Suspension feeders:
A Workshop to Assess What We Know, Don't Know, and Need to Know to Determine Their Effects on Water Quality

March 18-19, 2002
BWI Ramada Inn
Hanover, Maryland

Workshop Chair:
- Dr. Denise Breitburg, The Academy of Natural Sciences Estuarine Research Center

Steering Committee:
- Dr. Eileen Hoffman, Old Dominion University
- Dr. Roger Newell, University of Maryland Center for Environmental Studies
- Dr. Arthur Butt, Virginia Department of Environmental Quality
- Mr. Derek Orner, NOAA Chesapeake Bay Office
- Dr. Robert Magnien, Maryland Department of Natural Resources

Breakout Session Leaders:
- Oysters and Other Benthic Invertebrates:
  - Dr. Eileen Hoffman, Old Dominion University
  - Dr. Roger Newell, University of Maryland Center for Environmental Science
- Zooplankton:
  - Dr. Marie Bundy, The Academy of Natural Sciences Estuarine Research Center
  - Dr. Steven Bartell, Cadmus
- Menhaden:
  - Dr. Robert Wood, University of Maryland Center for Environmental Studies
  - Dr. Thomas Miller, University of Maryland Center for Environmental Studies

December 2002

STAC Publication 02-002

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Background and Workshop Goals

Phytoplankton standing stocks, production and species composition are potentially influenced by both the supply of nutrients to the bottom of the food web and removal by suspension feeders higher in the food web. Similarly, suspended sediment concentrations are determined by both their loading rates and their removal or settlement from the water column. Most management activities to date in the Chesapeake Bay watershed have addressed the supply end of these relationships by attempting to reduce nutrient and sediment loading to waters within the Chesapeake Bay watershed. However, to predict the relationship between nutrient or sediment loading and water quality, it is also important to understand and predict the potential top-down effect of suspension feeders such as menhaden, zooplankton, bivalves and other benthic invertebrates on phytoplankton and suspended sediment. These suspension feeders remove particles from the water column and potentially influence nutrient cycling, water clarity, phytoplankton dynamics, and other ecosystem processes. The impact of suspension feeders depends on population levels and distributions of the various species in space and time, which, in turn, can be influenced by both management actions and natural variation in physical and biological factors.

The current Chesapeake Bay Agreement includes the commitment: "*By 2004 assess the effects of different population levels of filter feeders such as menhaden, oysters and clams on Bay water quality and habitat."* The 'Suspension Feeders Workshop' was a response to this commitment. Its goals were:

1.) to assess current understanding of the biological and physical characteristics of the Chesapeake ecosystem needed to estimate suspension feeder effects,
2.) to assess the utility of currently existing models, and
3.) to identify critical features (processes, organisms, model capabilities) to include in future models designed to predict effects of suspension feeders on phytoplankton and sediment in Bay waters.

The workshop included plenary presentations and discussions, and three concurrent breakout groups - one each on menhaden, benthic suspension feeders (including oysters), and zooplankton. This workshop report summarizes plenary and breakout group discussions, and outlines steps recommended to meet the filter feeder commitment.

Each breakout group was charged with making three recommendations:

1.) A recommendation on how to estimate or model the effect of their focal taxa of suspension feeders on Chesapeake Bay phytoplankton in the *very best scientifically defensible manner if time and funding did not limit the effort.* (What biological, ecological and biogeochemical processes should be included? Of the suite of potential modeling techniques, which would be most appropriate? What levels of spatial and temporal resolution are required? How detailed should the food web be?),
2.) A recommendation on how to predict the effect of their group of suspension feeders on Chesapeake Bay phytoplankton *in the best way possible given a very modest amount of funding available and the need to meet the 2004 deadline* (Can available models be adapted or modified to answer the question

utilizing existing data as input? What level of confidence would you have in predictions? What level of linkage between suspension feeder models and the Bay Program water quality model is needed? Should suspension feeder effects be elaborated directly in the water quality model?); and

3.) A short list of the highest priority areas of research and model development that would greatly enhance recommendation #2 if a bit more time and funding were available.

A Recommended Framework for Estimating Suspension Feeder Effects

A 4-pronged approach (Fig. 1) to the task of estimating effects of suspension feeders on phytoplankton and suspended sediment will provide the most reliable, and ultimately, comprehensive assessment of the effects of current, higher and lower suspension feeder populations.

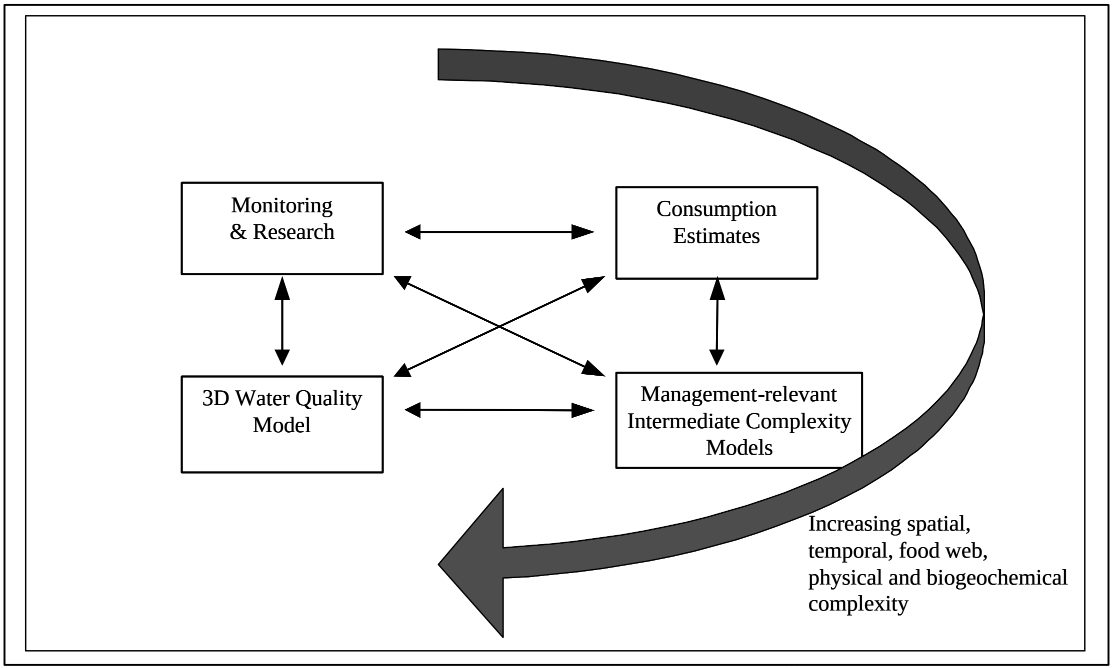

Figure 1 – Four pronged approach to the task of estimating effects of suspension feeders.

Monitoring and Research

Monitoring and research provide the information required for all estimates and models. Mathematical calculations, whether done with simple spreadsheets or complex models, are only as reliable as the data utilized to structure and parameterize them. Long-term monitoring has provided extensive spatial and temporal information on abundance, taxonomic composition, and distribution of a subset of Bay biota. Without data generated by these monitoring programs, the commitment to estimate suspension feeder effects would not be achievable. Targeted research programs, and short-term monitoring efforts provide additional spatial and temporal coverage of biota as well as estimates of consumption rates and the effect of biotic and physical factors on consumption and production. Nevertheless, there are important data gaps that limit the ability to perform even rudimentary estimates of effects of some potentially important suspension feeders. The most productive pathway for improved management and understanding of the Chesapeake ecosystem, as well as the path most likely to lead to success in achieving scientifically defensible estimates of suspension feeder effects requires a coordinated and collaborative program of monitoring, research and modeling with continuous feedback among component parts.

