1995a) reported that chlorophyll and total phosphorus concentrations decreased substantially in the inner bay during the initial zebra mussel invasion. Skubinna *et al*. (1995) reported that solids-related turbidity decreased substantially in the near shore zone. Johengen *et al*. (1995) reported significant decreases in inner bay annual mean values for total suspended solids and particulate phosphorus concentrations. Fahnenstiel *et al*. (1995b) reported substantial reductions in areal integrated and volumetric phytoplankton productivity in the inner portion of the bay.

Differences in responses between total phosphorus (Figure 7) and total suspended solids concentrations (Figure 8) reflect differences in the relative importance of external loads versus sediment resuspension. Total phosphorus concentrations, especially in the near shore zone on the eastern side of the bay, are more strongly influenced by Saginaw River loads than by sediment resuspension. In contrast, total solids concentrations are more strongly influenced by local sediment resuspension than by Saginaw River loads.

Vanderploeg *et al*. (1995) reported that zebra mussels exhibited a number of different mechanisms to selectively reject colonies of the blue-green alga, *Microcystis*, thus giving these algae a competitive advantage over other species. Zebra mussels were observed to filter water whether or not *Microcystis* was present; however, they spit *Microcystis* back into the water while continuing to filter out other algae, thus removing *Microcystis* competitors. These findings were the basis for including selective rejection of blue-green algae in the coupled phytoplankton-zebra mussel model.

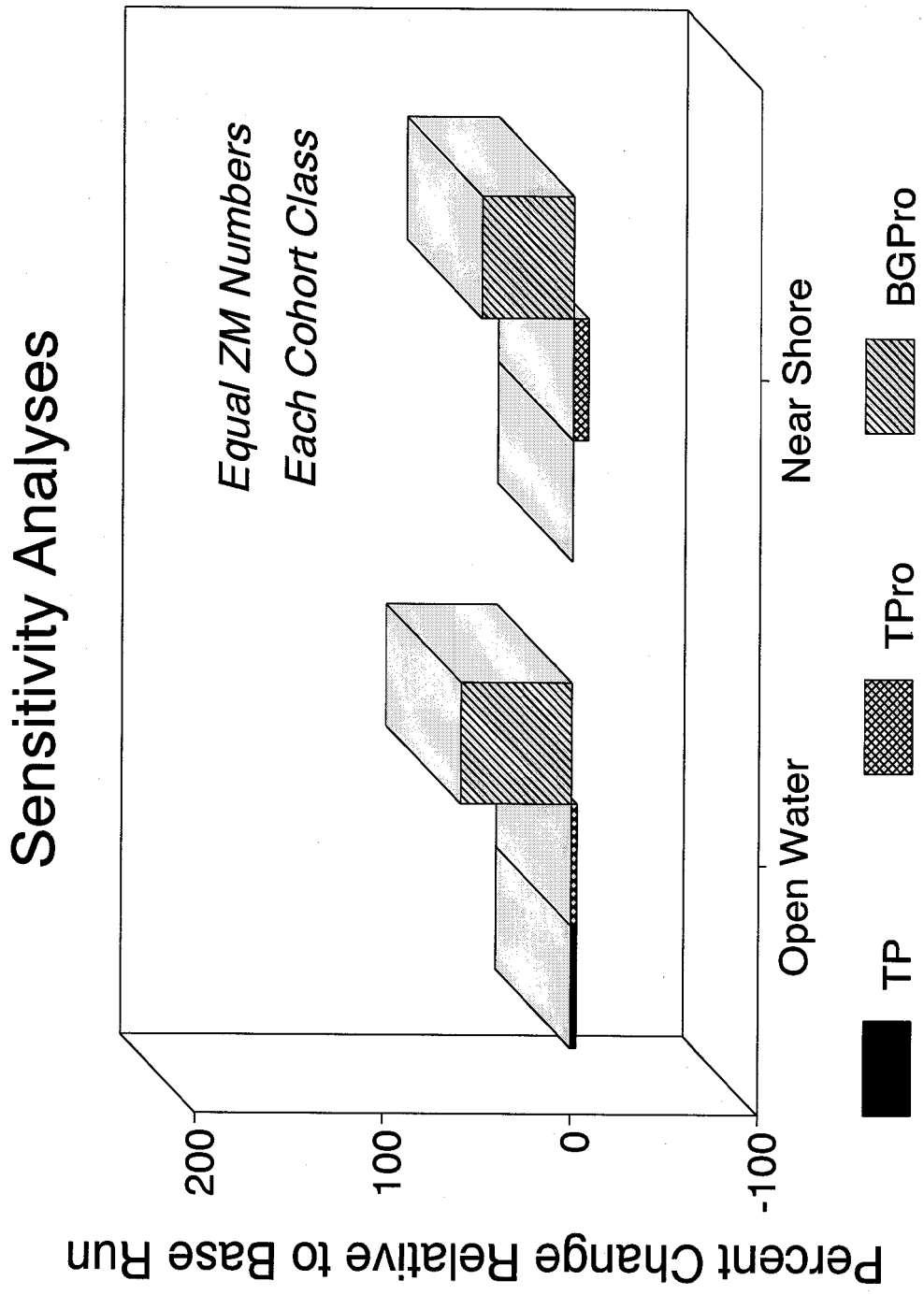


Figure 15. Model responses for sensitivity analysis to specification of equal zebra mussel numbers in each cohort class.

Nuisance blooms of *Microcystis* have occurred in Saginaw Bay every summer since 1994 (Vanderploeg 1996). It does not appear that changes in annual phosphorus loads since 1994 (Figure 5) were sufficient to cause these blooms. The blooms are qualitatively consistent with model responses showing large increases in blue-green phytoplankton production with increases in zebra mussel densities, especially the sharp step increases between the absence and presence of zebra mussels (Figure 10). Model responses for blue-green production also increased with enhanced sediment phosphorus fluxes attributed to presence of zebra mussels (Johengen and Cotner 1995); however, this enhancement occurred only when selective rejection of blue-greens was also included in the model (Figures 11-13).

Two observations with respect to the recent blue-green algal blooms in Saginaw Bay are unexplained: first, the initial zebra mussel invasion occurred during the period from 1990 to 1993 and the *Microcystis* blooms were not observed until 1994; and second, taste and odor problems have not been reported in the municipal water supplies. If zebra mussels were a causative factor in the *Microcystis* blooms, then differences in timing may have been due to population dynamics that are not fully understood. The serious taste and odor problems that occurred in Saginaw Bay in the 1970s involved *Aphanizomenon* (Bierman *et al*. 1984) not *Microcystis*. The absence of reported taste and odor problems may be due to physiological differences between these two species or because *Microcystis* biomass levels are not high enough to cause problems.

A major weakness in the present coupled phytoplankton-zebra mussel model is that it does not include explicit representation of zebra mussel population dynamics. Initial zebra mussel areal densities are externally specified and remain constant during each annual simulation. The model can not predict changes in spatial-temporal distributions of zebra mussels in the bay, nor can it predict distribution of zebra mussel numbers among different cohort groups. These factors are important because they appear to influence the degree to which zebra mussels impact bay water quality.

A deficiency in the current application of the coupled phytoplankton-zebra mussel model is that it has only been applied to actual field data for 1991. Water quality responses in Saginaw Bay are strongly dependent not only on annual phosphorus loads, but also on changes in advective-dispersive transport and actual nutrient loading time series among different years. These year-to-year variations can only be investigated by applying the model to year-specific external forcing functions and bay response data.

Conclusions

The following principal conclusions were drawn from the modeling research conducted in this supplementary study:

- Water quality responses in Saginaw Bay during the period from 1991 to 1995 were probably influenced by changes in both external phosphorus loads and zebra mussel dynamics.

- Total phosphorus concentrations in the bay are directly proportional to external phosphorus loads and inversely proportional to zebra mussel densities.

- Total solids concentrations are not strongly dependent on external phosphorus loads and are inversely proportional to zebra mussel densities.

- Total phytoplankton production is directly proportional to external phosphorus loads and inversely proportional to zebra mussel densities.

- Blue-green production is directly proportional to external phosphorus loads and zebra mussel densities.

- Responses to changes in external phosphorus loads and zebra mussel densities are generally greater in the near shore region than in the open water.

- Selective rejection of blue-green phytoplankton by zebra mussels appears to be a necessary factor in enhancement of blue-green production in the presence of zebra mussels.

- Enhancement of blue-green production in the presence of zebra mussels also appears to depend on:
  - ♦ zebra mussel densities;
  - ♦ distribution of zebra mussel densities among different cohort groups; and
  - ♦ sediment-water phosphorus fluxes.

Future research should include explicit representation of zebra mussel population dynamics in the model and application of the revised model to actual field data for the period 1991 to 1995. In addition, the revised model should be applied at finer spatial-temporal scales in the bay using the output of a fine-scale, site-specific hydrodynamic model for specification of advective-dispersive transport.

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Session 4 - Conceptual and Mechanistic Approaches to Development of Aquatic Ecosystem Assessment Models (Part 1)

Session Purpose

This session was designed to explore conceptual foundations of incorporating detailed process descriptions of demographic and bioenergetic processes into aquatic ecosystem assessment models, as well as spatially explicit descriptions of metapopulation dynamics and processes, based on the experiences of select speakers outside of WES and USACE. Discussions of session presentations focused on approaches to incorporating demographic and bioenergetic processes into aquatic ecosystem assessment models; linkages between demographic and bioenergetic processes in aquatic ecosystem models, and with existing biological and physical processes in water quality/contaminant models; and modeling biological processes in space associated with metapopulation dynamics.

Approaches to Large-scale Ecosystem Modeling Across Multiple Trophic Levels: Some Early Lessons from the South Florida ATLSS Experience

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Introduction

The Everglades region of South Florida offers one of the most complex challenges to natural system management currently faced in the U.S. The region has been greatly affected by many years of active human intervention to control the dominant environmental factor driving the system (water), with tremendous expenditures on a variety of canals, locks, and structures to drain certain portions of the system and control flooding. The effects of this intervention on natural components of the system have been extensive, including major declines in many species populations, greatly enhanced fluxes of certain nutrients, changes in plant community composition, and the release of high levels of toxicants including mercury. The complexity of hydrologic management of the system is enhanced by the mixture of agricultural demands, urban requirements from extensive human population growth, and calls for action by people concerned about further environmental degradation of the system. Davis and Ogden (1994) provide details on the system and its history.

The development of plans to restore the Everglades ecosystem to something closer to the original natural system is ongoing, with significant expenditures for physical modifications

being planned over the next several decades. As part of an effort to analyze the potential impacts of alternative restoration scenarios on the biotic systems of South Florida, a modeling project referred to as the Across-Trophic-Level System Simulation (ATLSS) has been ongoing with funding support from several government agencies (Fleming *et al*. 1994, USGS 1997). The Home Page for the ATLSS project is at http://www.tiem.utk.edu/~gross/atlss_www/atlss_frame.html.

Multimodeling and Other Approaches

The Everglades ecosystem is characterized by complex patterns of spatial heterogeneity and temporal variability, with water flow being the major factor controlling the trophic dynamics of the system. ATLSS uses a multimodeling approach, coupling compartment models for lower trophic levels, structured population/community models for intermediate trophic levels, and individual-based models for higher-level consumers. These are coupled in a spatially explicit manner through interactions on appropriate geographic information system (GIS) maps, with some of the map layers derived from or directly affected by various model components. The approach allows for direct use of both abiotic and biotic condition data, accounting for the spatial and temporal variability in these. A key objective of modeling studies for South Florida is to compare and evaluate the future effects of alternative hydrologic scenarios on the biodiversity of the system, and to provide a rational basis to prioritize monitoring activities for long-term adaptive ecosystem management.

The objective of multimodeling is to utilize a mixture of modeling approaches each of which takes account of the relevant spatial, temporal, and organismal resolutions necessary to address the questions for which the overall model is being developed. In ATLSS, the model types are associated with different types of species or functional groups of species in the ecosystem that have different-sized “ecological neighborhoods,” defined by Addicott *et al*. (1987) as “the region within which that organism is active or has some influence during an appropriate period of time.” The compartment models deal with variables representing spatially localized biota, mainly the biomasses of lower trophic levels such as periphyton. These biomass variables only interact locally. Therefore, one can represent these variables across a landscape by means of many local uncoupled spatial unit cell models, in which the cell size is chosen small enough to represent a tract relatively homogeneous in substrate and elevation, the linear resolution of which might be several tens of meters in a relatively flat landscape such as the Everglades. The age- and size-structured population and community models represent intermediate trophic levels, such as fish, macroinvertebrates, and small non-flying vertebrates. These may undergo short-distance movements in response to changes in water levels, so their ecological neighborhoods are larger, with a resolution perhaps on the order of up to a square kilometer, thus encompassing perhaps hundreds of unit cell models, coupled now to allow population movements. The individual-based models are employed to represent populations of top predators or other large-bodied species. Individuals of these species cover large areas of land and thus have large ecological neighborhoods. Their movements over short periods of time may span areas of tens of thousands of spatial unit cells.

The ATLSS approach therefore links a variety of modeling methodologies, each of which has been found to be an appropriate means to mimic select system components in many other studies. Thus, the approach offers the possibility to link together many of the methodologies presented at this Workshop, including matrix projections (discussed in the paper by Crowder *et al*.), bioenergetics, metapopulation approaches (Akçakaya), continuous structured population approaches (Hallam), and individual-based approaches (Rose). Through a combination of modeling approaches such as these, with underlying projections of environmental factors (in the case of ATLSS, this involves alternative future hydrologic scenarios), multimodeling offers a methodology for ecological risk assessment (Ginzburg) and uncertainty analysis which takes account of the detailed spatial and temporal interactions between biotic and abiotic factors in a natural system. Through its modular representation of the system, it also offers the capability to include, when feasible, other detailed modeling efforts such as the Everglades Landscape Model (Fitz *et al*. 1996), which focuses on nutrient fluxes in the system.

Although carrying out a detailed multimodeling analysis is data-intensive and time-consuming, many of the environmental management problems faced by agencies such as the U.S. Army Corps of Engineers (USACE) involve complex situations over large spatial regions. For these problems, simplified approaches such as Habitat Evaluation Procedures (HEP) and Hydrogeomorphic (HGM) assessment (Brinson 1996), which were designed for relatively quick analysis of small spatial domain problems for regulatory purposes, are inappropriate. One potential use of multimodeling approaches, however, will be to lead to more appropriate macrodescriptors of wetland systems, and in this way both provide details on the reference systems that are an inherent part of the HGM methodology (Brinson and Rheinhardt 1996), as well as indicate under what circumstances HEP approaches, which ignore the underlying demographics and dynamics of system components, may have sufficiently small errors to be useful.

Some Lessons from the ATLSS Experience to Date

The ATLSS project has involved a wide variety of individuals from government agencies (both U.S. and non-U.S.), academia, and private firms. Over the relatively short span of its existence (the initial funding of what eventually became part of the ATLSS project was in 1991), the main funding agency has changed three times (from the National Park Service, to the National Biological Survey, to the USGS). Involving as it does a highly contentious region, agencies and stakeholders with greatly varying agendas, and individuals from a diverse set of scientific backgrounds, we thought it would be appropriate to summarize our impressions of key take-home messages from the project to date. These are not meant to focus on the scientific aspects of the project, but more on our impressions of how to carry out a successful multimodeling project of this type. The lessons summarized below are not ranked in any particular priority order, though we have placed those dealing more with modeling aspects first.

Work closely with those having long experience in the system being modeled, and use their experience to determine key species, guild, and trophic functional groups on which to

focus the modeling effort. As with any model, there are parts of the system which will be investigated in more detail than others. We have fostered close relationships with individuals who are very knowledgeable from their own fieldwork about detailed components of the system, and encouraged them to become part of the various modeling teams.

Moderate the above based first on the availability of data to construct reasonable models, and then on the difficulty of constructing and calibrating the models. In deciding what components to include in the system models, not only is it necessary to have an appropriate set of data, but staff, time, and computational constraints may lead to selection of a more simplified modeling approach than was initially viewed as feasible or appropriate.

Don't try to do it all at once - start small, but have a long-term plan for what should be included in the overall suite of models, given realities of time and funding. This allows the team to obtain initial model results quickly for funding agencies, but at the same time provides a clear vision as to what could be accomplished with further support.

Leave room for multiple approaches; don't limit options. Accept the fact that other approaches will be taken, and that for some purposes these other approaches may add significantly to the overall effort.

In the face of limited or inappropriate data, take the opportunity to encourage further empirical investigations of key components of the system. As one example of this, due to initial efforts to develop an alligator model, it became obvious that a study of food habits of South Florida alligators was needed. Although the assumption had been made that fish constitute a major prey of alligators, the study found that fish comprise a relatively minor proportion of the diet.

Build as much flexibility into the program as possible. Such flexibility is needed to account for the possibility of different funding levels through time, the various needs of different funding agencies, and the potential for changing the criteria of success due to these factors.

Be flexible about what counts as success - e.g., don't expect the world suddenly to adopt your definition. Be willing to adjust your efforts regularly to meet short-term needs of stakeholders, but maintain an overall vision for longer-term project goals.