Consumption Estimates

The first step in predicting suspension feeder effects on the Chesapeake ecosystem is the development of estimates of consumption for each of the three functional groups of suspension feeders – benthic suspension feeders, zooplankton and menhaden. These estimates are calculated by multiplying the number or biomass of organisms of each relevant type by their taxa- and/or size-specific consumption rates. These simple calculations must be underpinned by extensive analysis and synthesis of available monitoring and research data.

The degree of temporal and spatial resolution that will be possible, and the confidence with which consumption estimates can be made, will be determined by available data, which vary greatly among taxa. In their most basic form, consumption estimates can qualitatively compare consumption with predicted reduction in phytoplankton biomass under management-relevant scenarios. For example, one could ask whether menhaden consumption is likely to be similar in magnitude to, or orders of magnitude less than, the reduction in phytoplankton predicted for a 40% reduction in controllable nutrient loadings. Such comparisons are useful to determine whether changes in suspension feeder populations are likely to make a substantial contribution to the magnitude of nutrient reduction required to meet water quality criteria, and whether more elaborate models are warranted.

Ideally, consumption estimates will have spatial resolution at least to the level of salinity zones within the mainstem Bay and major tributaries, temporal resolution at least to the level of season, and biologically meaningful taxonomic resolution. Management, harvesting, habitat degradation, habitat restoration, and important ecological processes all occur within spatial and temporal frameworks. Thus, consumption estimates are more useful if made at relevant spatial and temporal scales. In addition, spatial and temporal resolution of consumption estimates is critical to development of management-relevent ‘intermediate complexity’ models described below.

Numerical Models

Numerical models are required to go beyond consumption estimates and consider the fate of consumed nitrogen and suspended sediments. Phytoplankton nitrogen excreted as ammonia by suspension feeders potentially stimulates further phytoplankton production, while suspension feeder nitrogen that is harvested or remineralized and released from the system as N_2 gas is removed from the pool available to primary producers. Management-relevant models of ‘intermediate complexity’ (i.e., intermediate between consumption estimates and the 3-D water quality model) have great potential to address specific management questions at relevant spatial and temporal scales.

Intermediate complexity models should include as many of the following factors as possible:

1.) interacting consumer and producer populations,
2.) biogeochemical processes affecting the fate of nutrients, and other relevant processes affecting the fate of nutrients,
3.) phytoplankton production and biomass, and
4.) suspended sediments.

However, these models need not incorporate elaborate hydrodynamics and complex descriptions of other physical processes, and will only include a small portion of the Bay food web. Models should be able to be parameterized for specific sites within the Chesapeake Bay system to explore spatially explicit management alternatives.

The various suspension feeders in the Chesapeake Bay system do not occur in isolation. They may affect each other both directly through predatory and competitive interactions, as well as indirectly through their effects on shared prey and predators. The workshop consensus was that ultimately *models that incorporate relevant complexity* of the Bay food web will be needed to address the issue of suspension feeder effects in a comprehensive manner. In addition, the spatial complexity, hydrodynamic model and feedback between primary production and hypoxia contained within the 3-D water quality model are required.

The workshop participants did not reach consensus on how to proceed to the final stage of this process. The 3-D water quality model will not be able to incorporate the trophic complexity and extensive detail possible with network or dynamic food web models. However, existing and prototype network and detailed food web models do not incorporate the level of biogeochemical and hydrodynamic detail currently included in the 3-D water quality model. Further discussion and deliberation are needed to plan the next step beyond the intermediate complexity models. Nevertheless, the 3-D model should be enhanced and re-parameterized based on results of both the consumption estimates and intermediate complexity models. In addition, output of the current and enhanced 3-D models are required for appropriate parameterization of intermediate complexity models.

There was general agreement that the development of intermediate complexity models, as well as the general testing of management scenarios, would also greatly benefit from production of either or both of two simplified forms of the 3-D model – a whole-Bay model with reduced spatial resolution (e.g., a 20-box model), and a single tributary model. Training in the use of these models should be provided to interested researchers and managers. Output from these models could be used as input for the intermediate complexity models, and it may be possible to utilize some of the same model structure, relationships and parameter values in both sets of models.

It is important to emphasize that the strength of the overall approach is the interaction among all four proposed components. Monitoring and research, consumption estimates, intermediate complexity models, and a system of complex, linked models are all ultimately important, and the success of each depends on the validity and information generated by steps earlier in this chain of increasingly complex approaches.

Recommendations

Data needs

In order to estimate consumption and model effects of suspension feeders on phytoplankton standing stocks and production, additional data are needed on Atlantic menhaden, epibenthic invertebrates other than oysters, and soft-bodied microzooplankton. The highest priority data need is for the Atlantic menhaden. Lack of information on the abundance, sizes, and temporal and spatial distributions of menhaden in Chesapeake Bay severely inhibit the ability to produce even reliable consumption estimates.

Modeling

The workshop recommends the following framework for accomplishing the first two tasks.

1.) *Consumption estimates: $50,000 per functional group for a 1 year duration.* The estimate of effort required for each functional group is based on three months effort by a PI (i.e., senior researcher) with relevant expertise, or a smaller time commitment by a PI plus technical support, or equivalent effort that includes contributions by multiple PIs with support from technical staff. In addition, sufficient travel and communications support to meet with relevant Bay region researchers and managers, and standard institutional fees for computer support will be required.

Tasks for benthic suspension feeders and zooplankton:

a.) analysis, synthesis and evaluation of Chesapeake Bay monitoring and other relevant data sets on the abundance, and spatial and temporal distributions of relevant organisms;
b.) review of scientific literature to develop defendable estimates of consumption rates for relevant taxa;
c.) calculation of consumption with confidence limits and at least the following temporal and spatial resolution: season, salinity zone, and where relevant data exist, season and salinity zone within individual tributaries.

Task for menhaden:

a.) analysis, synthesis and evaluation of Chesapeake Bay monitoring and other relevant data sets on the abundance, and spatial and temporal

  distributions of relevant organisms;
  - b.) review of scientific literature to develop defendable estimates of consumption rates, and
  - c.) calculation of the range of potential consumption by utilizing several approaches to estimate menhaden biomass and, if possible, spatial and temporal distributions, with discussions of the strengths and weaknesses of various approaches for estimating menhaden biomass, distribution and consumption with existing data and an analysis of critical data needs.

2.) *Targetted models including nutrient cycling and consumption for benthic suspension feeders and zooplankton: $125,000 - $150,000/yr/functional group for two to three years.* Estimate of effort required for each model (models for benthic suspension feeders and zooplankton are recommended at this time), including production of management-relevant simulations for each model are: 1 full time (12 month/yr) postdoctoral researcher with guidance and collaboration by 1 PI with expertise in modeling (1.5 months/yr) and PI(s) with relevant biological and expertise (1 month/yr/PI), plus regional travel and computer support.

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Oysters and Other Benthic Invertebrates Working Group Recommendations

Roger I. E. Newell
Horn Point Laboratory, University of Maryland Center for Environmental Science

Eileen E. Hofmann
Center for Coastal Physical Oceanography, Old Dominion University

General Working Group Discussion Results

The presentations made at the Workshop indicated that considerable data exist on the distribution and abundance of specific benthic filter feeders, such as oysters, in Chesapeake Bay. Less extensive data sets are available on other benthic filter feeders, but these data are sufficient to develop general distributions of these animals. These data sets are the result of long-term studies, like the Chesapeake Bay Program, as well as targeted research programs and state-supported research and monitoring efforts. In some instances, concurrent environmental data were obtained along with the distribution and abundance measurements. The feeling of the working group participants was that considerable data for benthic suspension feeders exist but that the data are not generally available nor are they in a form that is readily accessible.