Be persistent, and have at least one member of the team who is totally dedicated to the project and willing to stake their future on it. Major projects such as ATLSS have the potential simply to fall by the wayside in relation to funding decisions, unless the project team includes a regular supporter willing to argue for support. This is particularly true for the long-term scientific aspects of the project, which may be considered of secondary interest to funding agencies more concerned with short-term management of natural systems.

Do whatever is possible to maintain continuity in the source of long-term support for the project. Associated with this is the need to maintain continuity in key technical staff

associated with the project, since no matter how well documented a programmer's code is, there is inefficiency associated with staff turnover.

Build a quality team who respect each others' abilities and won't second guess each other, but who accept criticism in a collegial manner. This is also important for publication aspects of the project, plans for which should be part of regular project meetings, with agreements on authorship clearly specified and agreed to by all involved.

Keep some part of the team out of the day-to-day political fray. The regular infighting that is typical of contentious public-policy projects can be very distracting to team members who do not need to be actively involved in responses on such matters to various agencies. Protecting team members from such distractions can greatly increase the overall efficiency of the project.

Constantly communicate with stakeholders - set up a liaison with a critical representative of each stakeholder.

Don't limit the project approach based on the desires of one stakeholder/funding agency - maintain the highest scientific standards possible can and be honest about the limitations of the chosen approach.

Be prepared for criticism based upon non-scientific criteria, including personal attacks.

Ignore any of the stakeholders at your peril.

Acknowledgments

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Development and Use of Matrix Models to Evaluate Alternative Management Approaches for Restoring Biological Populations

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The Problem

In the U.S., there are nearly one thousand species listed as endangered or threatened under the Endangered Species Act of 1973. Many marine organisms have declined, but documented extinctions are relatively rare (Sissenwine and Rosenberg 1993, NRC 1990). However, freshwater systems are at particular risk. While only 11-15 % of terrestrial vertebrates in the U.S. are classified as rare or extinct, 34% of freshwater fishes, 65% of crayfishes, and 75% of unionid mussels are now seriously threatened or extinct (Master 1990). Despite strong efforts to improve water quality, none of the 251 fishes listed as rare in 1979 were removed from the list in 1989, except via extinction (Williams *et al*. 1989). Major factors cited for these declines include habitat modification, effects of introduced species, chemical alteration of the habitat (including enrichment), hybridization, and overharvesting. Frequently, declines have been attributed to more than one cause (Williams *et al*. 1989).

The future of threatened aquatic populations depends upon effective management and recovery plans. Unfortunately, our knowledge of a threatened species' life history and of the potential costs and benefits of various management alternatives is extremely limited. In addition, research budgets are often limited and time to arrive at conclusions short. To manage effectively under these constraints, it is critical to evaluate the *relative* effectiveness of specific changes in vital rates (*e.g.*, juvenile survival vs. fecundity) on population responses (*e.g.*, population growth rate, abundance, or size/age structure), and the importance of uncertainty in our knowledge of these vital rates.

The philosophical basis for our approach dates to Thomas Chamberlain's (1890) paper on "The method of multiple working hypotheses." Most patterns in nature are driven by multiple mechanisms, not by single causative factors. Chamberlain (1890) proposed that we could more rapidly understand cause and effect by considering multiple hypotheses, including interacting effects, and then proposing experiments or observations which would allow us to narrow the list to those hypotheses most likely to produce the observed dynamics. In management of a threatened species, we can consider proposed management approaches as

alternative hypotheses and evaluate which management alternatives appear most (or least) likely to enhance population recovery.

Matrix Modeling

One set of tools for enhancing decision making involves deterministic matrix modeling; this approach focuses on relative changes in population responses as certain parameters in the population model are changed. One commonly used population response is λ, the population growth rate. The growth rate λ is related to the intrinsic rate of increase r obtained for Lotka's equation $r = \ln \lambda$. Elasticity analyses can reveal how changes in age- or stage-specific vital rates (*e.g.* survival, growth, or fecundity) affect λ. We can apply this approach to determine: 1) which stage-specific vital rates are most critical to population growth; 2) which processes or life history stages should be the focus of conservation; 3) which of an array of management alternatives is most likely to produce the desired results; and 4) where to focus limited research efforts to refine parameters for future analyses (Schemske *et al*. 1994, Heppell *et al*. 1997). In models which incorporate density dependence or stochasticity, the sensitivity of other response variables (such as population size) to changes in vital rates can also be examined.

It is outside the scope of this paper to outline fully the techniques for matrix modeling and analysis, but this is fully reviewed elsewhere (Caswell 1989, McDonald and Caswell 1993, Heppell *et al*. 1997). Deterministic, linear models are relatively simple to produce, easy to interpret, and provide analytic rather than simulation results. With a matrix model, we calculate the proportion of individuals in an age or stage class in each time period, dependent on the survival and growth rates of individuals within each class and the fecundity of individuals in each class. A transition matrix contains one row and column for each age/stage class in the model, with each entry representing the probability of survival and transition to another stage or fecundity. Using techniques from linear algebra, we can estimate λ, the stable age/stage distribution, and the reproductive value of individuals in each age/stage class. This approach assumes all individuals within a class are identical and that vital rates do not change over time. Deterministic models cannot be used to estimate future population size (despite being called projection matrices) and are inappropriate for small or isolated populations that are subject to high demographic stochasticity.

Matrix models require less data than individual-based or stochastic models. For conservation managers, this can be an advantage, because data are too limited for most threatened species to use more complicated modeling approaches. To produce a simple matrix model, we need age/stage specific vital rates information, similar to that included in a typical life table. The simplest matrix model is age-based (Leslie 1945), where surviving individuals grow into the next age class at each time step. In stage-based models, surviving individuals may remain in a stage for one or more time steps before making the transition to another life stage (Crouse *et al*. 1987). Organisms with complex life histories may make transitions to a variety of life stages (Heppell *et al*. 1994).

The real utility of matrix models hinges on elasticity (= proportional sensitivity) analysis; this analysis allows quantitative comparisons of the relative impact of model parameters on a population response which can be used to qualitatively compare management alternatives. Details of the methods for elasticity analysis are reviewed elsewhere (deKroon *et al*. 1986, Caswell 1989, Heppell *et al*. 1997). Elasticity analysis can help managers decide which life stages are in most need of protection and which model parameters need additional research (Schemske *et al*. 1994). If we can determine how a particular management proposal is likely to influence vital rates, we alter the particular vital rates in the model and examine projected population responses to each management alternative. The best use for this type of analysis is to eliminate management alternatives that are unlikely to lead to population recovery, as in the headstarting (*i.e.*, captive rearing) of Kemp's ridley sea turtles (*Lepidochelys kempi*) (Heppell *et al*. 1996).

Case Studies

Loggerhead Sea Turtles (Caretta caretta)

We evaluated alternative management scenarios for threatened loggerhead sea turtles in the southeastern U.S. using matrix models (Crouse *et al*. 1987, Crowder *et al*. 1994). By the mid-1980s, beach monitoring and nest protection programs had documented: 1) dramatic declines in adult nesting females; 2) nest, egg, and hatchling losses to erosion and predation; and 3) carcasses of drowned adult and juvenile turtles often washed ashore (these were termed "strandings"). Incidental capture of turtles in fishing gear, particularly shrimp trawls, appeared to account for most (but not all) of the strandings (Henwood and Stuntz 1987). In response to large numbers of stranded turtles, the National Marine Fisheries Service (NMFS) developed turtle excluder devices (TEDs) which could be installed in trawl nets to reduce turtle mortality. As managers considered requiring the use of TEDs in shrimp trawls, they encountered substantial resistance. Nest protection did appear to enhance egg survival, allowing the release of more hatchlings, at a minimal socioeconomic cost. Should managers require a strongly resisted approach (TEDs) of a industry already in financial trouble or opt for increasing low cost and widely popular nest protection projects?

Crouse *et al*. (1987) produced the first population model for loggerhead sea turtles. Elasticity analyses of the matrix showed that survival in the three juvenile stages, particularly the large juvenile stage (50-80 cm carapace length), as the most important to determining future population growth. Coincidentally, this was also the size class most often stranded dead on beaches. The model also documented that even 100% survival of the egg/hatchling stage was unlikely to reverse current population declines. Crouse *et al*. (1987) did not advocate terminating nest protection projects, but noted that nest protection projects without concurrent reductions in juvenile mortality (through the use of TEDs or some other method) would likely be futile. Subsequently the National Academy of Sciences review panel recommended requiring TEDs "in most trawls at most times of year" (NRC 1990). Recent estimates of reductions in strandings due to TEDs (Crowder *et al*. 1995) appear to be sufficient to allow loggerhead recovery (Crowder *et al* 1994). However, it will be decades before we can be sure of the effects

of current TED regulations, because only the nesting female populations are monitored and females first return to nest at 20-25 years of age.

Southern Appalachian Brook Trout (Salvelinus fontinalis)

Brook trout populations in the Southern Appalachians have declined in response to multiple anthropogenic effects including the introduction of an exotic salmonid (rainbow trout, *Oncorhynchus mykiss*); a decrease in pH (through acid deposition); an increase in siltation and allochthonous nutrients, and a decrease in shade (from road building and logging); and an increase in fishing pressure. We developed a population model based on a simple size-classified projection matrix to examine multiple anthropogenic effects and determine which factors are most (or least) important to population dynamics (Marschall and Crowder 1996). Density dependent survival was added to the model by multiplying the linear transition matrix by a second matrix with per capita survival probabilities on the diagonal entries; survival in the age 0 size classes depended on body size and number of age 0 fish (Marschall and Crowder 1995).

We evaluated the sensitivity of equilibrium population size and size-class structure to a variety of parameter perturbations (Marschall and Crowder 1996). Potential brook trout responses to rainbow trout include a decrease in survival rate of small fish, a change in density dependence in survival of small fish, and a decrease in growth rates of all sizes. When we included these responses in the population model, we found that population size tended to decrease with an increase in small fish growth rate (producing a population with fewer, but larger, fish). In addition, changes in the patterns of density-dependent survival also had a strong impact on both population size and size structure. Brook trout respond to decreases in pH with decreased growth rates in all size classes, decreased survival rates of small fish, and decreased egg-to-larva survival rates. This combination of effects, at magnitudes documented in laboratory experiments, had severe negative impacts on the modeled population. If siltation effects were severe, the extreme increase in egg-to-larva mortality could have strong negative effects on the population. However, even very strong increases in large fish mortality associated with sport harvesting were not likely to cause local extinction. In all of these cases, the interaction of drastic changes in population size structure with randomly occurring floods or droughts may lead to even stronger negative impacts than those predicted from the deterministic model.

Because these fish can reproduce at a small size, negative impacts on survival of the largest fish were not detrimental to the persistence of the population. Because survival of small juveniles is density dependent, even moderate decreases in survival in this stage had little effect on the ultimate population size. In general brook trout will respond most negatively to factors that decrease survival of large juveniles and small adults, and growth rates of small juveniles.

Finfish Bycatch in Trawl Fisheries

Bycatch is the incidental catch of non-target species that occurs to some extent in almost all commercial fisheries. In the U.S. shrimp trawl fishery, located in the estuarine, nearshore, and offshore waters of the Gulf of Mexico and the Atlantic Bight, bycatch comprises an average of 60-80% of the catch by weight. Shrimp trawl bycatch consists mainly of juvenile fishes and

invertebrates, including species that are highly valued as adults in other commercial or recreational fisheries. Commercial and recreational fishermen, as well as conservationists, have demanded reductions in bycatch on the grounds that these fish are "wasted." In addition, commercial and recreational fishermen in other fisheries face increasingly strict regulations because of declining fish stocks, and these fishermen are unwilling to accept new restrictions unless the incidental mortality is also reduced. For harvested populations, managers would like to know the tradeoff between bycatch and catch in targeted fisheries. For example, how much potential catch is lost due to bycatch?

Recent stock assessments for valuable species such as red snapper (*Lutjanus campechanus*) and weakfish (*Cynoscion regalis*) have clearly indicated that bycatch mortality is a significant factor in the decline of these species (Powers *et al*. 1987, Goodyear 1990, Vaughan *et al*. 1991). Because the shrimp trawl fishery is the most valuable fishery in the southeast, efforts to reduce bycatch have chiefly been aimed at developing bycatch reduction devices (BRDs), modifications of trawl gear that allow fish to escape while retaining shrimp. But managers looking to reduce bycatch are faced with several questions concerning bycatch reduction, including: How much should bycatch be reduced? What increase in the abundance of adults will result from a given level of bycatch reduction? How important to the population is juvenile bycatch mortality compared to other factors such as harvesting of adults, pollution, or winter cold spells that affect growth or survival in other stages of life?

In an ongoing study, we are using matrix models to analyze the effects of bycatch on fish populations in the Gulf of Mexico, where shrimping effort is high and bycatch is an order of magnitude higher than elsewhere in the U.S. (Diamond *et al*. in prep.). We used Atlantic croaker (*Micropogonias undulatus*) as a representative of the estuarine-dependent species complex, which accounts for 80-90% of the commercial fishes landed in the southeastern U.S. To investigate the effects of bycatch, we are using our model to examine the effects of different levels of Atlantic croaker bycatch and adult mortality, corresponding to management strategies aimed at reducing bycatch, reducing the harvesting of adults, or both. We are also exploring which parameters have the greatest effect on population growth rates and on the number of adult fish. It is premature to report our results here, but suffice it to say that survival in the large juvenile stage, which is heavily impacted by bycatch, is a highly sensitive process, suggesting that bycatch reduction for finfish, like sea turtles, may have strong population level effects.

Discussion

Matrix models may prove to be useful tools to focus research and management efforts and to enhance recovery of threatened populations. Because many declining populations also have poorly known population dynamics, information is often too limited to employ more robust approaches, including stochastic matrix models or individual-based models, which can examine more directly the effects of demographic and environmental stochasticity. Our approach explicitly considers that population declines are often due to multiple factors, some of which managers can respond to and others to which they cannot. These factors can be combined to

yield multiple working hypotheses (Chamberlain 1890) regarding causes of the decline. These causes impact different life stages and vital rates at different magnitudes. Matrix models provide a way to qualitatively compare the population-level effects of mitigation techniques that can influence stage-specific vital rates. This allows us to determine which of many proposed management approaches is most (or least) likely to contribute to population recovery.

Given the severe problems with threatened populations in aquatic ecosystems and the limited resources with which to address those problems, we recognize the need for a simple approach to address alternative management approaches and to focus critical research efforts. Like any simple approach, matrix modeling has real limitations. But often it provides a viable initial approach to the problem.

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Metapopulation Models and Ecological Risk Analysis: A Habitat-based Approach to Biodiversity Conservation

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Introduction

Natural environments usually show a high degree of spatial heterogeneity that determines the distribution and movement of organisms. For example, kelp (*Macrocystis pyrifera*) "forests" off the coast of southern California grow in patches determined mostly by the properties of the substrate on the ocean floor, the water depth and light (Burgman and Gerard 1989). There are numerous other examples of patchy distribution of habitats; *e.g.*, ponds in a forest, islands in an archipelago, woods in an agricultural landscape, and mountaintops in a desert. Species that occupy such patchy habitats exist not in a single population, but in a number of populations that are either isolated from each other or have limited exchange of individuals. Local populations occupy patches of high (or at least survivable) habitat quality, and use the intervening habitat only for movement from one patch to the other. Such a collection of populations of the same species is called a *metapopulation*.

In addition to the patchiness or heterogeneity of natural habitats, human-induced changes in the environment have increased the prevalence of metapopulations. For example, habitat loss often results not only in an overall decrease in the amount of habitat, but also in discontinuities in the distribution of the remaining habitat. Discontinuities can be created by opening land to agriculture, and by construction of buildings, dams, roads, power lines, and utility corridors. The result is the fragmentation of the original habitat, which now exists in disjunct patches. Any population that inhabited the original habitat will now be reduced to a smaller total size, and would be divided into multiple populations. Further fragmentation results in a decrease in the average size of habitat patches, makes them more isolated, and causes increased edge effects. Species that live in metapopulations are thus vulnerable to additional types of impact. In addition to impacts that decrease the survival or fecundity in a single population, a metapopulation can be subject to impacts that change the size, number, spatial distribution, and isolation of the habitat patches.

Species that live in multiple populations can also be managed in more ways than single populations. For example, they can be subject to management practices (such as the translocation of individuals from one patch to another) that increase the rate of migration. An important aspect of species conservation is reserve design, which involves selecting certain parts or patches of habitat for protection. The resulting network of reserves forms a metapopulation of the protected species. Which combination of nature reserves gives the endangered species the highest chance of survival can only be assessed by an analysis of metapopulation dynamics. The famous SLOSS controversy (whether a single large reserve or several small reserves of the same total area provide better protection) can best be answered on a case-by-case basis by a

metapopulation viability analysis. Other management options that can be evaluated at the metapopulation level include the reintroduction of species into their original habitat patches, and establishment and maintenance of habitat corridors that increase connectivity among habitat patches.

Dynamics of Metapopulations

Analyzing the dynamics of species that live in multiple populations, or evaluating management options such as those discussed above, requires a metapopulation approach. This is because in most cases, the dynamics of a metapopulation cannot be deduced from the dynamics of its constituent populations. Single population dynamics are determined by factors such as population size, life history parameters (fecundity, survivorship, density dependence), and demographic and environmental stochasticity that cause variation in these parameters. The dynamics of a metapopulation or a species depends not only on these factors, but also on other factors that characterize interactions among these populations. The additional factors that operate at the metapopulation or species level include the number and geographic configuration of habitat patches, and dispersal and spatial correlation among these patches.

Spatial correlation refers to the similarity (synchrony) of environmental fluctuations in different parts of the landscape and, in the case of a metapopulation, in different populations. If the fluctuations in the environment are at least partially independent, so would be fluctuations in population dynamics. Thus it would be less likely that all populations go extinct at the same time, compared to a case where the fluctuations were dependent, *i.e.*, synchronous (Akçakaya and Ginzburg 1991, Burgman *et al*. 1993, LaHaye *et al*. 1994). In most metapopulations, fluctuations in demographic rates are caused by large-scale climatic factors such as rainfall, temperature, flow rate, etc. These factors are often correlated even at relatively large distances. For such metapopulations, models based on an assumption of independent fluctuations among patches will underestimate the temporal variability of population dynamics and therefore the extinction risk of the metapopulation.

Correlation among the fluctuations of populations is often a function of the distance among them. If two populations are close to each other geographically, they will experience relatively similar environmental patterns, such as the same sequence of years with good and bad weather. This may result in a high correlation between the vital rates of the two populations. For example, Thomas (1991) found that Silver-studded Butterfly (*Plebejus argus*) populations that were geographically close tended to fluctuate in synchrony, whereas populations further apart (>600 m between midpoints) fluctuated independently of one another. Similarly, Baars and van Dijk (1984) found that in two carabid beetles, *Pterostichus versicolor* and *Calathus melanocephalus*, the significance of rank correlation between fluctuations declined with increasing distance between sites.

When modeling metapopulations, the correlation among population fluctuations may be modeled as a function of the distance among habitat patches. This can be done by sampling the

growth rates of each population from random distributions that are correlated, and the degree of correlation may be based on the distance among populations. This approach was used by LaHaye *et al*. (1994) to model correlated metapopulation dynamics of the California spotted owl. LaHaye *et al*. (1994) modeled this spotted owl metapopulation by making the growth rates of each population correlated with the growth rates of other populations. They calculated the degree of correlation based on the similarity of rainfall patterns among the habitat patches.

Dispersal among populations may lead to recolonization of empty patches (*i.e.*, extinct populations) by immigration from extant populations. Such recolonization would have a positive effect on overall metapopulation persistence. Dispersal rates depend on many factors, for example species-specific characteristics such as the mode of seed dispersal, motility of individuals, ability and propensity to disperse, etc. These factors will determine the speed and ease with which individuals search for and colonize empty habitat patches. However, the migration rate between any two populations of the same species may also differ drastically, depending on a number of population-specific characteristics. These characteristics include the distance between the populations, the type of habitat used during dispersal, and the density of the source population. Depending on these factors, migration from each local population to all others may not be possible. Consequently, the exact effect of migration on species extinction will depend on the topology (the network) of the migratory pathways or connections among populations.

The effectiveness of dispersal in reducing extinction risks depends to a large extent on the degree of similarity of environmental fluctuations experienced by different populations (*i.e.*, their correlation or interdependence). This is because when all populations decline simultaneously, there will be less chance of recolonization of empty patches. However, if the fluctuations are at least partially independent (uncorrelated), then when some populations decline or become extinct others may remain extant or even increase, thus providing recolonization opportunities. The dynamics of metapopulations are very sensitive to the spatial factors that operate at the metapopulation level. Thus, ignoring spatial correlations, geographic location of habitat patches, or dispersal patterns may bias the predictions.

Metapopulation Models

There are several different types of models for describing the dynamics of metapopulations, and several different ways to classify them. Here the models are grouped according to their variables and parameters.

Occupancy Rate Models

The variable of interest in these simplest metapopulation models is the proportion of habitat patches that are occupied by the species. Each patch is considered to be either occupied or empty, *i.e.*, there is no internal dynamics within a patch. Parameters of these models are the probability of recolonization of an empty patch, and the probability of extinction of an occupied patch. Examples of such models include one of the first metapopulation models, by Levins

(1970), as well as more recent models developed by Nisbet and Gurney (1982), Hanski (1983), Harrison and Quinn(1989), and Gilpin (1990).

Assumptions of Levins (1970) include (1) lack of local population dynamics, (2) infinite number of patches, (3) equal risk of extinction in all patches, (4) equal probability of recolonization of all patches, and (5) independent (uncorrelated) extinctions. More recent generalizations of this model have addressed some of these rather unrealistic and conflicting assumptions (see review in Burgman *et al*. 1993, pp. 188-193). However, all occupancy rate models are spatially unstructured, *i.e.*, the model parameters do not depend on the geographic configuration of patches. Chance of recolonization (rate of dispersal) and the correlation of extinction risks are the same regardless of the distance of a patch from the others. In addition, the patches are assumed to be identical. The model parameters are the same regardless of the size, quality, and other characteristics of habitat patches.

Occupancy State Models

These models are also based on the occupancy of patches, *i.e.*, as in all occupancy models, each patch is either occupied or empty, without any local population dynamics. In occupancy state models, the state of the metapopulation is characterized by the occupancy status of the metapopulation. For example, a metapopulation with 2 populations may be in one of four states: (0,0) if both patches are empty, (1,1) if both are occupied, and (1,0) or (0,1) is only one is occupied (Akçakaya and Ginzburg 1991). The parameters of the model are the rates of transition among these states, which can be arranged in a transition matrix. The transition rates are functions of the probability of extinction and recolonization, which may be different for each patch (Burgman *et al*. 1993, pp.193-205). However, the number of populations that can practically be modeled is very limited, and the parameters are difficult to estimate.

Spatially Explicit (Population-dynamic) Models

Populations differ in their size, carrying capacity, location, rate of growth, and many other characteristics that are important determinants of the metapopulation dynamics. Spatially explicit models can incorporate this complexity by describing the internal dynamics of each population separately, and the dynamics of the metapopulation through the correlation of stochasticity in internal dynamics, and through dispersal among populations. The internal dynamics can be described by a scalar (unstructured) model, or by a frequency-based model (such as a stage-structured matrix model, or an age-structured model based on a Leslie matrix). Because of the complexity of the interactions among these factors, these models can only be developed as computer algorithms that use stochastic simulation methods (Akçakaya and Ferson 1990, Akçakaya 1997).

Population dynamic models can be data-intensive. In addition to parameters related to the dynamics of each population, they require parameters that describe the metapopulation-level factors such as spatial correlation and dispersal. However, they can also be used to build simple models, by assuming the same growth model for all populations, the same rate of dispersal among any pair of populations, and the same rate of correlation (*e.g.*, zero or uncorrelated dynamics) among populations. Thus, they can be used with as little data as the occupancy

models, with the major difference that the simplifying assumptions are made explicitly, instead of the implicit assumptions of occupancy models.

Individual-based Models

In individual-based metapopulation models, each individual in the population is modeled separately, with parameters such as age, sex, mating status, location (*i.e.*, which habitat patch it is in), number of offspring, etc. In addition, a number of parameters describe the dispersal and reproductive behavior of the species. Individual-based models are the most data-intensive types of metapopulation models; the number of parameters required for individual-based models restrict their use to well-studied species with small populations, such as the Northern Spotted Owl (Lamberson *et al*. 1992).

Selecting the Right Model

One of the important decisions in building models concerns the complexity of the model appropriate for a given situation, *i.e.*, how much detail about the ecology of the species or the ecosystem to add to the model. Simple models are easier to understand, and more likely to give insights that are applicable in a wide range of situations. They also have more simplistic assumptions, and lack realism when applied to specific cases. Thus, they cannot be used to make reliable forecasts in practical situations.

Including more details makes a model more realistic, and easier to apply to specific cases. However in most practical cases, available data are limited and permit only the simplest models. More complex models require more data to make reliable forecasts. Attempts to include more details than can be justified by the quality of the available data may result in decreased predictive power and understanding.

The predictions of individual-based models are often very sensitive to assumptions and parameters related to the dispersal behavior, the mating behavior, and the physiological basis of the growth and reproduction of individuals. Frequency-based (population-dynamic) models, on the other hand, do not include these details because they use parameters that are “averaged” over larger temporal and spatial scales (such as survival rate from one year to the next, or average fecundity at the population level).

The question of the appropriate level of complexity (*i.e.*, the trade-off between realism and functionality) depends on: (1) characteristics of the species under study (*e.g.*, its ecology), (2) what we know of the species (the availability of data), and (3) what we want to know or predict (the questions addressed). In addition, portability of the model to other systems or locations may be a significant practical issue to consider when deciding on the level of complexity of a model.

Even when detailed data are available, general questions require simpler models than more specific ones. For example, models intended to generalize the effect of one factor (such as variation in growth rate) on a population's future may include less detail than those intended to forecast the long-term persistence of a specific species, which in turn, may include less detail

than those intended to predict next year's distribution of breeding pairs within a local population.

Risk Analysis with Metapopulation Models

The natural variability of populations and communities requires a stochastic approach to modeling. Ignoring variability in models of inherently variable systems results in biased and misleading conclusions, and confuses the end users with a false sense of predictability. Many questions in assessment of human impacts and in conservation of species are naturally phrased in terms of risk (Akçakaya 1992). Stochastic metapopulation models allow the calculation of risks of decline or extinction, or chances of recovery and increase to various levels of abundance. These results may be used to rank alternative management options in terms of their effect on the chance of recovery of a population, to estimate the risk of extinction of a threatened or endangered species under various scenarios, and to assess the relative impacts of different human activities on natural systems.

Incorporating Uncertainty in Metapopulation Models

In addition to the natural variability inherent in all natural systems, metapopulation models need to incorporate variability originating from lack of knowledge, measurement error, or uncertainty about parameter values and functions. Almost all parameters of a metapopulation model are known with some amount of uncertainty. In some cases, the uncertainty is large, because past efforts have not concentrated on that particular parameter.

These types of uncertainties, unlike natural variability, can be reduced when more data become available. Incorporating uncertainty in models provides a measure of the reliability of the model, and makes it possible to estimate the significance of the difference in models with different management options or types of human impact. In addition, sensitivity analyses can be performed to identify important parameters, and thus guide future empirical effort.

Future Directions in Modeling Aquatic Metapopulations

Incorporating Habitat into Metapopulation Models

Metapopulation models assume that the habitat is in discrete patches that are, or at least can potentially be, occupied by populations, and that are surrounded by unsuitable habitat. In some cases, the species in question has a specific habitat requirement that has sharp boundaries, making patch identification quite straightforward. In other cases, habitat quality varies on a continuous scale and designation of areas as habitat and non-habitat may be somewhat arbitrary. Or, the boundaries may not be clear-cut for human observers: what seems to be a homogeneous habitat may be perceived as a patchy and fragmented habitat by the species living there. If the suitability of habitat for a species depends on more than one factor, and some of these factors are not easily observable, the habitat patchiness we observe may differ from the patchiness from a species' point of view. In such cases, the information about habitat requirements may be combined by computer maps of each required habitat characteristic, using geographic information systems (Akçakaya 1997). This approach has been used to model the metapopulation dynamics

of a number of terrestrial species, including the Helmeted Honeyeater (*Lichenostomus melanops cassidix*), an endangered bird in Victoria, Australia, and of the California Gnatcatcher (Akçakaya and Atwood 1997), another endangered bird species. Similar methods may be developed for aquatic organisms by (1) statistically describing the species-habitat relationship; (2) creating maps of habitat suitability based on this relationship; (3) determining habitat patches based on distribution of suitable habitat; and (4) estimating population-level and metapopulation-level parameters based on habitat-related variables.

Metapopulation-based Community Models

Another approach is to expand the spatially explicit metapopulation models to include trophic interactions. In this approach, each trophic level is represented as a metapopulation. Each of these metapopulations is modeled at a different spatial scale. The lower trophic levels (due to the smaller size and lower motility of the individuals) are modeled at a finer spatial resolution, whereas the higher trophic levels are modeled at a lower resolution, perhaps even as a single (mixed or panmictic) population instead of a metapopulation. Similarly, the lower trophic levels are modeled at a finer temporal scale, because of their faster turnover rate. Higher trophic levels (such as fish), which often reproduce once a year, can be modeled at annual time steps, whereas phytoplankton may be modeled at a weekly time scale.

Several issues need to be addressed in building metapopulation-based ecosystem models. One of these is the coordination of multiple spatial and temporal scales. Another issue is determining the relationships (predation function, etc.) between the trophic levels. The complexity of these relationships makes it necessary to simplify the community model by aggregating species into functional groups (trophic level, guild). The level of aggregation may be different for different levels, depending on the availability of the data, and the questions that the model is to answer.

Multispecies Assessments Based on Habitat Relationships and Landscape Data

The habitat-based determination of the suitability and spatial structure of the landscape discussed above can be extended to multiple species by developing habitat suitability maps for several species in the same landscape, and combining these into a composite map. The habitat suitability maps may be combined by calculating a “multi-species habitat value” for each cell, as a weighted average of the values from the single-species maps. The averaging may be done with weights based on the extinction risk of the species involved. This approach can be used in management in two ways. One is the assessment of the “conservation value” of predefined parcels for purposes of conservation planning or mitigation. Another use is in identifying patches or locations with high “multispecies habitat suitability” for purposes of reserve design.

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Session 5 - Conceptual and Mechanistic Approaches to Development of Aquatic Ecosystem Assessment Models (Part 2)

Session Purpose

This session was intended to focus on alternative mechanistic approaches (*e.g.*, individual based models, physiologically structured models) to developing aquatic ecosystem assessment models that incorporate detailed descriptions of both demographic and bioenergetic processes across multiple trophic levels and spatial scales. Discussions of session presentations focused on advantages and limitations of alternative approaches (individual based models, projection matrix models, physiologically structured models, ...) to formulating biotic processes in aquatic ecosystem models, and on other plausible approaches to model formulation.

Individual-based Modeling of Fish: Linking to Physical Models and Water Quality

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Introduction

The individual-based modeling approach for simulating fish population and community dynamics is gaining popularity. Individual-based modeling has been used in many other fields, such as forest succession (Huston 1992) and astronomy (Barnes and Hernquist 1993). The popularity of the individual-based approach is partly a result of the lack of success of the more aggregated modeling approaches traditionally used for simulating fish population and community dynamics. Also, recent recognition that it is often the atypical (non-average) individual that survives has fostered interest in the individual-based approach (Crowder *et al*. 1992).

Two general types of individual-based models are distribution models and configuration models (Caswell and John 1992). Distribution models follow the probability distributions of individual characteristics, such as length and age. Configuration models explicitly simulate each individual in a population, with the sum over individuals being the population. DeAngelis *et al*. (1993) showed that, when distribution and configuration models were formulated from the same common pool of information, both approaches generated similar predictions. The distribution approach was more compact (a single equation, with an explicit, analytical solution) and general (changing parameter values was easy), while the configuration approach was more flexible. Simple biological changes, such as making current growth rate dependent on previous days' growth rates, were easy to implement in the configuration version but prevented simple analytical solution of the distribution version.

In this paper, I focus on the configuration approach to individual-based modeling of fish. I first outline advantages and disadvantages of the configuration and distribution approaches. I then present four examples from research being supported, to varying degrees, by the ongoing Compensatory Mechanisms in Fish Populations (CompMech) Program, sponsored by the Electric Power Research Institute. These examples were selected to highlight the themes of coupling fish models to hydrodynamic-water quality models such as those commonly used by the U.S. Army Corps of Engineers (examples 1 and 2), and to demonstrate methods for using individual-based models to examine the effects of dissolved oxygen (DO) (example 3) and zebra mussels (example 4) on fish population and community dynamics. The first two examples illustrate two types of coupling of fish models to physical models. The latter two examples focus on the population-level effects of two commonly encountered water quality problems.

Advantages and Disadvantages of Individual-based Modeling Approaches

Table 1 lists advantages and disadvantages of the distribution and configuration approaches to individual-based modeling. The advantages of individual-based modeling over other modeling approaches have been discussed previously (see papers in DeAngelis and Gross 1992; DeAngelis *et al*. 1994). I focus here on the relative merits of the two approaches to individual-based modeling. The advantages to the distribution approach (compactness, simplicity) arise from its mathematical tractability, whereas the advantages to the configuration approach result from the enormous flexibility associated with explicitly simulating individuals. Both the distribution and configuration approaches can encounter solution difficulties; analytical solution of distribution models quickly becomes impossible for even moderate levels of biological complexity, and numerical solution can require advanced mathematics (for the distribution approach) and excessive computer costs (for the configuration approach). Perhaps the most important disadvantage to both distribution and configuration approaches is the lack of individual-level variability associated with reported mean values of parameters and vital rates necessary to truly simulate inter-individual variation.