The working group participants made the observation that the issues of interest to the Chesapeake 2000 Agreement concern understanding and quantifying processes that control the distribution and abundance of benthic suspension feeders. However, the existing historical data sets and ongoing monitoring programs are not designed to address process-oriented research questions. The Working Group participants indicated that understanding changes in the abundance and distribution of benthic suspension feeder biomass required long-term studies that are directed at quantification of the space and temporal distribution of the dominant species. A concurrent effort directed at understanding seasonality in feeding of these species and the resultant effect on food availability is also needed. These types of studies are needed to address issues of nutrient cycling, light attenuation and water clarity, which are of primary interest to the Chesapeake 2000 Agreement.

Needed Data Sets and Existing Models

The Working Group noted that many distribution and abundance data sets exist for benthic suspension feeders in Chesapeake Bay. However, data are lacking for many animals that may potentially be of importance in removing particles from the water column. Also, the existing data sets tend to focus on specific areas of the Bay, rather than being inclusive of the entire Bay-tributary system. Thus, the Working Group suggested that a high priority area is the collection of distribution and abundance data such that the full suite of benthic suspension feeders can be identified.

The Working Group noted that filtration relationships and basic bioenergetics information is lacking for many of the important benthic suspension feeders in

Chesapeake Bay. Filtration relationships are a basic requirement in order to make even crude estimates of the amount of biogenic material that can be removed by benthic feeders. These relationships need to be known as a function of animal size, temperature, salinity, dissolved oxygen concentration, and ambient food supply. Bioenergetics relationships are needed to make mass balance estimates for material cycling and nutrient cycling due to the benthic feeder biomass. These need to be known as a function of animal size and ambient environmental conditions. Thus, obtaining filtration relationships and bioenergetics information for the dominant benthic filter feeders was given a high priority. The Working Group felt that studies of benthic suspension feeder reproduction, spawning and recruitment were also needed, but that these can be deferred to a later time.

The presentations made during the Workshop indicated that several models already exist for the Chesapeake Bay system that can be used to study aspects of benthic suspension feeder impacts on particle removal. These include models for population dynamics of single species (e.g., oysters), biogeochemical cycling, the effect of submerged aquatic vegetation on water clarity, and a three-dimensional water quality model for Chesapeake Bay (see Workshop abstracts for more information on these models). Each model has components that can be used to address issues related to those of interest to the Chesapeake 2000 Agreement. The Working Group felt that the existing models could be better used to address these issues. However, the Working Group also noted that one model does not (and will not) address all of the science and management questions of interest and expecting this of a single model is unrealistic. The Working Group recommended the development of a hierarchy of models for addressing the issues of interest. The existence of a range of models will potentially provide more understanding of the process that control benthic suspension feeder populations.

Role of Ecosystem Modeling

During the course of the Workshop and Working Group deliberations it became apparent that there is a fundamental schism between the scientific researchers and environmental managers in the use and benefits of ecosystem models. This dichotomy is not new nor is it confined to the Chesapeake Bay but it is important that it be explicitly recognized because there may be very different expectations from both groups as to what ecosystem modeling can accomplish.

Managers have very clear needs to understand the long-term consequences of management actions. There was considerable concern among researchers that managers may believe that ecosystem modeling will provide a definitive answer as to how the Chesapeake Bay ecosystem will change in response to management actions. Specifically, there was concern among some researchers that the Chesapeake Bay water quality model is perceived by many in the management community as being the definitive tool to be used to understand how changes in abundance of oysters may ripple through the ecosystem leading to water quality and habitat improvements. The obvious desire is to understand if a tenfold increase in oysters will decrease the amount of phytoplankton, increase the abundance of sea grasses, increase the bottom dissolved oxygen concentrations, reduce the abundance of jellyfish, etc.

Research scientists realize that the tremendous complexity of marine systems as large as Chesapeake Bay defy our attempt to understand all of the possible myriad interactions between the various components. From their perspectives no model is ever going to predict with a high level of certainty what the outcome will be if another component far removed within the model is altered. Most importantly the concern is that each parameter put into a model has a certain error, which is often quite large. This means that the errors in prediction can accumulate as more and more parameters are involved in complex models. Obtaining realistic estimates of the consequences of such error propagation is complex. For example, a model will likely be able to predict the effects of changing oyster abundance on phytoplankton because this is a closely related direct effect. It is less likely that a model will predict with the same level of accuracy the magnitude of changes in adult sea nettle abundance because that is farther removed from the influence of the oysters. Many scientists prefer simpler models in which specific interactions can be modeled that are then used to further understand ecosystem interactions and develop new experimental hypotheses.

This dichotomy in expectations between both groups has to be understood by both sides before progress can be made in developing requirements for future ecosystem models.

Strategy for Implementing Models

The Working Group developed a short-term and long-term strategy for addressing issues related to the effect of benthic suspension feeders on the Chesapeake Bay ecosystem. The general consensus was that in the short-term much can be gained from analyses of existing historical data sets on benthic suspension feeders. In particular, analyses focused on determining the species present and their distribution, how many of each are present, and how much food is required to support the biomass were given a high priority. Following from the data analysis, simple calculations of filtration effects of dominant benthic filter species can be done. These calculations can draw upon the physiological data in the scientific literature and should include environmental effects of temperature, salinity and possibly low dissolved oxygen concentrations. The output of the data analyses and filtration calculations need to be such that they can interface with larger more complex models for the Chesapeake Bay or specific Bay tributaries. These efforts were viewed as necessary for constraining and validating the output from the more complex models.

For the longer term, the Working Group discussed several approaches for implementing models of the Bay. The first was to develop multiple models for the Chesapeake Bay system, which will allow a range of questions to be addressed, such as those related to water clarity and those related to multiple species effects. These two topics require fundamentally different types of models. The Working Group stressed that a single model was not the way to go and noted that multiple models is the approach taken in the climate modeling research community. Also, having a range of models allows development of uncertainty relationships associated with model predictions that arise due to choices made for model dynamics and parameterizations. This is not currently possible with the water quality model used by the Chesapeake Bay Program. Implementation of this approach will require the Chesapeake Bay modeling community to maintain strong communication and exchange of model results.

An alternative approach is to develop a single model with multiple participants, as has been done by the European Community for the North Sea. This latter approach was thought to be less of an option due to logistical and funding constraints. A third approach discussed was to put effort into developing a detailed model or a series of models (e.g., zero-dimensional to three-dimensional) of a limited system, such as a specific tributary.

The Working Group noted the importance of obtaining spatial and temporal resolution in existing and future models such that the models can be used to address issues of biological importance. In particular, the ability of these models to provide estimates of benthic consumption rates was noted and given a high priority.

The Working Group noted that there are important management questions that can be addressed with existing models and data sets. Thus, providing resources to do analyses of historical data, to refine existing models, and to do simple first order calculations can result in information that can potentially be used by managers, especially for the short-term questions of interest. The Working Group felt that this provided a viable and alternative approach to simply continuing support for the existing Chesapeake Bay water quality model. The results of these research efforts, such as bivalve and phytoplankton parameterizations, can then be folded into more complex models that can be used to address the longer-term questions.

Zooplankton Working Group Recommendations

Marie H. Bundy
Academy of Natural Sciences Estuarine Research Center

Steven Bartell
The Cadmus Group, Inc.

The current understanding of the biological characteristics and the spatial distributions of zooplankton suspension feeders in Chesapeake Bay is rather good. There is an extensive database, associated with the Chesapeake Bay Program Zooplankton Monitoring effort, which provides species-specific information on the abundance and biomass of mesozooplankton and microzooplankton. Detailed information on phytoplankton biomass, abundance, and species composition, along with data on physical parameters, have been collected concurrently, but enumeration of “soft-bodied” microzooplankton has been conducted for only the past few years, so those records are less extensive. Trophic interactions between phytoplankton, mesozooplankton, and microzooplankton are less well understood. However, recent work in Chesapeake Bay and studies in other systems show that microzooplankton grazing may be more important than mesozooplankton grazing in the removal of phytoplankton biomass.

Any initial modeling effort should include enough detail to capture the variability in feeding rates among the major zooplankton taxa. A breakdown by size class within major taxa and functional groups should be made, and then grazing rates ascribed to each. Grazing estimates should include mean, error, and range of grazing rates. This first step can be considered a “spreadsheet model”. An earlier effort by Sellner and Jacobs (1993) used this approach, and their work can serve as a template for future work.

The role of physical parameters such as salinity, suspended solids, and water temperature in constraining the temporal and spatial distributions of micro- and mesozooplankton must also be considered. If ample resources are available for the modeling effort, the spreadsheet model can be tailored to several temporally and spatially explicit domains. If resources are limited, the temporal resolution of the model should be able to capture seasonal differences in zooplankton grazing pressure, and the spatial resolution should be able to distinguish between salinity regions, and deep and shallow regions of the Bay.

When grazing rates are calculated for functional groups of zooplankton, it will be important to consider the relative food quality of phytoplankton taxa. For example, cyanobacteria may be very abundant, but they are rarely grazed effectively by zooplankton. Alternatively, large dinoflagellates may be high quality food for copepods, while large diatoms may be high quality food for some copepod species and poor food for others. With ample funding, the taxonomic differences in mesozooplankton, protozoan and protistan microzooplankton feeding rates, and differences in feeding rates on various phytoplankton taxa (including different developmental stages of zooplankton) should be included in these estimates. If funds are limited, phytoplankton assemblages could be broken down into size classes by major taxa.

The spreadsheet model is a necessary first step to the modeling effort, and may be able to provide more accurate grazing parameters to water quality models. However, as a final product, a model should also serve to predict grazer responses to changing abundances or species composition of primary producers. The final model, which may function at an intermediate level between the large scale water quality model and the more simple spreadsheet model, should also be dynamic enough to predict effects of management strategies on zooplankton populations and consequently on grazing pressure. It should include information on feed-backs between zooplankton and other grazers, and should provide estimates of the relative magnitude of zooplankton grazing compared to other grazers. We should ultimately be able to answer the following questions: If nutrients and chl a are reduced to result in a "clean Bay", what will happen to fish food (i.e. zooplankton)? At what levels of reduced nutrient and sediment loadings does the pelagic food web run out of gas?

Existing models of zooplankton production dynamics should be identified and examined for possible adaptation and application to the objectives of the Bay assessment program. For example, the Chesapeake Bay Estuary Model (CE-QUAL-ICM) and the tributary refinements to the Chesapeake Bay model (Cerco and Meyers) that include microzooplankton (44-201 um) and mesozooplankton (> 201 um) should be evaluated to determine strengths and limitations in addressing Bay water quality and production issues. Models of other similar and relevant systems should also be included in a systematic model evaluation (e.g., Narragansett Bay (Kremer and Nixon 1978, Kremer and Kremer 1982, Dwyer and Kremer 1983), Rhode River Estuary (Dolan and Gallegos 1991), European tidal estuaries (Heip and Herman 1995), Dublin Bay coastal/estuarine system (Wilson and Parks 1998), Caete estuary, North Brazil (Wolff et al. 2000), Atsumi Bay, Japan (Suzuki et al. 1987)).

In using or adapting existing models or in developing new models of Bay zooplankton dynamics, issues concerning model structure, process formulations, forcing functions, and parameter estimation will have to be considered. A more detailed food web model will be necessary to examine the implications of nutrient control on differential growth of phytoplankton species (or functional groups), subsequent availability of algal production to different zooplankton grazers (e.g., microzooplankton, macrozooplankton), and potential changes in zooplankton community composition resulting from competitive and predator-prey interactions. However, it may prove necessary to develop several differently structured and differently scaled models of zooplankton dynamics to address the objectives outlined in the Bay Agreement of 2000. The level of detail in model structure (e.g., number of state variables, parameters, external forcing functions) should be guided by the specific objectives of the modeling activity. For example, a simple linear food chain model might be useful for examining the broader scale implications of nutrient control on overall zooplankton production. The degree of spatial detail in model implementation (e.g., several point locations, transects, full spatial coverage of the Chesapeake Bay) will also be guided by the nature of the modeling questions and Bay 2000 objectives.

Careful consideration will be required in specifying the mathematical form of biological and ecological processes used to describe the production dynamics of Bay zooplankton. Simple linear donor-dependent equations may prove useful in formulating models used to examine broader scale questions concerning nutrient dynamics and consumer population biomass in the Bay. More detailed, nonlinear equations that describe zooplankton feeding in relation to food availability, food quality, food preferences, and environmental factors might be necessary to explore more complex relations between feeding behavior, Bay zooplankton production, and zooplankton community composition in space and time.

A risk assessment framework may prove useful in quantifying the production of Bay zooplankton (and other suspension feeders). Uncertainties inherent to modeling the complexities of zooplankton production can be addressed in part through the specification of model inputs as statistical distributions, fuzzy sets, or intervals that characterize variability and uncertainty. The corresponding methods (e.g., Monte Carlo simulation, fuzzy arithmetic, interval analysis) used to propagate such uncertainties through model calculations can be incorporated into the overall structure and implementation of selected zooplankton (other suspension feeders) models to characterize the impacts of uncertainty on model results. The model results can be used to estimate the probability (i.e., risk) of failing to achieve Bay 2000 objectives. Importantly, these uncertain results can be further analyzed to identify the key contributors of uncertainty in the overall model calculations (i.e., sensitivity/uncertainty analysis). These analyses can be used to guide the efficient collection of new information (e.g., data, design experiments, etc.) to refine models and more precisely address zooplankton production dynamics in relation to the Bay 2000 objectives.

Menhaden Working Group Recommendations

Robert J. Wood
University of Maryland Center for Environmental Science, Chesapeake Biological Laboratory

Thomas Miller
University of Maryland Center for Environmental Science, Chesapeake Biological Laboratory

Introduction

The Atlantic menhaden is a unique trophic component of the Chesapeake Bay ecosystem. These fish are often associated with the Chesapeake Bay, which serves as an important nursery area and feeding ground for the coastal Atlantic population. However, menhaden spawn and spend much of the adult life spans in the coastal Atlantic Ocean. Newly spawned larval menhaden travel into Chesapeake Bay and spend their late larval and juvenile life stages in habitats of the upper tidal reaches of Chesapeake Bay and its tributaries. As a filter-feeding forage fish, the menhaden serves as a direct link between the Bay's phytoplankton and organic detrital production and many ecologically and economically important piscivorous predators that occupy the upper echelons of the ecosystem's food web. Examples of piscivores that depend upon menhaden for a significant portion of their diet, at least seasonally, include striped bass, weakfish, bluefish, and osprey.