Table 1. Advantages and disadvantages of the distribution and configuration approaches to individual-based modeling.

Advantages:	Distribution	Configuration
Compactness of model and solution equations	X	
Conceptually simple	X	X
Ease of representing size-based interactions	X	X
Ability to simulate stochasticity		X
Ability to mimic plasticity		X
Ability to represent spatial heterogeneity		X
Ease of simulating movement		X
Disadvantages:		
Solution difficulties	X	
Use of average values in lieu of true inter-	X	X
Problems visualizing multivariate results		X
High computational costs		X

Examples of Linked Individual-based Models of Fish

Example 1 - Walleye Pollack Transport in the Gulf of Alaska

The first example involves a model of walleye pollack eggs and larvae in the Gulf of Alaska (Hinckley *et al*. 1996). Individual fish are tracked as particles using filtered output from a three-dimensional (3-D) hydrodynamics model. Eggs are introduced in a small area (Figure 1). Simple biological rules were imposed on the particles: vertical migration, degree-day development, and temperature-based growth. While the rules imposed were simple, the resulting behavior of the particles in space and time was quite complex.

This example illustrates a direct, hard coupling between physical and biological models, and also the use of hydrodynamics predictions in a Lagrangian rather than the usual Eulerian perspective. The Lagrangian perspective allows for the histories of experiences of individual particles to be tracked and recorded in order to evaluate what experiences distinguish survivors from those that perish. The usual Eulerian approach of tracking the mass (number of individuals) at fixed locations would not allow such interpretation. The model is still under development; initial results suggest that survivors tend to be those that get transported along the coast, rather than those transported out to sea. Figure 1 provides an example of a single model simulation. These results are based on unpublished data (Sarah Hinckley, National Marine Fisheries Service, Seattle, WA., personal communication), but are similar in concept to other simulations shown in Hinckley *et al*. (1996).

Example 2 - Striped Bass Populations in San Francisco Bay

The second example involves application of an individual-based young-of-the-year (YOY) model coupled to an age-structured adult model to simulate striped bass population dynamics in San Francisco Bay (Rose *et al*. in prep.). The striped bass population has been declining over the past several decades; a variety of causes (including reduced food, increased diversion of water for agricultural use, and reduced adult survival rates) have been blamed for the decline (Stevens *et al*. 1985).

The adult model tracks the number and mean length of age-1 and older fish on an annual time step. Age-based maturation determines the number and size distribution of female spawners each year, which is used to initiate the individual-based YOY model. The YOY model computes the number of age-1 survivors from each year's spawners, based on their daily spawning, and the subsequent development, growth, mortality, and movement of their progeny. Four spatial boxes are simulated for the YOY life stages. The upper Sacramento River box leads to the lower Sacramento River box; the lower Sacramento River box joins with the San Joaquin River (Delta) box to form the most downstream Suisin Bay box.

Movement of YOY individuals among the four spatial boxes was based on predictions from a two-dimensional (2-D) hydrodynamics model. One hundred simulations of the hydrodynamics model with particles started in historical spawning areas were used to estimate transition probabilities. The transition probabilities represent the daily likelihood an individual in

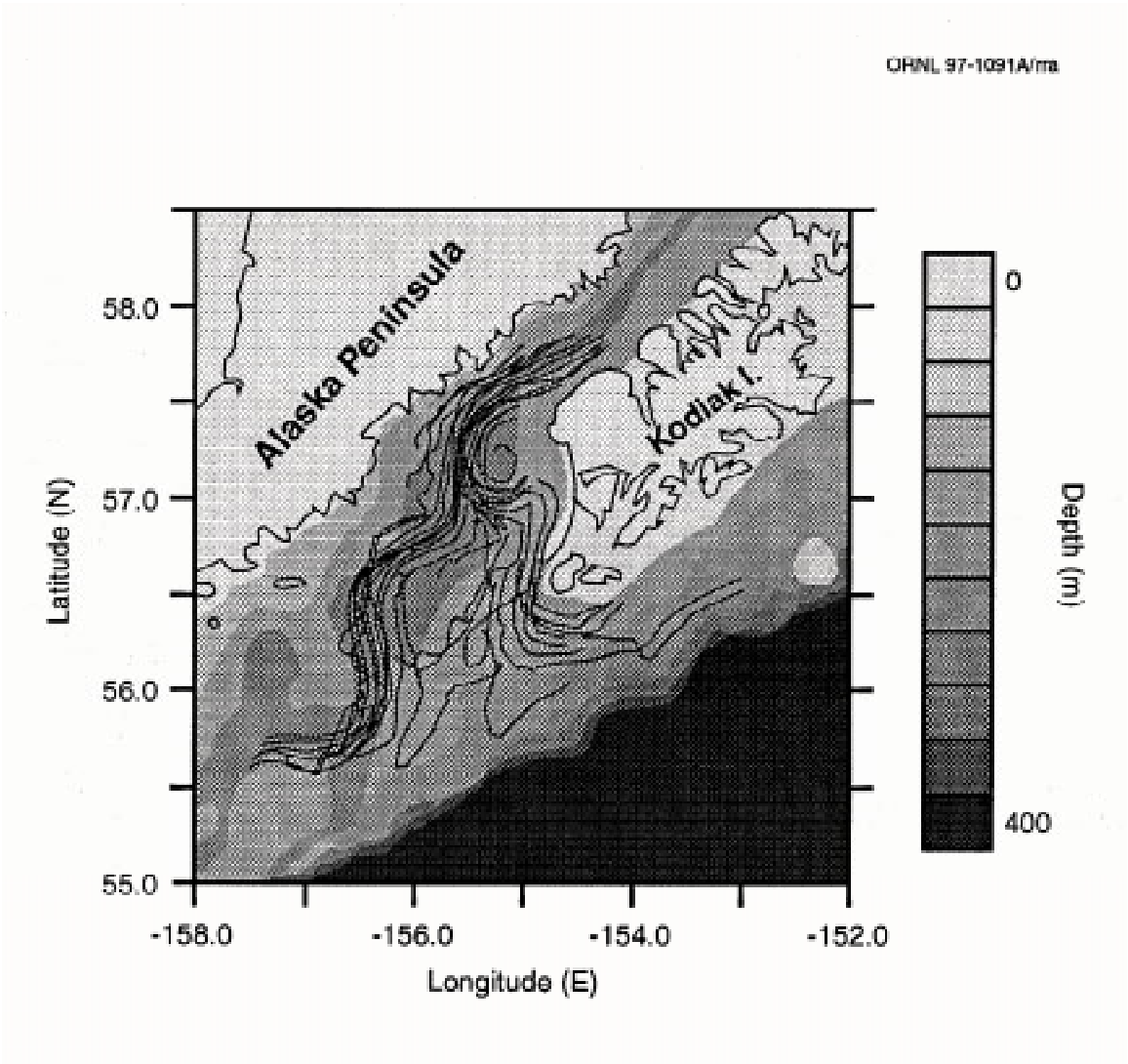

Figure 1. Example simulation of the predicted fate (float or particle tracks) of larval walleye pollack in the Gulf of Alaska. Eggs were introduced roughly where the float tracks begin between Kodiak Island and the Alaska Peninsula. These results are based on unpublished data (Sarah Hinckley, National Marine Fisheries Service, Seattle, WA, personal communication), but are similar in concept to other simulations shown in Hinckley *et al*. (1996).

one box moves to each of the other boxes or is lost due to water diversions. These transition probabilities were applied to eggs, yolk-sac larvae, and larvae for their first 10 days after spawning. Two flow conditions were simulated: 5,000 ft^3/sec Delta outflow which is considered a critically low flow condition, and 20,000 ft^3/sec which is considered an above-normal flow condition.

Predicted spatial distributions of individuals mimicked observed distributions. I summarize the spatial distribution by life stage, as the fraction located in the most downstream Bay box (Figure 2). Under higher flow conditions (20,000 ft^3/sec), a greater proportion of yolk-sac larvae, larvae, and juveniles are found in the Bay. Effects of transport on egg densities are difficult to see because egg densities in the Bay box are low under both low and high flow conditions. Most eggs are found upstream of the Bay box. The striped bass population model is now being used to evaluate the likelihood that reduced food, increased diversions, or reduced adult survival were the cause of the observed population decline (Rose *et al*. in prep.).

This example, and the walleye pollack example above, both illustrate a direct coupling of biological and physical models; they differ in that the walleye pollack example used hydrodynamic predictions (*e.g.*, velocities) themselves and could have been run simultaneously with the hydrodynamics model, whereas the striped bass example used processed predictions from the hydrodynamics model and was run separately from the hydrodynamics model.

Example 3 - Larval Fish Survival under Varying DO Conditions in Chesapeake Bay

The third example is based on a model that predicts larval fish survival exposed to juvenile fish and sea nettle predators under different DO conditions in a vertically-stratified water column (Breitburg *et al*. in review). Larval prey are based on naked goby and bay anchovy; predators simulated are sea nettles, and a fish predator sensitive to low DO and tolerant to low DO. The water column is divided into 3 layers (surface, pycnocline, and bottom). The daily growth, survival, and movement of individual fish larvae in a cohort are tracked for 30 days from hatching. Larval growth is fixed at 0.21 mm/day. Larval survival is determined based on encounters with and successful captures by individual predators. Encounter rates and capture success depend on the swim speeds and lengths of the prey and predators. Movement among the surface, pycnocline, and bottom layers is updated daily by randomly assigning individual prey and predators to layers based on specified proportional densities.

DO concentrations affect larval growth rates, predator capture success, and the vertical distributions of prey and predators. All baseline parameter values are based on high DO levels. Larval growth rates are specified to decrease with decreasing DO concentrations. Sea nettle capture success increases, while fish predator capture success decreases (more so for the sensitive predator), with decreasing DO concentrations. Proportional densities by layer shift from a distribution proportional to the water volume in each layer under high DO concentrations, to distributions that progressively avoid the bottom layer with decreasing DO concentrations. DO concentrations in the surface layer are always set to no-effects levels. DO concentrations in the pycnocline layer depend on the concentrations specified for the bottom layer (3 mg/L when bottom layer is 0 mg/L and 4 mg/L when bottom layer is 0 to 1 mg/L).

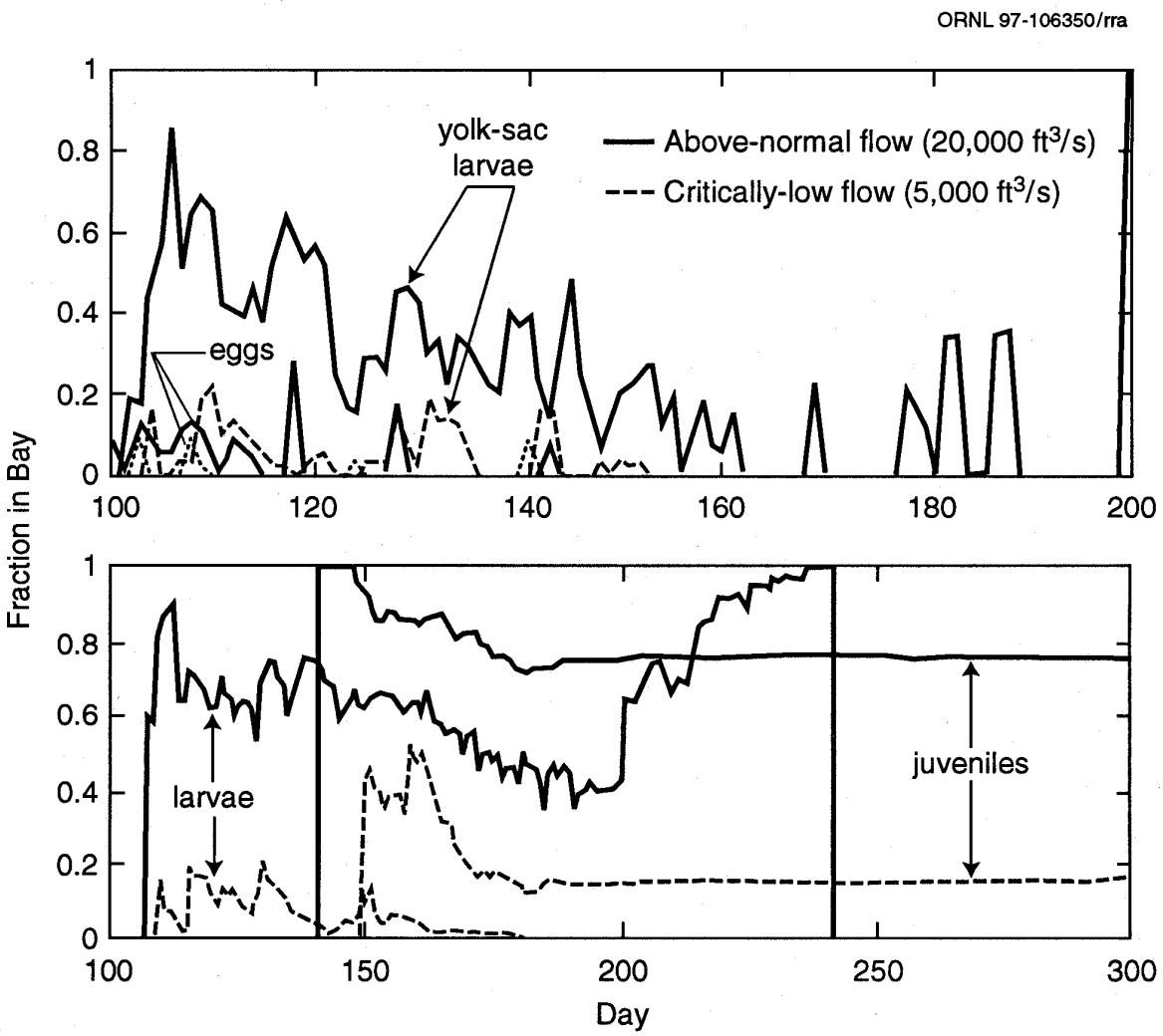

Figure 2. Predicted fraction of total striped bass by life stage in the most downstream (Bay) box under the critically low (5,000 ft^3/sec) and above normal (20,000 ft^3/sec) flow conditions. Results are from Rose *et al*. (in prep.).

Parameter values are based on a variety of laboratory, mesocosm, and field experiments; the model is configured to resemble the mesohaline region of the Chesapeake Bay.

Predicted larval survival peaked at intermediate bottom DO concentrations (Figure 3). A variety of simulations involving different shaped water columns and mixes of predators were performed. I show only the results for one of the water column configurations (termed "intermediate" in Breitburg *et al*. in review).

This example illustrates a soft link between water quality and individual-based fish modeling. One could envision configuring a spatial array of independent water columns and specifying DO concentration by layer based on spatially explicit predictions from a hydrodynamic-water quality model of the same system. A spatial map of larval survival rates could be generated over time (perhaps seasonally) for different water quality scenarios.

Example 4 - Zebra Mussel Effects on Yellow Perch and Walleye in Oneida Lake

The fourth example illustrates use of an individual-based prey-predator (yellow perch-walleye) model to predict the population-level effects of zebra mussels (Rutherford *et al*. in review). The model follows the daily spawning, growth, and mortality of individuals of yellow perch and walleye throughout their lifetimes. Adult walleye predation is the major source of mortality on YOY juvenile and yearling yellow perch. The model was developed and corroborated using the extensive 35-year database collected on Oneida Lake.

Zebra mussels are rapidly spreading from their introduction in the Great Lakes area. Zebra mussels are expected to increase water clarity and macrophytes, increase blue green algal blooms, reduce chlorophyll concentrations, and shunt energy from the pelagic to benthic pathways. The increased water clarity and energy shunt effects were imposed in the model, and predicted yellow perch and walleye population dynamics were compared to baseline (no zebra mussel effects) predictions. The increased water clarity effect was imposed by increasing the yellow perch's ability to feed, decreasing the walleye's ability to feed, and increasing the larval mortality rate of both species. Yellow perch can feed under high light conditions, while walleye prefer low light conditions. Larval mortality is assumed to increase with zebra mussels because increased macrophytes will result in increased predation pressure on larval yellow perch and walleye. The energy shunt effect of zebra mussels was imposed by increasing benthos densities and production rates and decreasing zooplankton densities and production rates.

Zebra mussels were predicted to reduce walleye adult abundances but have little net effect on yellow perch adult abundances (Figure 4). Walleye population abundance decreased from an average of 18/ha under baseline conditions to 12/ha with zebra mussels due to the elimination of years of high recruitment. Average annual walleye yield declined 33% based on numbers (13.5 to 9.1/ha), but due to density-dependent growth of walleye, annual yield based on biomass declined only slightly from baseline values (9.0 to 8.4 kg/ha).