In addition to its ecological importance, the Atlantic menhaden that inhabits Chesapeake Bay and the coastal Atlantic supports are commercially exploited by baitfish and reduction fisheries. Fish harvested by the former are used as bait by commercial and recreational fishers. The reduction fishery harvests the majority of fish however. This harvest is processed or 'reduced' into fishmeal, used in agricultural or aquacultural feed, and into refined oils, used as chemical additives (in paints, printing inks, etc.), as lubricants, and in agricultural and human food products (e.g. margarines). The most recent amendment to the current ASMFC Atlantic menhaden fishery management plan (ASMFC, 2001) reflects the emerging consensus of fisheries scientists that fisheries management should begin to adopt multispecies and ecosystem-based management approaches (NMFS, 1999). This amendment specifically acknowledges the ecological importance of this filter-feeding forage fish in one of its management goals which is to, "*Protect and maintain the important ecological role Atlantic menhaden play along the coast* " and suggests that the spawning stock biomass targets and thresholds, which dictate management actions, *"should be more conservative to alleviate concerns over the ecological role of menhaden (to provide more forage and filtering capacity)"* With this new emphasis on the ecological role of menhaden, the objective of the FMP intersects the 2000 Chesapeake Bay Agreement (C2K) commitment to, "*assess the effects of different population levels of filter feeders such as menhaden, oysters and clams on Bay water quality and habitat."*

Modeling Approaches

There exist at least four recent examples of models that have been used to assess menhaden consumption. These are: Peters and Schaff (1981), Baird and Ulanowicz (1989); Gottlieb (1998); and Lou et al. (2001). Each of these research efforts utilized different approaches and their chronological order roughly corresponds to an ever increasing level of complexity in their approach. This should not however be taken as an endorsement of model complexity. In fact, complex models require more assumptions and much more data than simpler models. These characteristics can create great uncertainty in model calculations. Together, this suite of models provides valuable insights into possible modeling approaches that can be used to address the C2K filter feeder commitment and assess and prioritize research and data needs to do so by the 2004 target date.

Of the four models considered here, Baird and Ulanowicz (1989) is the only method that does not estimate menhaden population consumption from daily ration calculations or using bioenergetics submodels. In this landmark work, Baird and Ulanowicz used dietary information, population biomass estimates, and network analysis to characterize the mesohaline Chesapeake Bay food web. While this research provided valuable insights into the trophic dynamics of Chesapeake Bay, the authors' approach was designed to provide seasonal 'snapshots' of the mid-Bay food web and therefore it does not provide spatial or temporal resolution required to effectively address the filter feeder C2K agreement commitment. Further, conclusions drawn from this study regarding the impact of the Atlantic menhaden population likely could be improved by more recent and future studies of menhaden diet composition.

There is however, an ongoing effort to construct a Chesapeake Bay food web model (see, http://noaa.chesapeakebay.net/ecosystem.htm) that utilizes the same network analysis approach used by Baird and Ulanowicz. The computer software package currently being used in these efforts, Ecopath with Ecosim (http://www.ecopath.org/), when accurately parameterized by species-specific biomass and diet composition information, will characterize the food web of Chesapeake Bay as in Baird and Ulanowicz (1989) and also allow dynamic and interactive modeling of the ecosystem food web. Plans currently exist to couple this model with the Chesapeake Bay Water Quality model. Because the Ecosim module of this software allows for interactive dynamic modeling, these efforts may represent a viable method of effectively assessing the impact of various sizes of the menhaden population on the Bay's water clarity, nutrient budget, and trophic dynamics within the time frame set forth (2004) by the filter feeding C2K agreement commitment.

Peters and Schaff (1981) represents the simplest method of directly estimating menhaden population consumption. Focusing on the entire coastal Atlantic population, these authors use a daily ration approach where population consumption is estimated by multiplying the number of menhaden times the daily consumption of a single fish. Both the advantage and disadvantage of this method is its simplicity. The information needs of this ration-based approach are modest, as are the number of required assumptions and calculations. An updated ration-based approach may be the best option for a rapid assessment of the effects of Atlantic menhaden on Chesapeake Bay water quality. However, the consumption estimate derived from such a model would provide only a rough approximation of consumption (with no spatially-explicit information) and should be considered accurate only within perhaps an order-of-magnitude. It does not, for example, consider that ration estimates based on a single fish may be non-linearly related to (not a constant multiple of) menhaden abundance because of the species' schooling behavior. That is the cost inherent in using an approach with broad and simplifying assumptions such as; menhaden are not food limited, each menhaden consumes and behaves like all others, menhaden foraging is independent and additive.

Gottlieb (1998) constructed a much more complex model designed to estimate the impact of menhaden on Chesapeake Bay's nutrient budget. This model was comprised of three components: a bioenergetics submodel; a phytoplankton-nutrient response submodel; and a menhaden mortality model, which accounted separately for natural and fishing morality. In effect, the bioenergetics model is used to simulate the daily food consumption requirements of a single fish (either a YOY or an age 1-3 individual) over the growing season for a year (e.g. 183 days for YOY). An initial number of recruiting fish was chosen and consumption levels were calculated daily after accounting for natural and fishing mortality. There is no spatial dimension in this model so menhaden and phytoplankton production are assumed to be equally distributed throughout the Bay. This model did allow for manipulation of various parameters such as temperature (affecting menhaden bioenergetics), menhaden abundance, and primary production rates therefore it does begin to address the C2K commitment of interest to this workshop. As the author acknowledges, this model has a number of limitations, many of which are imposed by a lack of available data. With respect to addressing the C2K filter feeder commitment, the most important limitations of the model are the model's lack of realistic feeding dynamics, its over-simplified treatment of menhaden prey, which is modeled as primary production instead of species-specific abundance or biomass, and the lack of spatial resolution.

A more recent model that does not suffer from a lack of spatial resolution is that of Lou et al. (2001). This model couples foraging and bioenergetics models with the Chesapeake Bay water quality model and attempts to estimate the carrying capacity of Chesapeake Bay for Atlantic menhaden by comparing the bioenergetics (focusing on food requirements) of newly recruited (YOY) fishes to prey availability in each of 4000 geographical cells comprising the estuary. The water quality model is used to provide dissolved oxygen, temperature, and chlorophyll (*chl a*) concentrations for each of these grid cells.

Unfortunately, this model does not realistically depict menhaden feeding dynamics. For example, menhaden were assumed to consume only phytoplankton. Further generic phytoplankton biomass (not species-specific) was derived from *chl a* concentration provided by the water quality model and, due to data limitations, the authors assumed that only 10% of the phytoplankton in the environment was available for menhaden consumption, assuming the rest was consumed by other filter feeders. While the spatial maps provided by this study are informative, substantially more information regarding menhaden diets, behavior, and prey availability will be required before this methodology can provide and an accurate assessment of the menhaden's effect on Chesapeake Bay water quality.

What Do We Need to Know?

The menhaden workgroup of this workshop was challenged to recommend viable methods and approaches for assessing the filtering effects of Atlantic menhaden on Chesapeake Bay water and habitat quality. We were charged with providing a number of possible approaches, each of which would be appropriate for different funding levels. The various approaches should be expected to yield information and provide answers to these questions with increasing specificity corresponding to their cost of implementation.

Despite the wide range of approaches that could be employed to assess the effect of Atlantic menhaden on Chesapeake Bay water quality, all require a few pieces of basic information, including:

Menhaden abundance and distribution

- How many are there?
- How are they distributed (size specific information needed)?
- When are they there?

Feeding, Diet, and bioenergetics information

- How do menhaden feed?
  - Mechanics
  - Behavior -e.g., changes in response to prey densities
- What and how much do they consume?
- What happens to what they eat? (to what extent are consumed nutrients lost to the system versus cycled throughout the system)

Menhaden prey dynamics

- Spatial and temporal distribution patterns of menhaden food items
- Response of menhaden prey to changes in grazing pressure

Considering the long history of menhaden exploitation and research, much of this basic information is not well known.

Current Status of Knowledge

Perhaps the most basic requirement needed for these calculations is an accurate estimate of menhaden abundance in Chesapeake Bay. Both the Maryland Department of Natural Resources and the Virginia Institute of Marine Science conduct extensive fishery-independent monitoring programs in the major Bay tributaries within their respective states, from which, annual abundance indices are calculated. Unfortunately, these surveys effectively monitor only relative changes in young-of-the-year (YOY) menhaden and, due to their sampling design, cannot provide absolute abundance estimates of even this age-class.

While these surveys effectively capture YOY fishes using beach seines, older and larger menhaden are much more difficult to capture. This is because as menhaden age, they are less closely associated with the littoral zone, moving into more open and often deeper waters in early summer. While fishery-independent open water fish survey programs now exist in both states, older menhaden appear to effectively avoid the various trawling gears employed in each case. The most efficient method of capturing these fishes in open water is that practiced by the industrial menhaden fishery fleet. This fleet employs spotter planes, which guide vessels equipped to quickly deploy and retrieve relatively large purse seine nets, after surrounding large schools. Because the fishery is designed to maximize catch-per-unit-effort and prohibited from Maryland waters, deployment of the gear is highly selective. This selectivity drastically reduces the utility of the catch information with respect to estimating menhaden distribution and abundance.

Information is available for menhaden diets, however it may not be sufficient to support a detailed assessment of the population's effects upon Chesapeake Bay water quality. Much of this information is the result of detailed investigations of the feeding structures of menhaden (e.g. Friedland 1984, 1985), though a few studies have studied menhaden diet in a more direct way, through, for example, stomach content analysis. Larval menhaden are strict zooplanktivores (June and Carlson, 1971), however morphological changes dictate a dietary shift to phytoplanktivory during the juvenile life stage (Friedland et al. 1984), and another ontogenetic shift occurs later in life so that adults filter copepod-sized particles most efficiently (Durbin and Durbin 1975). A recent stomach contents study by Lewis and Peters (1994) found that juvenile and adult menhaden stomach contents in estuarine creeks contained 81% amorphous aggregated detritus, 17% phytoplankton, and 1% zooplankton in estuarine creeks and 47%, 36% and 18% of those same components, respectively, in open coastal and estuarine waters of North Carolina.

While these numbers provide some guidance, additional field studies will be required in order to depict menhaden consumption with the spatial and temporal resolution and accuracy required to accurately assess the water quality impact of menhaden on the Bay's water quality. Prey selectivity information is an important aspect of the menhaden diet and behavior that is unknown. For example, what composes the amorphous aggregated detritus found in menhaden stomachs, how much of this is processed, and how does the composition change with menhaden size, distribution, and abundance of both menhaden and various types of detritus in the water column.

Of the basic informational needs to model the effects of varying levels of menhaden abundance on Chesapeake Bay water quality, bioenergetic and prey distribution information are perhaps the least problematic to obtain. As Gottlieb (1998) and Luo et al. (2001) have demonstrated, the Wisconsin bioenergetics modeling framework can be effectively applied to provide this information using data currently available. Similarly, because of the strong and continued water quality and living resource monitoring that occurs in Chesapeake Bay, relatively detailed phytoplankton and zooplankton data exist for most months since the mid 1980's in many stations, and since the late 1980's for stations throughout the mainstem Bay and its tidal tributaries.

Strategy

To accomplish the goal of assessing the effect of varying levels of menhaden population abundance on Chesapeake Bay water quality, the menhaden workgroup recommends a multi-faceted approach that attempts to utilize the strengths of each modeling approach that has been outlined in this report. Because the C2K filter-feeding commitment requires an assessment be completed as early as 2004, modeling and additional data collection and research efforts should begin as soon as possible.

Early and rough estimates of the potential effect of the menhaden population on, for example, phytoplankton density, could be calculated relatively quickly using the ration-based approach. This approach could be used to effectively address a key question underlying the C2K filter feeding commitment: *Can menhaden fisheries management be used to supplement land-based nutrient management activities?* For example, using the ration of a single fish, a relatively simple set of calculations could determine whether the number of menhaden removed from the system by the fishery might have otherwise consumed enough detritus, phytoplankton, and zooplankton to have substantially improved the Bay's water quality. While the calculation would require a number of assumptions, it would be an appropriate and informative first step to determine whether menhaden fishery management could be used as a vehicle to augment land-based nutrient reduction efforts. As mentioned with respect to the Peters and Schaff (1981) model, one of the first research questions that would help improve the accuracy of these calculations is, *what is the quantitative relationship between total menhaden ration of a single independently swimming individual and that of a large number of schooling fishes*? Results from these calculations could be used to guide more complex efforts, such as those underway to use the Ecopath with Ecosim modeling suite to model the Bay's food web, and to prioritize research and data gathering activities. As new information becomes available, it could be incorporated in updates of these models and provide stronger guidance to managers and research scientists.

With continued interest and resources, future efforts should include more models of increasing complexity. These could include a much more detailed effort that builds upon that of Luo et al. (2001) but accounts more realistically for factors such as species-specific prey selection and dynamic behavioral responses of menhaden to prey concentrations and distributions.

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Appendix A
Workshop Agenda

March 18, 2002

7:20 - 8:00	Breakfast meeting for steering committee and discussion leaders *Washington Room*
8:00 - 8:30	Coffee & Snacks *Lobby*

General Session: Baltimore/Hanover Room

8:30 - 8:40	**Denise Breitburg:** Introduction, Workshop Organization & Workshop Goals
8:40 - 9:10	**Roger Newell:** Beyond Water Clearance: Incorporating Other Aspects of Benthic Suspension-feeder Ecology into Estuarine Water Quality Models
9:10 - 9:40	**Eileen Hofmann**: Oyster models and Coupling Biological and Physical Models
9:40 - 10:10	**Marie Bundy**: The Potential for Zooplankton to Affect Water Quality in Chesapeake Bay: a Working Group of the STAC Suspension Feeder Workshop
10:10 - 10:40	**Steve Bartell**: Modeling the influence of zooplankton on phytoplankton and other particulate matter in the Chesapeake Bay
10:40 - 10:55	**Break with Snacks: Lobby**
10:55 - 11:25	**Bob Wood**: Simulating Menhaden (*Brevoortia tryannus)* filtering capacity in Chesapeake Bay: Acknowledging ecological complexity and research needs
11:25 - 12:05	**Tom Miller**: Modeling the ecosystem level impacts of Menhaden (*Brevoortia tryannus*) in Chesapeake Bay
12:05 - 12:35	**Jan Thompson**: San Francisco Bay Experience
12:45 - 1:30	**Lunch: Washington Room**
1:30 – 1:45	**Arthur Butt**: Explanation of afternoon schedule and charge to breakout groups

Breakout Sessions: Baltimore, Hanover or Washington Room

1:45 – 3:45 **Breakout groups**
Oyster and Other Benthic Invertebrates: *Washington Room*
Zooplankton: *Hanover Room*
Menhaden: *Baltimore Room*

3:45 - 4:00 **Break with Snacks**

General Session: Baltimore/Hanover Room

4:00 - 5:00 **Breakout Group Progress Reports**

March 19, 2002

8:00 - 8:30 Coffee & Snacks
Lobby

General Session: Baltimore/Hanover Room

8:30 - 8:50 **Rob Magnien**: Defining the "Filter-Feeding" Commitment of the Bay Agreement

8:50 - 9:20 **Carl Cerco: Filter** (fix bold) Feeders in the Chesapeake Bay Environmental Model Package

9:20 - 9:30 **Denise Breitburg:** Charge to workgroups

Breakout Sessions: Baltimore, Hanover or Washington Room

9:30 - 12:00 **Breakout groups**
Oyster and Other Benthic Invertebrates: *Washington Room*
Zooplankton: *Hanover Room*
Menhaden: *Baltimore Room*

12:00 -1:00 **Lunch: Washington Room**

General Session: Baltimore/Hanover Room

1:00 - 4:00 **Breakout group summaries and plenary discussion**

Appendix B
Workshop Handout

Workshop Overview and Objectives

Phytoplankton standing stocks, production and species composition are potentially influenced by both the supply of nutrients to the bottom of the food web and removal by suspension feeders higher in the food web. Similarly, suspended sediment concentrations are determined by both their loading rates and their removal or settlement from the water column. Most management activities to date have addressed the supply end of these relationships by attempting to reduce nutrient and sediment loading to waters within the Chesapeake Bay watershed. However, to predict the relationship between nutrient or sediment loading and water quality, it is also important to understand and predict the potential top-down effect of suspension feeders such as menhaden, zooplankton, bivalves and other benthic invertebrates on phytoplankton and suspended sediment. These suspension feeders remove particles from the water column and potentially influence nutrient cycling, water clarity, phytoplankton dynamics, and other ecosystem processes. The impact of suspension feeders depends on population levels and distributions of the various species in space and time, which, in turn, can be influenced by both management actions and natural variation in physical and biological factors.