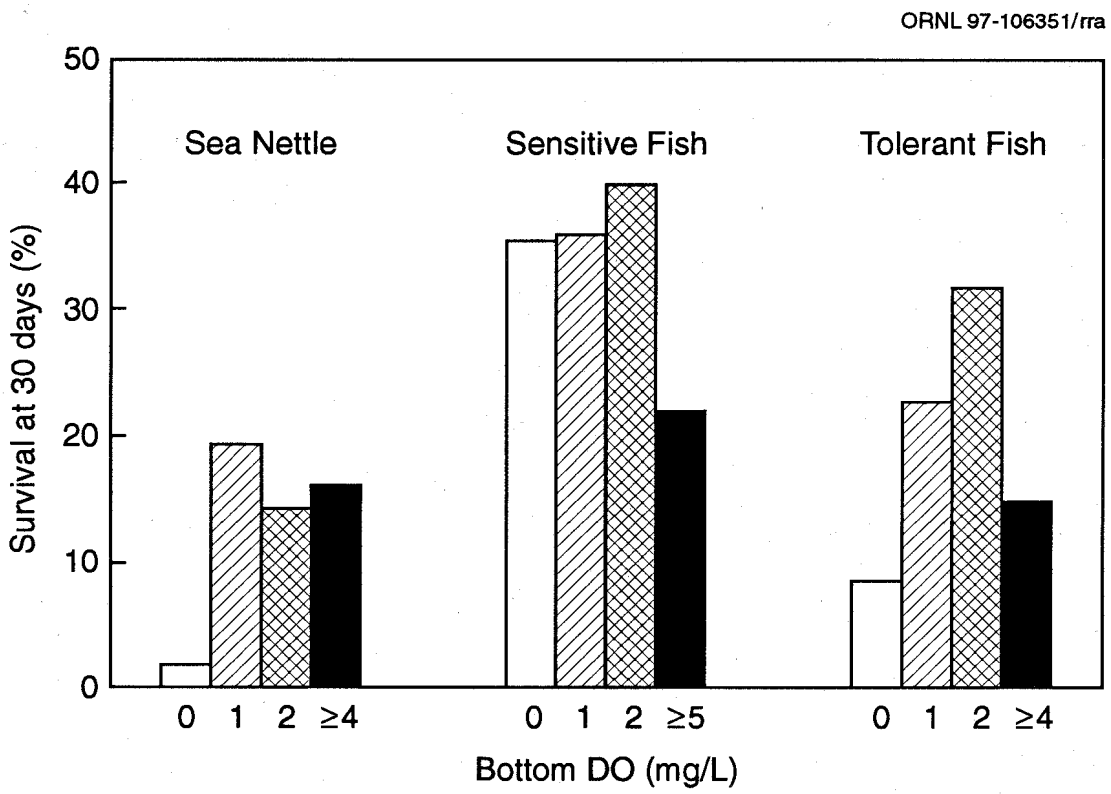

Figure 3. Predicted larval survival for the sea nettle, sensitive fish, and tolerant fish predators under 0 mg/L, 1 mg/L, 2 mg/L, and no-effects (≥4 or ≥5 mg/L) bottom layer DO concentrations. These results correspond to the intermediate water column results reported in Breitburg *et al*. (in review).

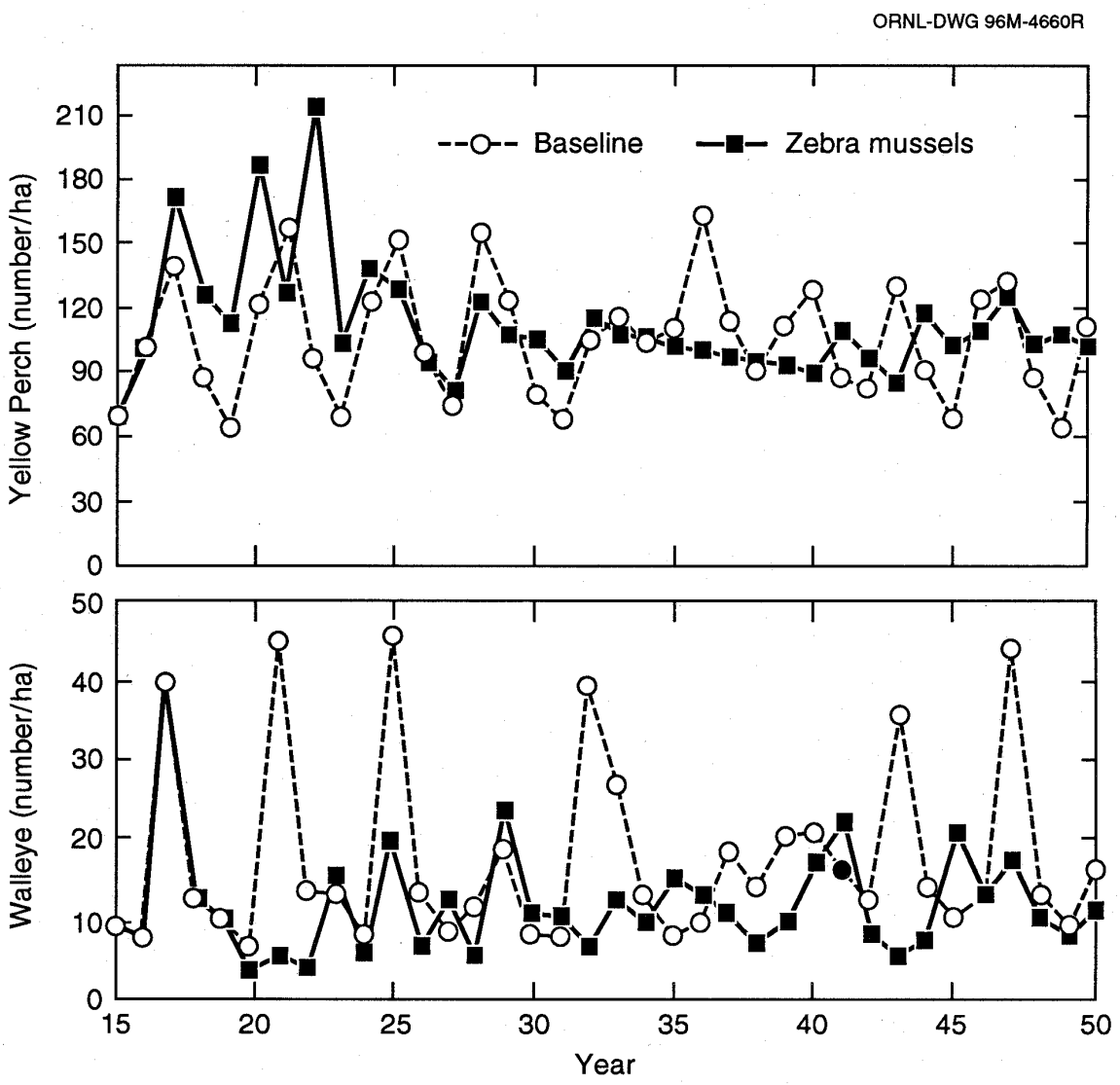

Figure 4. Predicted adult abundances (number/ha) of yellow perch and walleye under baseline and zebra mussel simulations. Results are from Rutherford *et al*. (in review).

Summary Remarks

The two general types of individual-based modeling (distribution and configuration) were described and their advantages and disadvantages were discussed. Four examples that use the configuration approach were presented that illustrate direct use of hydrodynamics predictions, use of hydrodynamic predictions to estimate movement probabilities, DO effects on larval survival, and zebra mussel effects on fish population dynamics. Linkages between biological and physical models can vary from highly coupled, in which the models can be run together simultaneously, to soft linkages, in which predicted water quality variables can be used as input to a biological model. As with any modeling analysis, the questions of interest must be clearly specified first, and then used to properly scale the temporal, spatial, and biological resolution of the models. The configuration approach to individual-based modeling offers many advantages for hard and soft coupling to physical models and for predicting water quality effects on fish populations.

Acknowledgments

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Applications of Physiologically Based Population and Community Models to Stress Ecology

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Stress at the Individual Organism Level

The Individual and Its Stressors

An individual-based (IB) approach to investigating population and community ecology assumes that the individual is the functional ecological force (Lomnicki 1988, DeAngelis and Gross 1992). IB models are particularly appropriate for representing effects of chemical, physical, or biological stressors because characteristics of individuals, such as physiological processes or behavioral strategies, can be intricately linked with the organism's environment. IB formulations can be relatively simple or complex depending on the biological detail included about the modeled individuals. However, the ability to relate important individual characteristics to both ecology and stressor biology requires development of models that are generally detailed in formulation and difficult in analytical tractability. The advantage of increased complexity derives from increased biological detail in IB models and the ability to incorporate differences between individuals. For example, in the individual-based setting, survival of large organisms but die off of very young organisms because of environmental conditions can be observed. Death caused by narcotic chemical toxicity in females immediately after reproduction, when lipid stores are low, can also arise (Hallam *et al*. 1990b). Hence, IB approaches allow inclusion of the atypical individual, maybe the unique individual type, that survives a stress. Another advantage of IB approaches is that basic ecological principles, such as conservation of mass and energy, can be utilized and coupled with IB models derived from first principles or, minimally, with well delineated assumptions.

Individual based approaches are particularly appropriate for organisms with a complex life history or when spatially explicit constraints are important. A basic thesis -- that investigations of ecological effects observed in stressed systems require an individual perspective -- is implicitly supported by several directions of reasoning. Academic areas of stress biology, such as toxicology, and most biological areas as well, generally investigate problems relating to individuals or small groups of individuals and, thus, most available data reflect this individual viewpoint. This level of information allows parameters for the individual to be directly estimated, a property not shared by models framed at higher levels of ecological organization. Sound parameter estimation is fundamental for stress biology because stress modifies individual parameters. Thus, at the individual level, we have the best chance of utilizing existing data, and then extrapolating to make reasonable dynamic projections. Individual-based models incorporate state of the art biological processes and parameters, hence, already at the formulation stage, the model validation process is initiated.

In my opinion, an individual perspective is necessary for any ecotoxicological or stressor investigation, from the microbial level to that of the top predator. Some constituents about the individual can be suppressed; important ecotoxicological detail cannot; and aggregation, the combining of ecological structural detail, should not be utilized to a high degree for relevant ecotoxicological factors. Aggregated models tend to handle neither chemical stressor exposure nor effects adequately. Even microbial organisms have characteristics that merit structural perspectives; for example, with lipophilic stressors, knowledge of organism composition partition fractions in bacteria is essential to determine effect exposure times, and ultimately, dynamical behavior. Utility of IB models is often regarded as most appropriate at the higher trophic levels where organisms have complex physiological and behavioral mechanisms. To explicitly indicate the modeling viewpoint being addressed, I do not advocate detailed modeling of each individual, only that an individual perspective, that is relative to specifics of the stressor scientific problem and is capable of accounting for both exposure and effects, be imposed.

Stress affects individual organisms. Hence, in ecotoxicology, chemical exposure models, generally first-order ordinary differential equations, are coupled with an individual growth model to determine the effects of chemical stressors (FGETS, Barber *et al*. 1988, Lassiter and Hallam 1990, Nichols *et al*. 1990). After the individual model is coupled with an exposure model, some method to measure effects, such as a qualitative structure activity relationship (Hermens *et al*. 1985), is needed. Physical stresses tend to affect processes directly, and the stress can be noted in parameter values associated with those processes.

Types of IB Models

IB models can usually be put into two categories: dynamic or rule based. Dynamic IB models are formulated in terms of dynamic systems such as ordinary or partial differential equations. Rule based IB models formulate the behavior of the organism according to a set of operational procedures. Physiologically based models usually are in the class of dynamic IB models (Hallam *et al*. 1992). Individual oriented, rule based approaches have been utilized to investigate dynamics of populations and communities (Wolff 1994, Fleming *et al*. 1994, Hallam *et al*. 1997, Jaworska *et al*. 1996a, b, c), especially when behavior is fundamental.

A recent approach to physiologically based models is stoichiometric, where individual chemical species are followed in the ecological model based upon the conservation properties (Kooijman *et al*. 1997). This approach is promising for stressor ecology, especially for investigation of effects of chemical stressors; however, this approach is in its infancy stage of development.

Assessment Using Physiologically Structured Population Models

The Population and Stress

Representation of populations as a complex of individuals that differ in their susceptibility to chemical or physical stressors via their variation in physical, behavioral, and physiological properties is possible in a structured population model. Techniques where

adequate variation in individual attributes is coupled with chemical fate and effects models provide a spectrum of assessment tools for individuals, populations, and communities (Hallam *et al*. 1990a, Jaworska *et al*. 1995, Kooijman 1993, 1995).

Risk assessment is primarily developed for, and focused upon, the higher organizational levels of ecological systems where there is a general lack of both biological and stressor dose - biological response information. An individual-based perspective allows integration of both stressor and physiological information so that indicators of the effects of stress can possibly be extrapolated to the population, community, or higher organizational level. Stressor effects on individuals are much different than effects at the population level. For chemicals with a nonpolar narcosis mechanism of action, sublethal effects on growth in a *Daphnia* population model (Hallam *et al*. 1992) led to the population extinction threshold, as a function of chemical concentration, that was less than the effect concentration that reduces growth by 50%, the EC50 for growth. Hence, apparently concentrations well below the LC50, the concentration that kills 50% of the individuals in laboratory tests, can lead to ultimate population extinction.

The last decade has seen an explosion of knowledge about structured, individual-based population models, including applications in areas such as ecotoxicology and stressor ecology (*e.g.*, Thomann 1989, Hallam *et al*. 1992, DeAngelis and Gross 1992, Kooijman 1993). The nature of results about structured dynamical systems prevents widespread application and reasonable interpretation for the management and regulation of ecosystems. Indeed, even though needed for assessment purposes, there is traditionally a considerable time lag in implementation for most methodologies. Another difficulty is that data for structured dynamic model verification seldom exist at the population or community level, even for the simplest ecological systems, although there are community systems that have allowed model replication (*e.g.*, Kooijman *et al*. 1997). Hence, significant advances in dynamic ecological assessment methodologies, especially at ecological organizational levels above the individual, remain elusive because of the biological detail and the temporal-spatial scales required.

The Search for Indicators

Integrative ecological indicators that link cause and effect mechanisms are necessary for almost all aspects of assessment. A critical set of spatial and temporal relationships obtained from empirical data and models should be identified as ubiquitous for specific systems. At the population level, these include integrated indicators such as dynamic maternity and survivorship relationships and their dependence upon system parameters associated with environmental, physiological, and ecological processes. A combination of indicators might provide insight into assessment problems.

Knowledge about population ecology rarely provides physiological or population level indicators for properties that govern dynamics. It has been, and will continue to be, a major concern to relate dynamic scale factors to natural systems, to ascertain what features of population models are found in stressed and unstressed natural systems, and to be able to generate hypotheses that can be tested in order to determine if the risk assessment scheme is effective. While there exist several key stress indicators associated with structure and

population dynamics that appear consistent with physiological and population ecology literature, such as mean total biomass and length of juvenile period (Hallam and Funasaki 1997), it is clear that validation in highly complex natural systems is still somewhat removed from the present state of empirical techniques and knowledge. Indeed, with the dynamic sensitivity and scale problems observed during model analyses, it seems clear that the primary focus should not be on specific dynamics which are often subject to great variability that depends on many life history attributes as well as system temporal and spatial scales. Indicators that integrate dynamical perspectives need to be developed rather than focusing on specific dynamics of systems.

Environmental Stressors

In most physiological modeling approaches, toxicological and environmental factors are assumed to affect rate parameters in physiological process formulations but not the process representation itself. Seasonal variations in environmental factors, such as temperature and dissolved oxygen, have been incorporated as driving forces for the physiological variables in a *Daphnia* population model to permit interaction with toxicants and physical stressors (Koh *et al*. 1997). In general, it has been concluded that a characteristic of stressed systems is that distribution of structure is a good indicator of adverse effects of stress. For example, a model *Daphnia* population that consists of individuals with a wide spectrum of ages, with a young robust subpopulation, is generally a healthy population. A chemically stressed population close to extinction can exhibit a bimodal age distribution, with one mode consisting of old, small, relatively unproductive individuals, and the other of young subsisting organisms that do not grow much during their lifetime (Hallam *et al*. 1992, Kersting 1975). Temperature and dissolved oxygen effects also reinforce the concept that *Daphnia* population structure is a good indicator of stress.

Sublethal and Lethal Effects of Chemicals

Under a set of well-defined assumptions -- (1) the environment is spatially homogeneous; (2) stress is caused by a chemical that is lipophilic, reversible, nonmetabolizable, and nonpolar (Schultz 1989), and is measured only in terms of mortality; and (3) only physiological processes are relevant to the assessment -- theoretical developments have indicated that two outcomes are to be expected: The first, *survival of the fattest*, occurs for acute exposures (Lassiter and Hallam 1990), but this outcome is not robust in that many factors can destroy this property. For chronic exposures, the second outcome, *survival of the fittest of the fortunate*, results where a dominant individual ecotype, the fastest growing morph, is ultimately the successional winner over all other surviving ecotypes in the population (Hallam *et al*. 1990b, Henson and Hallam 1994). A conclusion important for stress ecology is that the successional dominance behavior of individuals in a structured population can be modified -- to situations where there is a distribution of individual ecotypes -- by utilizing a suitable toxic chemical and an appropriate exposure duration. A chemical stress can disrupt, and completely change, outcomes of dynamic population composition processes.