The current Chesapeake Bay Agreement includes the commitment: "*By 2004 assess the effects of different population levels of filter feeders such as menhaden, oysters and clams on Bay water quality and habitat.*" The 'Suspension Feeders Workshop' is a response to this commitment. Its goals are:

1.) to assess current understanding of the biological and physical characteristics of the Chesapeake ecosystem needed to estimate suspension feeder effects,
2.) to assess the utility of currently existing models, and
3.) to identify critical features (processes, organisms, model capabilities) to include in future models designed to predict effects of suspension feeders on phytoplankton and sediment in Bay waters.

The workshop will include plenary presentations and discussions, and three concurrent breakout groups - one each on menhaden, benthic suspension feeders (including oysters), and zooplankton. A workshop report will summarize plenary and breakout group discussions, and outline steps recommended to meet the filter feeder commitment.

We are asking each breakout group to come up with three recommendations:

1.) A recommendation on how to estimate/model the effect of your group of suspension feeders on Chesapeake Bay phytoplankton in the *very best scientifically defensible manner if time and funding did not limit the effort.* (What biological, ecological and biogeochemical processes should be included? Of the suite of potential modeling techniques, which would be most appropriate? What levels of spatial and temporal resolution are required? How detailed should the food web be?);

2.) A recommendation on how to predict the effect of your group of suspension feeders on Chesapeake Bay phytoplankton *in the best way possible given a very modest amount of funding available and the need to meet the 2004 deadline* (Can available models be adapted or modified to answer the question utilizing existing data as input? What level of confidence would you have in predictions? What level of linkage between suspension feeder models and the Bay Program water quality model is needed? Should suspension feeder effects be elaborated directly in the water quality model?);

3.) A short list of the highest priority areas of research and model development that would greatly enhance recommendation #2 if a bit more time and funding were available.

Each of you will be assigned to one working group. Please bring data and ideas to share with the group. Think about, but do not limit yourself to the questions we have listed in this packet. Think about spatial and temporal considerations, the simultaneous occurrence of all suspension feeders, linkages between water quality and consumer models, the range of modeling techniques available, how much of the consumed nitrogen is actually removed from the system, and the range of other considerations that should go into both the optimal and practical approaches that could be pursued.

We will have LCD and overhead projectors available in each room for planned and impromptu presentations. One 35-mm slide projector will be available for plenary sessions.

Appendix C
Presentation Abstracts

Beyond Water Clearance: Incorporating Other Aspects of Benthic Suspension-feeder Ecology into Estuarine Water Quality Models

Newell, Roger, Jeff Cornwell, Raleigh Hood, and Evamaria Koch
Horn Point Laboratory,
University of Maryland Center for Environmental Science,
PO Box 775, Cambridge, MD 21631, USA,
newell@hpl.umces.edu

Benthic suspension feeders, such as bivalve molluscs, sponges, tunicates, polychaetes, etc. serve to couple pelagic and benthic processes because they filter particles with high efficiency from the water column and transfer undigested remains in their biodeposits to the sediment surface. This feeding activity, combined with their often high abundance in shallow coastal waters, can make them extremely important in regulating water column processes. Of all species worldwide, eastern oysters are among the most powerful in this regard because of their unusually high weight specific filtration rates (7 to 10 l h^{-1} g^{-1} dry tissue weight at typical summer water temperatures of 25°C.) The eastern oyster is well adapted to living in estuaries where inorganic particles comprise a large fraction of the seston because it sorts filtered particles prior to ingestion and rejects less nutritious particles as pseudofeces. Currently, in the nutrient enriched Chesapeake Bay, where phytoplankton are in high abundance, eastern oysters maintain high filtration rates but now reject large amounts of undigested algal cells in their pseudofeces. Newell (1988) initially drew attention to the possible ecosystem benefits of the original huge stocks of eastern oysters in Chesapeake Bay by comparing water column turnover times before oysters were commercially exploited to the situation today when oysters are at all time low abundances. The objective of this workshop is to take us to the next level in understanding the ecosystem effects of filtration by historic and present days population of suspension feeders.

In contrast to Newell's (1988) proposition that oyster populations may once have exerted "top-down" control on phytoplankton stocks others have claimed that oysters may have simply recycled inorganic nutrients rapidly back to the water column and hence there would not have been any long-lasting reduction in phytoplankton biomass. To help distinguish between these scenarios, Newell et al. (2002) explored in laboratory incubations changes in nitrogen fluxes and denitrification under anoxic and oxic conditions in response to loading by different amounts of phytoplankton cells, representing an experimental analog of oyster biodeposits. When organics were regenerated under aerobic conditions, typical of those associated with shallow water oyster habitat, coupled nitrification-denitrification was promoted, resulting in denitrification of ~20% of the total added nitrogen. In contrast under anoxic conditions, typical of current summertime conditions in main-stem Chesapeake Bay where phytoplankton is microbially degraded beneath the pycnocline, nitrogen was released solely as ammonium from the added organics. Such denitrification of particulate nitrogen remaining in the biodeposits of benthic suspension feeders will enhance nitrogen removal from estuaries and needs to be incorporated into revised ecosystem models.

The removal of particles from suspension by oysters will reduce turbidity. In aerobic incubations with sufficient light (70 :mol m^{-2} s^{-1}), Newell et al (2002) found that a benthic microalgal/cyanobacterial community grew that not only absorbed the inorganic nitrogen released from oyster biodeposits but also fixed N_2. This suggests that an ecosystem dominated by benthic primary production may develop in shallow waters when reduced turbidity associated with bivalve feeding increases light penetration to a level that can sustain benthic microalgal production.

Seagrass beds either are in decline or have disappeared throughout much of the Chesapeake Bay due to high water turbidity/reduced light availability. It is likely that reduced oyster filtration by the much diminished oyster populations has contributed, in part, to observed higher turbidities and the consequent reduction in light reaching the sediment surface. In order to explore these interactions, Hood et al. (2001) and Newell et al. (2001) have developed a numerical model to simulate the interaction between wave-induced sediment resuspension, bivalve filtration, and seagrass growth. This model, which is parameterized based upon direct measurements of oyster filtration and seagrass wave dampening effects, shows that under high wave height conditions, the presence of oysters can reduce suspended sediment concentrations by nearly an order of magnitude, which significantly increases water clarity and the depth to which seagrasses can grow. Such ecosystem level effects associated with increasing oyster stocks in Chesapeake Bay also need to be incorporated into new water quality models.