Physiologically Based Population Models: An Illustration

An example of a physiologically structured population model is the spatially homogeneous, extended McKendrick-von Foerster hyperbolic partial differential equation (see Hallam *et al*. 1992 for the modeling philosophy and development employed here):

$$\frac{\partial \rho}{\partial t} + \frac{\partial \rho}{\partial a} + \Sigma_i \frac{\partial(\rho g_i)}{\partial m_i} = -\mu\rho$$

In this equation, $\rho = \rho\ (t, a, g_1, g_2, \ldots, g_n)$ represents the density of the population; t is time; a is age; g_i is the growth rate of the ith physiological variable, m_i, of the individual, with $g_i = g_i\ (m_1, m_2, \ldots, m_n)$; and μ is the mortality rate. Subscripts t, a, and m_i above indicate partial derivatives. This conservation equation contains implicitly the individual model given by the equation $dm_i / da = g_i\ (m_1, m_2, \ldots, m_n)$. Typically we have utilized lipids, structure (proteins and carbohydrates), and aqueous compartments as physiological components in our individual models. Reproduction, formulated at the individual model level, is accumulated to form the boundary condition, which is coupled with an initial condition to yield a well posed problem. Each partial differential equation represents the population dynamics of a single ecotype where all individual characteristics are identical except for age. In general, our approach is to consider a population composed of n ecotypes, so the model becomes a system of n partial differential equations which are usually coupled through resource and mortality.

The model population dynamics are extremely sensitive to the particular individual model employed (Hallam *et al*. 1992, Hallam and Funasaki 1997). Assumptions about the life history of the individual include a juvenile period determined by attainment of a fixed size, after which periodic reproduction occurs throughout the individual's lifetime. It is these two assumptions that determine the dynamic behavior of the population. For example, if all individuals have identical physiology, the asymptotic synchronization of births in time intervals occurs within the assumed period of reproduction.

Computational Aspects

Physiologically Based Populations

The simulation of physiologically based populations can be numerically intensive. Parallel codes have been implemented, not only to handle population level computations but in anticipation of the coupling of IB population models into a community setting, on a number of different platforms including a Thinking Machines CM-5, IBM SP-2, and a distributed PVM environment. The reproductive temporal and physiological scales of individuals determine population dynamics. Understanding these biological scale issues helps determine important numerical computational scales. Serial and parallel implementations of McKendrick-von Foerster population models indicates that expansion to parallel computing environments are

appropriate for physiologically structured models. The speedup attained is significant (Ramachandramurthi *et al*. 1996, 1997).

Spatial Heterogeneity

Recent numerical and analytical investigations of physiologically structured populations in a spatially heterogeneous environment that emphasizes the relationships between dynamics and scale have demonstrated again that bioavailability and structure are fundamental to understanding chemical stresses. Investigations in this area are just beginning, with associated computational aspects, such as implementation on high performance computers, at the forefront. Spatially explicit and spatially heterogeneous individual-based models are beginning to emerge, with good examples provided by models such as ATLSS (L.J. Gross *et al*. this volume) and the fish models of K.A. Rose (this volume). We have incorporated a structured fish model into a spatial environment, merging consumer dynamics and physiology with a dynamic, heterogeneous, unstructured resource. Recent investigations have shown that, even in a spatially heterogeneous environment, assessment issues such as "survival of the fattest" are resolvable (Lika and Hallam 1997). In higher trophic levels such as the fishes, behavioral mechanisms (*e.g.*, territoriality, migration) should be modeled so that, for example, toxicant avoidance mechanisms can be implemented; however, this is biological and chemical species-specific and, at present, has been not been considered.

Advective movement in a resource-directed flow (Lika 1996) formed an initial excursion into spatial heterogeneous models of McKendrick-von Foerster populations. When coupled with water quality and chemical transport models, a computationally intensive complex model will result. In my opinion, this is not an intractable task.

Conclusions

Considerable progress in understanding individual-based approaches to ecotoxicology has occurred during recent years, leading to a good understanding of the biological, ecological, and computational aspects of some basic physiologically based population models. Physiologically or individual based, structured approaches to modeling populations present new perspectives for population ecology (Murdoch *et al*. 1992) and for ecotoxicology (Hallam *et al*. 1990b, Kooijman 1993, 1995, Nisbet *et al*. 1996). Some disadvantages of IB models include the fact that the models are very data intensive with parameterization, while direct, being nontrivial. These models are also highly computational, so when coupled to physical system models using geographical information systems, hydrological models, and water quality models, high performance computing platforms will probably be a requirement. Structured population models can be coupled in order to study stressed communities, but this work is not as advanced from an application perspective.

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Session 6 - Special Topics Associated with Development of Aquatic Ecosystem Assessment Models: Assessing Risk and Uncertainty

Session Purpose

This session was intended to focus on the incorporation of risk and uncertainty analysis capabilities into aquatic ecosystem models for use at CE projects. Discussions of session presentations focused on the desirability of including risk and uncertainty analysis capabilities in aquatic ecosystem assessment models, and on the implications of their inclusion for model structure and utility.

Aquatic Ecosystem Models for Ecological Risk Assessment: From Single Species Populations to Communities

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Overview

Assessing risks for whole communities rather than single species is important for management, and requires that the trophic relationships between species are taken into account. The methods and data requirements for including trophic dynamics in aquatic risk assessment are illustrated using RAMAS/ecotoxicology, a software system that implements food chain, toxicokinetic and concentration-response models in Monte Carlo form. A need for further development including spatial dynamics and integration with water quality models is discussed.

The Problem: Assessing Human Impacts to Ecosystems

Ecologists attempting to characterize impacts to natural ecosystems are usually interested in questions of the form, "Will a given impact affect the structure or function of an ecosystem?". Sometimes, we may not be concerned about individual species so long as the ecosystem is substantially unchanged in terms of the abundance of broad functional groups (such as primary producers or predators) or the flow of energy. At the other extreme, only one species may be important, but that species is influenced by its prey, predators, or competitors. In either case, a quantitative understanding of at least part of the ecosystem will be needed to predict the anthropogenic effects. For example, Bothwell *et al.* (1994) exposed algae and chironomids to different levels of ultraviolet light (UV). In the short term, higher UV reduced the abundance of both algae and chironomids. However, in the long term, algae were more abundant in high-UV treatments, because their abundance was controlled by chironomid grazing, and the reduction in grazing caused by UV effects on chironomids more than compensated for the direct negative effect of UV on algae. Although single-species bioassays can indicate the potential for community and ecosystem level effects, they cannot directly predict responses of this kind, which must be understood for reliable ecosystem management.

Approaches to Multispecies Modeling for Ecological Risk Assessment

One approach to describing multispecies systems is to include population-level effects estimated from bioassays in an ecological model that takes account of the interactions between

individuals of the same species (intraspecific competition), and of different species (interspecific competition or predator-prey interactions). Age-structured or individual-based models may provide a more comprehensive description of population dynamics (Kooijman 1993) in certain cases, but will usually require too much data to be practical for whole communities. It is worth experimenting with the simplest models until they are found to be inadequate.

The major component of a multispecies model which is usually subdivided into predator-prey and competition interactions is the effect of species on each other. Competition between species is important, but in many cases it can be represented in the form of predator-prey interactions, where two or more species act as 'predators' on a common resource. Mathematical models for predator-prey systems have two important components: the rate at which individual predators capture prey (the functional response), and the rate at which captured prey are transformed into new predators (the numerical response). Several kinds of functional response have been proposed (Ginzburg and Akçakaya 1992), including the Lotka-Volterra form (where per capita prey consumption is a linear function of prey density); hyperbolic relationships such as the Holling type II function (which include a maximum rate at which predators can consume prey); ratio-dependent models (Arditi and Ginzburg 1989) in which predators also interfere with each other (so that per capita consumption is a function of prey density per predator); and intermediate forms (Hassell and Varley 1969, DeAngelis *et al*. 1975). The choice of functional response can have major effects on population dynamics (*e.g.*, Yodzis, 1994), and is still a matter for debate (*e.g.*, Oksanen *et al.* 1981, Ginzburg and Akçakaya 1992, Gleeson 1994, Sarnelle 1994, Akçakaya *et al*. 1995). The numerical response is generally approximated as a linear function of the functional response, assuming that consumed prey are transformed into new predators with constant efficiency.

Community and ecosystem models can become very complex, and it will often be necessary to reduce the system to a few functional groups. Aquatic communities are often modeled as food chains containing phytoplankton, zooplankton, planktivorous fish, and piscivorous fish (Figure 1).

The properties of these food chains at equilibrium are relatively well-understood, although once again these properties depend on the choice of functional response (Ginzburg and Akçakaya 1992). Although there may be considerable variation in sensitivity to various impacts within functional groups, this will not matter provided the functional rather than taxonomic structure of the system is of interest. Food webs may quickly grow in complexity, but assessing parameter values for complex models is very difficult. We can expect that models such as that shown in Figure 2(a) can be built with the data ecologists are able to collect, but the web in Figure 2(b) is probably too complex for ecologists to deal with on a routine basis.

The dynamics of multispecies models can be very sensitive to measurement error in parameter values such as feeding rates, which are difficult to estimate. For example, Yodzis (1988) constructed plausible models for sixteen real communities, and simulated the effects of changing the density of a single species on the rest of the community. Given the accuracy with which parameters could be estimated, it was difficult to predict either the magnitude or the

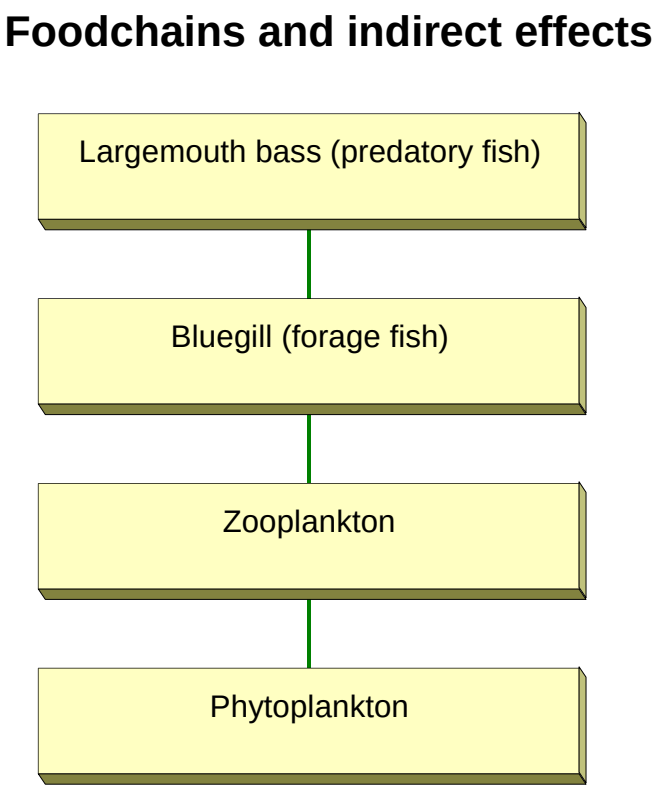

Figure 1. Example of an aquatic food chain.

direction of responses to this kind of disturbance. In many cases, temporal variability in parameter values will also be important. For example, the feeding and growth rates of many species are influenced by unpredictable weather conditions, which can have strong effects on the long-term behavior of populations (Burgman *et al.* 1993). Both kinds of uncertainty can be included in multispecies models through the use of Monte Carlo methods. Measurement error should be sampled at the start of each replicate simulation, while environmental variability should be sampled at regular time intervals throughout each replicate (Kirchner 1997). These methods are important because they can reveal how much confidence should be placed in predictions concerning the effects of toxicants on ecosystems. Although the answers will in many cases be unpleasant (*e.g.*, Yodzis 1988), they will at least indicate when and by how much we should err on the side of caution in setting management objectives.

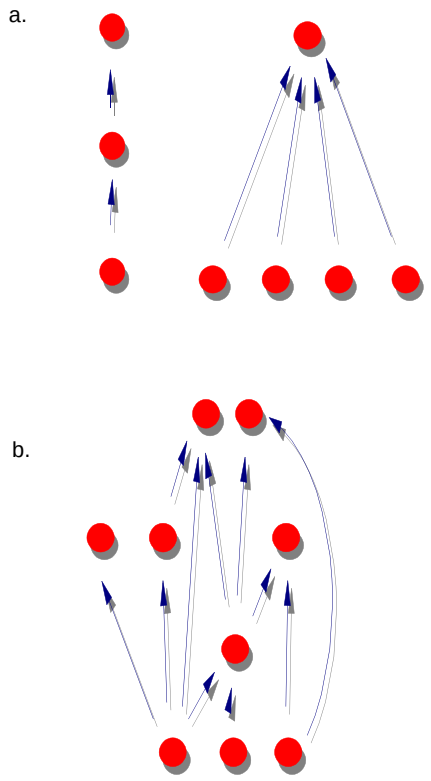

Figure 2. (a) Sample web for which ecologists are able to collect data. (b) Sample web which is too complex to deal with: aggregating species into functional groups like ‘fish’ and ‘benthic detritivores’ may help.

The RAMAS/ecotoxicology software system (Spencer and Ferson 1997) was developed to carry out Monte Carlo simulations of predator-prey systems affected by toxicants. User-specified parameters for population growth, toxicant kinetics, and concentration-response functions are added to a system of differential equations. Replicate simulations are used to deal with measurement error and environmental variability as described above, and the equations are integrated numerically (Spencer *et al*. 1997).

RAMAS/ecotoxicology allows for a comprehensive description of ecological interactions but it is not spatially explicit. Metapopulation models taking spatial configuration into account like RAMAS/GIS (Akçakaya 1997) have focused on multiple populations of single species. At the same time, management decisions require predictions about ecological communities on large spatial scales where an ecological system cannot be treated as homogeneous.

A significant gap exists between water quality models, which comprehensively describe physical and chemical processes in large scale systems, and ecological models of communities, which still commonly assume homogeneity. It is the connection between water quality models (such as the ones developed at the U.S. Army Engineer Waterways Experiment Station) and spatially explicit biological community models which represent a major challenge for the next few years in the development of applied aquatic ecology.

Organisms at different trophic levels have very different generation times and visit neighborhoods of very disparate sizes during their lifetime. It is possible that models of the lower levels of a food chain may require much higher spatial resolution in the description of their dynamics than models of higher trophic levels. Fish populations may react to an average condition in a large water body while planktonic species may respond to a much more local situation. It might be the case that we can build satisfactory models of decreasing levels of spatial and temporal resolution as we move up to higher trophic levels. Fish population dynamics may often be modeled on annual time scales and without geographic differentiation for a sizable body of water. Phytoplankton and zooplankton may require at least monthly time scales and a detailed representation. As a first approximation, water quality models will drive aggregated models of planktonic dynamics which, in turn, drive even more aggregated models of fish population dynamics. While admittedly simple, such a structure, if developed, would represent a significant step for aquatic ecosystem modeling from where we are today.

Both models and field studies (*e.g.*, Cohen *et al.* 1994) stress not only the importance of considering interspecific interactions, but also the high degree of uncertainty associated with predicting the behavior of complex ecological systems. The additional uncertainty introduced by multispecies models is unwelcome, but the impression of precision given by focusing on single species can be misleading. If none of the species in a community are likely to be individually affected, then it is safe to ignore interspecific interactions. However, if any single species is affected, then effects may cascade through the system. Models which explicitly describe the interactions between species are necessary to determine whether this will happen, and therefore provide the context in which the importance of population-level effects should be assessed.

More complex models will have to be associated with more uncertainty in their predictive power. We therefore have to learn to analyze uncertainty in both of its foci: objective natural variability in time and space, and subjective uncertainty due to our inability to measure ecological variables accurately.

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Session 7 - Summary of Workshop Discussions

Session Overview

As explained in the opening paper in this proceedings volume (Waide this volume), this workshop was designed to be highly interactive, with short, focused presentations on specific topics by both USACE and other speakers, followed by extended time for discussing issues raised pertinent to the subject matter of the workshop. Discussions occurred following individual presentations, at the end of each workshop session, and during an extended discussion period at the end of the workshop. The specific discussion topics intended for each of these focused discussion sessions were identified in each of the overviews of the prior workshop sessions and in the workshop agenda (Appendix A). The purpose of this concluding section of the workshop proceedings volume is to provide a concise summary of the key points and issues that emerged during the workshop discussions.

Summary of Workshop Discussions

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Introduction

Discussions during the workshop occurred following individual presentations, at the end of each workshop session, and during an extended period at the end of the workshop. Rather than simply present the discussion points and themes as they occurred sequentially, we have organized them into three broad categories: (1) a category of specific items which reflect general discussion points not directly related to individual presentations or sessions, (2) a second category of select points made following or in reference to individual presentations, and (3) a final category containing comments which capture both the broad theme of the discussions that occurred and the essence of the expertise and advice provided by workshop participants, along with select individual comments that were particularly pertinent to the overall theme of the workshop. Discussion points in this third category are further organized into ten subcategories. We have taken editorial license in grouping related comments together under common themes without altering the intent or essence of the original comments. We have made no attempt to filter any discussion points, to assess their relevance to the workshop themes, or to alter the intent or essential content of comments made by any participant. Discussion points and comments are summarized here without individual attribution.

General Discussion Points

1) The USACE has developed strong capabilities in water quality and hydrodynamic modeling, but not in ecological and ecosystem modeling. Current USACE models are based on significant advances in the understanding and numerical representation of many chemical and physical processes. Other existing modeling capabilities within the USACE include some habitat and statistically based fisheries models.

2) The USACE needs more quantitative descriptions of the effects of management actions on biological resources by using ecosystem modeling, with both terrestrial and aquatic systems being targets for this modeling. Presently the agency lacks a complete tool box to manage resources and assess impacts at a particular organizational level and spatial scale.

3) There is current interest and need within the USACE to link ecosystem modeling to high performance computing. Historically ecological modeling has been decoupled or isolated from detailed numerical consideration of underlying physical processes and from computational aspects of modeling. Now is an excellent time to achieve better linkages among all these apsects.

4) It is critical that, if the Corps undertakes a major new effort in developing ecosystem models, they show a return on the resources invested in the effort. In that sense the resulting products or models must be fully functional to the end user. Therefore, the USACE needs to define who the end user is and what that end user wants or needs. In this undertaking the Corps must define clear objectives. As one part of the identification of objectives, the Corps must define the purpose of the tool/model -- for example, will be tool be a forecast tool, a risk-based decision tool, or an [*sic* impact] assessment tool. There will be pressure to defend the scientific acceptability of the resulting models and to demonstrate their prediction accuracy.

5) The framing of modeling approaches must be dependent on early and open dialogue with the appropriate stakeholders. What the stakeholders feel they need as a modeling approach will vary across spatial scales. Therefore, adaptive management approaches provide an appropriate organizing framework for modeling.

Comments Pertinent to Individual Presentations

1) There is strong need within the USACE for models of higher trophic levels. Models such as the ATLSS model (see Gross *et al.* this volume) are multiple models which transcend trophic levels via levels of aggregation, and which have explicit space and time scale components. Determining the appropriate time and space scales for such models is often based on best professional judgement, on the defined level of model resolution, and on the ability to parameterize the model based on existing data and knowledge. For such a multi-level model, geographic information system (GIS) techniques are used to identify or drive the couplings or interactions within the model. Therefore, such a model is a landscape or GIS-based model. The nature of the model couplings is dependent on the specific biotic component on which interest is focused in a given application. The limitations of such a model relate to the fact that it is a long-term modeling framework (with a 20-30 year time frame for predicting). One cannot expect that this model will provide accurate predictions at a time scale of single years.

2) The appropriate approach for validating a multiscale model is to validate individual model components rather than the model as a whole. It is difficult if not effectively impossible to validate ecosystem models as whole, intact entities. In addition, predictions from such a model should be compared with monitoring data, and a monitoring program should be developed and linked to the large-scale modeling effort. One suggested approach for ecosystem modeling was to base validation on specific biological indicators rather than attempting to understand and predict the dynamics of the “complete” ecosystem.

3) Because there are often multiple causes underlying the decline of a specific biological resource, managers frequently end up with ineffective management or restoration alternatives or practices, which when implemented do not have any actual effect on the target species or population. Models are therefore good tools for evaluating and comparing management alternatives for the species or population in question. However, one mistake frequently made is that management actions often focus on a life stage of the target species for which it is most convenient to collect data or on which management is easiest. A good example provided by

Crowder *et al.* (this volume) focused on the protection of sea turtle nests. The management or protection of this single life stage may or may not play a significant role in the overall management and protection of the sea turtle population. In such cases, it is critical to collect information on all life stages of the species. Once the most sensitive stages are identified, a model can be developed to focus management actions on the most sensitive stages (or ages) in the life history of the organism.

4) The new mission of the USACE is to be the environmental (green) agency (see Juhle this volume). In implementing this new mission, Corps managers must be able to assess the consequences of human actions and management alternatives on the health and sustainability of ecosystems. The USACE feels that this can best be done at the watershed scale, in that the Corps is interested in managing ecosystems rather than individual species. Corps administrators feel that broad-scale modeling tools, that can be applied across many watersheds to protect and manage sustainable ecosystems, are needed. An index or some other indicator of watershed/ ecosystem health is desired. Through development of a coarse modeling approach such as this, the USACE can assess human impacts on sustaining ecosystem functions and evaluate risks associated with proposed management actions. The Corps hopes to alter its mode of action from being more of a reactionary agency, responding to fires, to being a forward thinking agency based on preventing the degradation of important functions important to ecosystem sustainability. Examples of management questions at this scale of analysis would be: (1) what are impacts of changes in land use? and (2) what are impacts of changes in zoning laws? Examples of target inputs would be buffer zones and fragmentation, while examples of target outputs or responses would be fishable/swimmable criteria.

USACE administrators, therefore, feel that modeling (at least for the sorts of applications outlined in the paragraph above) must move away from reductionist approaches that can't be transferred from watershed to watershed and that only address issues of local concern. Models need to be developed at a coarse scale, dealing with broad-scale ecosystem functions. However, it also recognized that no single ecosystem model can address all of the Corps' environmental concerns, even at broad spatial scales.

Considerable discussion occurred in response to these points. The index or coarse-scale modeling approach is not appropriate for many environmental issues of interest to the USACE. Modelers have been building coarse-scale models for years, and have learned via these efforts that species do matter and do alter ecosystem structure and functions in critical ways, and must therefore be included among the new modeling approaches to be developed. Indeed, different suites of models are required to answer the sorts of environmental questions of interest to the Corps across an array of scales and organizational levels. Models are problem and use specific, so that model structure boils down to the specific problems or issues that an agency, administrator, or natural resources manager wants to resolve. It is also the case that upper-level agency managers require different sets of tools to answer broad-scale national questions than local resource managers require to deal with environmental issues at local or regional scales. What matters to local resource managers are often tangible items of interest to defined stakeholders such as the quality of the fishery for recreational use or water quality for drinking or recreation. Moreover, it is it is often site-specific issues or problems that result in breakthroughs in modeling approaches and advances in modeling capabilities.

Broad Discussion Themes

Conflicting Modeling Needs in the USACE

As follow-up to the discussion of different modeling needs, for example, of upper-level agency managers vs local resource managers, suggestions were made that several (3-5 ?) case studies could be initiated nationwide to develop coarse-level models and indices for broad-scale resource management. This could be done by identifying a limited number of watersheds from the 1,000+ watersheds of interest to the Corps nationwide. These watersheds could be used as demonstration areas for model and index development. Selection of watersheds should be based on significant, non-overlapping differences in key physical and biotic attributes. A hierarchy of models could be developed for each watershed at different scales of resolution. Watershed selection should also be based on definition of "real" management issues and systems of interest. Indices developed from this approach would be used as screening tools to identify and evaluate relationships between management and other human impacts and the condition of the watershed ecosystem.

Approaches to Modeling

Key issues and concerns defined from the perspective of the major stakeholders for a given project must be identified early in the modeling process. It is equally important to identify who the major stakeholders are, in that pertinent issues and concerns can be very different for different types of stakeholders. In many large-scale ecosystem management projects, there may be two or more sets or levels of stakeholders - *e.g.*, both technical and political. Technical stakeholders are good for long-term studies and may serve as an advisory group to the political stakeholders. It is important for the stakeholders to get involved directly with the biologists who know the system. A schematic of such interactions are:

biologists ↔ modelers ↔ political/technical stakeholders

Planning is an important part of the process of model development. Examples given were the EPA Estuary Program, where workshops were conducted to assemble the issues, develop a modeling plan, and identify key endpoints. In these meetings it is important to listen to the issues articulated by the participants and then to develop a candidate model of the system. This can be presented to the technical and political stakeholders, along with the spatial and temporal scales of interest; the tentative model can be modified iteratively based on input received, followed by agreement on the defined approach by all stakeholders.

Alternative Modeling Approaches

During the workshop a number of different modeling approaches were presented and discussed, including: projection matrix models, individual based models, physiologically based models (bioenergetics), metapopulation models, dynamic compartment models. The relative advantages and limitations of the different approaches were treated in several of the papers presented and will not be reviewed further here. Deciding which of these models to use in a given project is often linked to the question and how much data are available. One should begin with a simple model construct if sufficient data don't exist to answer the question. The presence

of adequate data may provide the basis for employing a more complex model. Other comments offered concerning specific modeling approaches included: projection matrix models are increasingly moving toward stochastic/risk analysis and metapopulation models; individual-based models are compatible with metapopulation models; and stage-based models are developing in the direction of individual-based models.

Issues of Scale

Workshop participants recognized the critical role that space and time scales play in defining problems and modeling approaches. Suggestions were made that the USACE should consider a "bottom-up" vs a "top-down" approach with respect to scale, in that less process detail is typically required at higher trophic levels. The rationale for this relates to the fact that there are fewer compartments, larger time steps (*e.g.*, breeding cycles are longer), and organisms are larger and require greater space. Organismal size is generally related to generation time, and space is related to both size and territory needs.

The scale of a problem is related to the required simulation time step. Models at larger scales, such as a population, require a longer time step vs models of individuals (smaller scale), which function at a smaller time step. Nonetheless, it was suggested that the USACE should increase the spatial and temporal scales at which it addresses problems. However, as the spatial scale increases, the meaning or interpretation of model parameters also changes, which must be considered carefully in any project.

It is clear that there does not exist a single modeling approach or scale appropriate to all problems. The relevant endpoints and "control knobs" (*i.e.*, controlling variables or processes) are quite different at different scales. Definition of the appropriate scale for the problem at hand, and the endpoints, control knobs, and controlling processes pertinent to that scale, determines how to structure model at that scale.

In some instances one can use appropriate averaging or filtering functions to retain the same answer in moving across scales. However, if this leads to averaging out the dominant forcing functions, one can and will lose information. For example, for individual behaviors or other types of nonlinear effects or responses, one probably shouldn't average. In conducting population studies and models, one can use this general approach if the effects or responses of interest are linear.

Other comments offered in relation to the issue of scale included: in modeling, as one reduces the temporal or spatial scale (*i.e.*, make them finer), one also needs more detailed information in the model. Models formulated at an individual scale are acceptable when there are only a small number of individuals, such as with threatened and endangered species. In other cases, the model should be based on some sort of aggregated variable or "proxy measure" (*e.g.*, a compartment of wading birds) quantified in terms of biomass, size class, or water depth. Metapopulation models become quite useful when the spatial scale of the problem gets very large.

Model Linkages

Workshop participants seemed to be in agreement that ecosystem modeling will require considerable work on model linkages. It will also require a change in the currency of model outputs and inputs. Softening the linkages between models or coupling models can provide

greater model flexibility. One example given was the McKendrick-von Foerster model (*e.g.*, Hallam this volume) for chemical contamination, where each ecotype affected is represented by a partial differential equation. These partial differential equations are then coupled to obtain information on the entire population.

Projection matrix models typically are not linked to hydrodynamic or water quality models, but individual based models (IBMs) can be linked to hydrodynamic models, habitat models, and stage-based models. IBMs are spatially explicit models that allow individual movement, and are thus easier to link to hydrodynamic models. One of the crucial steps in linking models is that one must have the data required to define or formulate the linkages. The outputs of one model must be the same as the drivers (inputs) for the linked model, for the linkage to be successful. There needs to be some sort of numerical relationship between them, which can be formulated with appropriate functions.

Ecological Theory as the Basis for Ecosystem Models

Recent advances in the development of water quality models have occurred because of the underlying first order principles -- *i.e.*, recent advances in understanding and formulating the underlying transport and chemical transformation processes. We currently do not have such "first principles" for ecosystems or other areas of ecology, but we do have access to "conservation of energy" principles (*i.e.*, the laws of thermodynamics). In order for progress to be made in ecosystem modeling, we must consider energy conservation as providing the fundamental basis for many of our model constructs. In other words, we can't make significant progress in ecosystem modeling without access to or development of first order principles. Individual based models can provide for the conservation of mass and energy not available with other types of models. If modelers ignore the basic physiology of organisms, and models do not take account of conservation of energy and mass along with fundamental physiological processes, then we are left with statistical mechanistic approaches to modeling. Similarly, we can employ theories from evolutionary biology or ecology as a source of guidance for ecosystem models (*e.g.*, habitat-choice models). The key point is that significant advances in ecosystem modeling of the sort being considered in this workshop must be firmly based in sound ecological theory and first principles.

Attributes of Management-Oriented Models

Models must have both utility and scientific credibility. To make a model defendable or credible, one must have access to a good data base. If the model formulation includes too many processes and computations that lack support from available data, it could lead to problems with model credibility. If sufficient supporting data are lacking, then efforts must be made to collect the required data. Data richness and compatibility lead to higher model credibility.

Costs of data collection vs model development, however, often have a ratio of 10:1. Hence, it is much cheaper to develop the model than collect the data required to support its credibility. Therefore, when one is thinking about developing a model, the availability of data should be considered, and the cost of collecting new data built into the overall modeling budget.

Risk and Uncertainty

There is considerable confusion in the modeling literature between uncertainty and variability. Uncertainty is subjective and is related to measurement (or prediction) error, whereas variability is objective and is related to natural fluctuations in processes or variables of interest. Uncertainty is related to the probability associated with a particular prediction. Confidence is based (inversely) on the uncertainty associated with the prediction. Modelers often distinguish between two sources of uncertainty: natural variability (= variability), and measurement variability (or error, which = uncertainty). Uncertainty compounds in models as the number of parameters increases. The larger the number of parameters in a model, the more important it is to evaluate and deal with uncertainty. The tendency in most ecological models, however, is to ignore it.

One can run parallel models or use Monte Carlo simulation (in which case the underlying models are stochastic) to evaluate natural variability. The number of runs one would need to make is dependent on the degree of variability reflected in different model realizations. If they are highly variable, then many runs are required. Supercomputing capabilities may be required to perform Monte Carlo analyses of ecosystem models.

Risk Communication

Communicating risk to stakeholders typically involves use of a similar plot or graphical representation - *i.e.*, a plot of the probability of decline or impact vs the % decline or impact. Once stakeholders see this plot several times they begin to and can understand the risks that are being communicated. Effectively communicating risk works best if one makes the transition from the specific to the general, and requires someone who is good at explaining to lay people that ecological systems are inherently variable systems naturally.

When all the underlying variability and uncertainty in model predictions are incorporated into the final results, it may be the case that the model is not capable of making a reliable prediction, in which case one ends up providing a qualitative answer to the issue at hand. But one can say in such a situation that a certain parameter is the most uncertain parameter in the model, that a specific assumption was made relative to this parameter, and that based on this assumption one obtains a certain answer.

Modelers need to employ uncertainty analysis, in order to express how much uncertainty is associated with the model results. Often the public wants more certainty, in which case it is important to explain what it would cost to be more certain. Uncertainty analysis results can also be used to explain to the public or stakeholders that some parts of the resulting uncertainty are inherent and can't be reduced any further, no matter what resources are applied to the problem. One can only say that the best available science was used in reaching the answer provided.

Examples were given as to how risk has been communicated in two large-scale federal assessment programs: (a) NAPAP provided a qualitative index of uncertainty in its communication of risk to Congress and the public, and (b) the Global Climate Change Program is using a structural uncertainty analysis, where four separate groups are completing uncertainty analyses of model predictions and the Program will take the mean of the difference between the four groups.

Zebra Mussel Modeling Approaches

As the initial test case for the new modeling approach under discussion at this workshop, discussions of the devlopment of a zebra mussel model focused on the desire to develop a model of the impacts of mussels on other organisms, trophic structure, and water quality conditions in aquatic ecosystems, rather than on a model to be used for zebra mussel control.

The suggestion was made that, if funding is limited, WES should focus model development efforts where they are rich in data and where it will be easy to demonstrate an impact when the model is implemented. Use of the Ohio River data set was discussed, leading to the idea that available demographic and spatial data could lead to a two-dimensional (2-D) model. However, the Ohio River data set has only limited data on water chemistry and water quality. Also, ongoing studies (papers by Miller this volume) indicate that zebra mussels do not represent a significant impact or issue in high velocity, flowing systems, but have more of an effect in quiescent waters, so that a riverine system may not the best to be modeled. Other suggestions indicated that a reservoir system, particularly one where reasonable amounts of water chemistry, water quality, fish, and other biological data are available, would be a better site for model development. Possible sites include Lake Oneida in upstate New York, Saginaw Bay on Lake Huron, or Taylorsville Lake in Kentucky, where zebra mussels have already been identified in the lake. The limnology group at the University of Wisconsin was suggested as a contact for lake models that have already been developed.

Some time was spent discussing the time and spatial scales (especially watershed vs lake) appropriate to a zebra mussel model. The scale selected will depend on the objective defined for the model application. For example, the target may be the entire watershed but the effects of concern may be focused more specifically than on the entire watershed.

The desired modeling approach or platform could include reservoir operations as a possible management tool. It is easy to see the effects of reservoir operations at all levels of the aquatic ecosystem, from dissolved oxygen to zooplankton and fish. This gets back to the issue of whether this is to be a control or an impact assessment model. Reservoirs are operated based on rule curves for lake staging that times when and how the stage increases or decreases. A possible management question for this scenario might be framed as, “How can one alter the rule curve in order to mediate the impacts of zebra mussels on other organisms in the reservoir?” It was agreed that if the focus of the modeling effort was on the control of mussel populations, that whatever management actions did to alter the survival of zebra mussels would also affect other trophic levels and populations within the reservoir ecosystem.

Discussions emphasized the fact that quite a bit has been done on the spread of zebra mussels, but that this work has been fairly crude, mostly involving multiple regression type analyses. The focus of this effort should be placed on the effects of zebra mussels on water quality, zooplankton, and higher trophic levels. It was suggested that this might be done in Lake Oneida, where WES could study the effects of zebra mussels on walleye, other food sources, and water quality.

A suggestion was made that the zebra mussel model that is to be developed could serve as a surrogate for other bivalves that may infest USACE projects in the future.

On several occasions the question was raised of whether it is necessary to include demographic processes in the desired model, or whether population levels should be specified as

an initial condition since not enough is presently known about demographic processes in this species. A related question is whether WES has sufficient information concerning links between zebra mussels and other species to incorporate into a model.

The following specific items were suggested as possible approaches or considerations for the development of the desired zebra mussel model:

a) Begin with a model of the bioenergetics and life history of a single zebra mussel, and then couple that model to other models. This should be a stand alone bioenergetics model that produces reasonable results for mussel biomass. A bioenergetics model may be available (*i.e.*, developed by Snyder).

b) The model might focus either on numbers of zebra mussels or biomass (structure) and reserves.

c) The model should then be linked to water quality variables and conditions, through parameters such as filtering rates.

d) The model could follow the dynamics of calcium carbonate.

e) The mussel bioenergetics model could be coupled with a demographic model.

f) The sequence of steps followed in developing the desired model will be dependent on time, cost, and the types of predictions WES wants to make with the model.

g) Totally aggregated compartment models won't be useful for predicting the dynamics of chemicals through the aquatic food chain.

h) It was suggested that if the model is initially developed for the Ohio River, one can employ a stage-based model and then link it to a metapopulation model that tracks the distribution and dispersal of different stages and their transition to the next growth stage.

i) WES was cautioned that one key to the success of this modeling effort was the ability to develop appropriate links between zebra mussel biology and water quality; therefore, careful attention needs to be given to whether (and how) mussel demographics are formulated in the model (*e.g.*, dispersal, settling and establishment/early development).

j) It was suggested that it may be critical to select a semi-closed system in respect to mussel dispersal for the purpose of this zebra mussel model demonstration.

k) As part of this effort, it may be possible to demonstrate or evaluate the benefits and limitations of several different models or modeling approaches.

l) Several questions were raised as to whether it would be best to employ a stage-based model or an individual-based model. Resolution of this issue may be dependent on the specific questions being asked and on the specific information needed to evaluate mussel impacts on

other attributes of the aquatic ecosystem selected for study. If the desire is to build a more robust model, then life history processes should be incorporated into the final modeling approach.

m) It is critical that specific linkages among various possible models that could contribute to this effort be defined early in the model development process, so that these linkages can be built into model structure from the outset.

n) The model or suite of models assembled for this effort must include a model of zooplankton dynamics, to create linkages to higher trophic levels. The zooplankton model should be dynamic, should account for both numbers and biomass, and should include several functional groups of zooplankton (*e.g.*, both herbivorous and predatory). The model should allow for vertical migration as well as growth from one size class to the next. A starting point could be provided by existing zooplankton population models developed by Park and Carpenter. The zooplankton model should be linked to models of fish, water quality variables, and other organisms (which can be linked to early life stages). It was suggested that formulations of zooplankton couplings to water quality and to higher trophic levels may have very different requirements in terms of the level of detail needed in the model formulationss. The example given was: WES can ignore rotifer feeding in terms of links to water quality, but this is an important linkage in terms of fish feeding. This point was made to show that WES may need to make compromises in the level of detail to be included in this component of the overall model.

o) The suggestion was made that the model developed under this effort should include all major levels in the aquatic food chain including algae. Most current models of algal processes include fixed stoichiometric relations for algal nutrient concentrations, which may or may not be appropriate for other components of the food chain.

p) Carbon fixation is important to energy flow/trophic transfers. However, this process is usually not well represented in models that work at a higher level of aggregation than that of carbon chemistry reactions.

q) It was pointed out that if WES wants to include higher trophic levels in this model, they need to be careful in regards to maintaining mass balance. The concern was expressed that they don’t have closure on all processes affecting nitrogen dynamics.

r) It was agreed that one particularly viable approach would be to develop a population model for zebra mussels focused on Omstead Lake, OH; this model could then be transported to other water bodies in order to build confidence both in the formulation of population dynamics and in the predictive capabilities of the resulting model.

Appendix A

Workshop Organization & Agenda

Workshop on Aquatic Ecosystem Modeling and Assessment Techniques for Application within the U.S. Army Corps of Engineers

Final Workshop Organization & Agenda

Tuesday, July 1

7:00 AM BREAKFAST

8:00 AM Registration and Informal Discussions

Session 1: The Institutional and Resource Management Context

Session Purpose - this initial session is intended to provide background information to all workshop participants on the broad organizational context for the workshop, and on the resource management issues and challenges at CE projects that will motivate subsequent modeling activities.

8:30 AM Welcome and Introductions, and Overview of Workshop Purpose, Organization, and Logistics - Jack B. Waide, Lead Workshop Organizer and Facilitator, FTN Associates, Ltd., Little Rock

8:45 AM Brief Welcome on Behalf of WES: the Purpose and Organizational Context for this Workshop (CHSSI, ZMRP, EMRRP, EMI) - Dr. Robert H. Kennedy, Lead Workshop Sponsor, WES Environmental Laboratory, Vicksburg

9:00 AM The Resource Management Challenge in the Corps of Engineers - the Mandate to Manage and Restore Ecosystems at Corps Projects: a Corps-Wide Perspective - Mr. Pete Juhle, Headquarters, US Army Corps of Engineers, Washington, DC and Dr. L. Jean O'Neil, WES Environmental Laboratory, Vicksburg

9:15 AM The Resource Management Challenge in the Corps of Engineers - the Mandate to Manage and Restore Ecosystems at Corps Projects: the Perspective of a Research Biologist - Dr. Richard E. Price, WES Environmental Laboratory, Vicksburg

9:30 AM The Institutional Context - Needs for Expanded Ecosystem Modeling and Assessment Capabilities in the Corps of Engineers: an Ecologist's Perspective - Dr. Robert H. Kennedy, WES Environmental Laboratory, Vicksburg

9:45 AM The Institutional Context - Going Beyond Current Water Quality and Contaminant Modeling Capabilities to Assess Project Impacts on Aquatic Ecosystems and Biota: a Modeler's Perspective - Dr. Mark S. Dortch, WES Environmental Laboratory, Vicksburg

10:00 AM BREAK

10:15 AM Conceptual Issues Underlying Development of New Approaches to Modeling and Assessing Human Impacts on Aquatic and Terrestrial Ecosystems at Corps Projects - Jack B. Waide, FTN Associates, Ltd., Little Rock and Dr. Robert H. Kennedy, WES Environmental Laboratory, Vicksburg

10:45 AM Extended Discussion of Session Presentations, with particular focus on: (1) the Corps resource management challenge to manage and restore aquatic (and terrestrial) ecosystems; (2) the contribution of models and related assessment tools to this process; and (3) desirable characteristics and capabilities of models to be useful for this purpose

12:15 PM LUNCH

Session 2: Test Application - Assessing & Managing Zebra Mussel Impacts at CE Projects
Session Purpose - this session is designed to provide essential background information on the extent and nature of zebra mussel impacts -- on water quality conditions, on trophic dynamics and food web processes, and on biotic composition and species interactions -- to aquatic ecosystems and biota at CE projects, and on current understandings of the biology and ecology of zebra mussels as prerequisite to understanding and managing such impacts.

1:15 PM Current Understandings of the Physiological Ecology and Life History of Zebra Mussels (*Dreissena polymorpha*) - Dr. Drew C. Miller, WES Environmental Laboratory, Vicksburg

1:35 PM Potential Impacts of Zebra Mussels (*Dreissena polymorpha*) on Aquatic Ecosystems - Dr. Drew C. Miller, WES Environmental Laboratory, Vicksburg

1:55 PM Extended Discussion of Session Presentations, with particular focus on: (1) the zebra mussel “problem” at CE projects as a central focus for developing an assessment-oriented aquatic ecosystem modeling approach and capability; (2) key linkages of zebra mussel biology to other ecosystem components and processes (specifically, linkages to water quality processes, to trophic dynamic/food web processes, and to biotic composition/species interactions); (3) development of a conceptual model of critical biotic components, processes, and linkages to serve as the conceptual underpinnings of the proposed modeling framework

3:10 PM BREAK

3:30 PM Extended Discussion of Session Presentations (continued)

Session 3: From Water Quality/Contaminant Models to Aquatic Ecosystem Models
Session Purpose - this session is intended to stimulate discussion both of extensions of current WES water quality and contaminant modeling capabilities and approaches required to deal with the resource management challenges identified in the initial workshop session, and of potential linkages of new modeling approaches to existing water quality and transport models and modeling approaches.

3:55 PM Going Beyond Current Water Quality/Contaminant Models and Approaches to Assess Human Impacts to Biological Components and Processes in Aquatic Ecosystems: a Coupled Phytoplankton-Aquatic Food Web-Zebra Mussel Model for Saginaw Bay, Michigan - Dr. Victor J. Bierman, Jr., Limno-Tech, Inc., Ann Arbor, MI

4:15 PM Extended Discussion of Session Presentation, with particular focus on: (1) processes and characteristics to include in desired modeling framework/approach, not included in existing water quality and contaminant models, in order to develop capabilities to model and assess human impacts to biotic components and processes in aquatic ecosystems at multiple spatial scales and organizational levels; (2) desired linkages of new modeling framework to, and compatibilities with, existing water quality/contaminant models

5:30 PM ADJOURN

6:30 PM DINNER

8:00 PM Evening Session - Informal Discussion of Main Issues and Ideas from Day 1: (1) key ideas underlying use of models to assess human impacts on aquatic ecosystems, (2) key features and attributes to be included in new models/model constructs to be used for this purpose; and (3) the zebra mussel problem as a focus for initial model development activities. Discussion prompted by review of highlights from day's discussions by Jack B. Waide and Dr. Lisa M. Gandy, FTN Associates, Little Rock

SOCIAL & Informal Discussions

Wednesday, July 2
7:00 AM BREAKFAST

8:00 AM Logistics issues, carry-over thoughts from previous day

Session 4: Conceptual and Mechanistic Approaches to Development of Aquatic Ecosystem Assessment Models (Part 1)
Session Purpose - this session is designed to explore conceptual foundations of incorporating detailed process descriptions of demographic and bioenergetic processes into aquatic ecosystem

assessment models, as well as spatially explicit descriptions of metapopulation dynamics and processes, based on the experiences of select speakers outside of WES and COE.

8:15 AM Approaches to Large-Scale Ecosystem Modeling Across Multiple Trophic Levels: Some Early Lessons from the South Florida ATLSS Experience - Dr. Louis J. Gross, University of Tennessee, Knoxville; Dr. Donald L. DeAngelis, USDI-GS/BRD, South Florida/Caribbean Ecosystem Ecosystem Research Group and University of Miami, Coral Gables, FL; and Dr. Michael A. Huston, University of Tennessee, Knoxville and ORNL Environmental Sciences Division, Oak Ridge, TN

8:35 AM Development and Use of Matrix Models to Evaluate Alternative Management Approaches for Restoring Biological Populations - Drs. Larry B. Crowder and Selina S. Heppell, Duke University Marine Laboratory, Beaufort, NC; and Elizabeth A. Marschall, Ohio State University, Columbus

8:55 AM Models of Bioenergetic Processes and Trophic Dynamics and Their Incorporation into Aquatic Ecosystem Assessment Models: Development and Use of Bioenergetic Models to Assess Contaminant Exposure and Effects in the EPA - Dr. Craig Barber, USEPA/ORD/NERL, Ecosystems Research Division, Athens, GA **[NOTE - presentation cancelled due to last minute logistical conflict]**

9:15 AM Metapopulation Models and Ecological Risk Analysis: A Habitat-Based Approach to Biodiversity Conservation - Dr. H. Reþit Akçakaya, Applied Biomathematics, Stony Brook, NY

9:35 AM Extended Discussion of Session Presentations, with particular focus on: (1) approaches to incorporating demographic and bioenergetic processes into aquatic ecosystem assessment models; (2) linkages between demographic and bioenergetic processes in aquatic ecosystem models, and with existing biological and physical processes in water quality models; (3) modeling biological processes in space associated with metapopulation dynamics - a necessary feature of aquatic ecosystem assessment models?

10:15 AM BREAK

10:30 AM Extended Discussion of Session Presentations (continued)

Session 5: Conceptual and Mechanistic Approaches to Development of Aquatic Ecosystem Assessment Models (Part 2)

Session Purpose - this session is intended to focus on alternative mechanistic approaches (*e.g.*, individual based models or IBMs, physiologically structured models) to developing aquatic ecosystem assessment models that incorporate detailed descriptions of both demographic and bioenergetic processes across multiple trophic levels and spatial scales.

11:20 AM Approaches to Development of Aquatic Ecosystem Assessment Models: Individual-Based Models of Fish and Their Coupling to Physical and Biological Processes in Aquatic Ecosystem Models - Dr. Kenny A. Rose, ORNL Environmental Sciences Division, Oak Ridge, TN

11:40 AM Approaches to Development of Aquatic Ecosystem Assessment Models: Physiologically Structured Population Models and Model Stoichiometries - Dr. Thomas G. Hallam, University of Tennessee, Knoxville, TN

12:00 Noon LUNCH

1:15 PM Extended Discussion of Session Presentations, with particular focus on: (1) advantages and limitations of alternative approaches (individual based models, projection matrix models, physiologically structured models, ...) to formulating biotic processes in aquatic ecosystem models, and (2) other plausible approaches

Session 6: Special Topics Associated with Development of Aquatic Ecosystem Assessment Models - Assessing Risk and Uncertainty

Session Purpose - this session is intended to focus on the incorporation of risk and uncertainty analysis capabilities into aquatic ecosystem models for use at CE projects.

2:45 PM Use of Aquatic Ecosystem Models for Ecological Risk Assessment: From Single Species Populations to Communities - Dr. Lev R. Ginzburg, SUNY-Stony Brook and Applied Biomathematics, Stony Brook, NY

3:05 PM Evaluating Uncertainty and Risk in Projections of Aquatic Ecosystem Assessment Models - Dr. Steve M. Bartell, SENES Oak Ridge/Center for Risk Assessment, Oak Ridge, TN **[NOTE - presentation cancelled due to last minute scheduling conflict]**

3:25 PM BREAK

3:45 PM Extended Discussion of Session Presentations, with particular focus on: (1) desirability of including risk and uncertainty analysis capabilities in aquatic ecosystem assessment models; (2) implications of their inclusion for model structure and utility

5:15 PM ADJOURN

6:00 PM DINNER

7:30 PM Evening Session - Informal Discussion of Main Issues and Ideas from Day 2: (1) incorporation of demographic and bioenergetic processes into aquatic ecosystem assessment models; (2) alternative mechanistic approaches to model

formulations; and (3) advantages and implications of incorporating risk and uncertainty assessment capabilities into aquatic ecosystem assessment models. Discussion prompted by review of highlights from day's discussions by Jack B. Waide and Dr. Lisa M. Gandy, FTN Associates, Little Rock

SOCIAL & Informal Discussions

Thursday, July 3

7:00 AM BREAKFAST

8:00 AM Logistics issues, carry-over thoughts from previous days

Session 7: Workshop Wrap-Up and Conclusions

8:05 AM Final Extended Discussion of Key Workshop Conclusions and Promising Approaches: (1) identify key conclusions from workshop; (2) summarize discussions of desirable features to build into aquatic ecosystem assessment models; (3) refine conceptual models underlying model development; (4) outline specific tasks required to develop such models

10:00 AM BREAK

10:15 AM Concluding Discussion of Workshop Discussions from a Broad Perspective - In looking back over our discussions and their relation to the initial objectives established for the workshop, have we formulated an approach to development of aquatic ecosystem assessment models that is (1) useful for managing and restoring aquatic ecosystems at Corps projects?, and (2) generalizable to the array of similar problems faced by the Corps in both aquatic and terrestrial settings?

11:10 AM ADJOURN and LUNCH, transportation to airport

Appendix B

List of Workshop Participants

Workshop on Aquatic Ecosystem Modeling and Assessment Techniques for Application within the U.S. Army Corps of Engineers

List of Workshop Participants

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