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Oyster Models and Coupling Biological and Physical Models

Eileen E. Hofmann,
Center for Coastal Physical Oceanography,
Crittenton Hall,
Old Dominion University, Norfolk, VA 23529
hofmann@ccpo.odu.edu

Coupled circulation-biological models provide a framework for integrating and synthesizing information about estuarine systems and for investigating hypotheses about controlling processes in these systems. Also, in many environments prediction and forecasting are goals for these models. Thus, this presentation will briefly review some existing circulation-biological models that have been developed for estuarine systems. The models to be discussed were designed to address issues related to larval transport and dispersion, whole ecosystem dynamics, and population dynamics of specific species. Emphasis will be placed on potential model shortcomings as a basis for recommending improvements to future models developed for estuarine systems such as Chesapeake Bay. Discussions will also highlight data limitations, space and time scale resolution in coupled circulation and ecosystem models, and model structure and parameterization. The final portion of the presentation will focus on combined circulation-oyster models. Current efforts in this area of modeling show the need to include environmental factors, as well as oyster physiology, when attempting to predict the response of oyster populations, because it is the superposition of a combination of these factors that determines the state of the population. This is of particular importance when attempting to address issues related to climate change or habitat alteration, such as may occur by dredging. The final portion of the presentation will focus on future directions for improving the predictive capability of models developed for estuarine systems. Suggestions for improving the state of estuarine modeling include the development of integrated sampling systems, the concurrent measurements of physical and biological properties, the development of data assimilation techniques, and advances in model construction

The Potential for Zooplankton to Affect Water Quality in Chesapeake Bay: a Working Group of the STAC Suspension Feeder Workshop

Marie H. Bundy
Academy of Natural Sciences Estuarine Research Center,
10545 Mackall Road, St. Leonard, MD 20685.
bundy@acnatsci.org / 410-586-9710

The goals of this working group are to (1) assess the current understanding of zooplankton feeding on phytoplankton in Chesapeake Bay and (2) evaluate the utility of existing models and the potential for new or adapted models to predict top-down effect of zooplankton on phytoplankton abundance and biomass. Zooplankton communities have the potential to remove significant portions of the phytoplankton standing crop and to structure phytoplankton populations by feeding selectively on different phytoplankton size classes or taxa. Trophic interactions within the zooplankton community are complex, and there is also the potential for feedback loops between metazoan and protistan zooplankton to influence the magnitude of the grazing pressure on primary producers.

Several factors, aside from the abundance and biomass of zooplankton grazers, should be considered to accurately estimate the top down effect of zooplankton on phytoplankton production and abundance in Chesapeake Bay. In particular, the species composition of the zooplankton assemblage, and the size and taxonomic composition of phytoplankton assemblages will help determine whether the potential for top down control exists. For example, the two species of copepod grazers that dominate Chesapeake Bay feed most effectively on particles that are greater than 5 μm, but their feeding preferences for phytoplankton vs. protozoan prey, their selectivity for different sized prey, and their spatial distributions over the course of the year differ dramatically. What mesozooplankton taxa, other than calanoid copepods, are important grazers? Microzooplankton (e.g., ciliates, heterotrophic dinoflagellates, and rotifers) can be more important than crustacean zooplankton in the top down control of smaller phytoplankton; it is therefore important to consider their impact, as well as the role of predation by mesozooplankton in structuring microzooplankton populations.

For the purposes of modeling, decisions will need to be made about the levels of taxonomic detail required to characterize metazoan and protistan zooplankton assemblages, and the detail needed for classifying phytoplankton size and taxonomic classes. The potential for working with larger functional groups should be discussed. Does the existing literature provide the means, through numerical models or empirical studies, to relate zooplankton species abundances to clearance rates of phytoplankton? The Chesapeake Bay program plankton monitoring data set provides an extensive species-level record of zooplankton and phytoplankton abundances and spatial distributions. Abundances of soft-bodied microzooplankton, which may make up as much as 90% of total microzooplankton carbon, are now being enumerated, and their inclusion in the modeling effort should be evaluated. What can we predict about grazing on picoplankton? How do suspended sediments and detritus affect zooplankton feeding? Temperature and salinity can constrain feeding rates and species distributions, and the timing of nutrient loading may affect the potential for top-down control. What geochemical and physical parameters should be considered to make an accurate assessment of grazing pressure?

The Zooplankton Working Group will discuss these and other questions relevant to the prediction of the effects of zooplankton feeding on phytoplankton standing stocks in Chesapeake Bay. Participants are encouraged to bring supporting materials and relevant data to the breakout session, and to communicate ideas about theories, models, and pertinent literature prior to and during the workshop. Please Email Marie Bundy (bundy@acnatsci.org) with thoughts and concepts to be distributed to the group. The discussion begins now!

Modeling the Influence of Zooplankton on Phytoplankton and Other Particulate Matter in the Chesapeake Bay

Steve M. Bartell.
The Cadmus Group, Inc.
78A Mitchell Rd., Oak Ridge, TN 37830
sbartell@cadmusgroup.com

The characterization of zooplankton production can contribute to the development of a comprehensive description of the influence of filter-feeding organisms on phytoplankton and other particulate matter in the Chesapeake Bay. Current data limitations and incomplete understanding of the production dynamics in this complex ecosystem suggest that ecological models will play an important role in describing the impacts of filter feeders on the Bay's phytoplankton and other particulate matter. Models provide formal frameworks for analyzing and integrating existing information; models also permit the translation of current data and understanding into estimates of the influence of zooplankton on phytoplankton production, phytoplankton community structure, and the dynamics of organic and inorganic particulate matter in the Bay.

This workshop presentation will briefly summarize the historical role of ecological models in quantifying zooplankton feeding and production in the Chesapeake Bay and similar estuarine ecosystems. Current capabilities in modeling zooplankton feeding and production in the Bay will be reviewed and evaluated. One major challenge lies in determining the necessary and appropriate level of structural detail (e.g., food web complexity) to include in models of Bay zooplankton. The implications of structural complexity on model performance will be discussed using results from different aggregations of a detailed lower trophic level model constructed to simulate experimental estuarine mesocosms. Issues concerning the formulation of feeding terms in describing filter feeding by zooplankton will also be discussed. The effects of sparse data and associated model parameter uncertainty on model results will be discussed in terms of ecological risk assessment and numerical uncertainty analysis using a version of the mesocosm model adapted for the Patuxent River and estuary.

The presentation will also underscore the direct and indirect effects of filter feeding by zooplankton on the flow of energy and the cycling of nutrients within the Bay. The intensity of grazing by zooplankton directly influences the flow of energy (or carbon) through the pelagic food web and can impact phytoplankton standing crop. At the same time, selectivity in zooplankton feeding can alter the composition and size structure of the phytoplankton and indirectly affect nutrient cycling via pathways influenced by organism size. Future modifications and refinements in the modeling of zooplankton will be offered in the context of a comprehensive model of Bay filter feeders.

Simulating Menhaden (*Brevoortia tryannus*) filtering capacity in Chesapeake Bay: Acknowledging ecological complexity and research needs

Robert J. Wood
Chesapeake Biological Laboratory
University of Maryland Center for Environmental Science
P.O. Box 38, Solomons, MD 20688
bwood@cbl.umces.edu / 410-326-7211

Atlantic menhaden is one of two numerically dominant forage fish species in Chesapeake Bay. Together with bay anchovy, Atlantic menhaden serve as an important trophic conduit, linking the Bay's prolific primary productivity to many economically and ecologically important piscivorous fishes and fish-eating birds (gulls, terns, cormorants, ospreys). Atlantic menhaden feed directly on phytoplankton, grow to a relatively large size, spend significant portions of their life cycle in the coastal ocean, and are commercially harvested. These characteristics distinguish Atlantic menhaden populations as a key component of the Chesapeake Bay ecosystem, influencing the flow of nutrients and biomass within the estuary and their export to the coastal ocean.

A primary goal of this workshop is to discuss modeling approaches that hold the greatest promise for assessing the influence of Atlantic Menhaden on Chesapeake Bay water quality. Certainly, Atlantic menhaden filtering capacity can be calculated using a variety of modeling approaches that utilize measured or estimated parameters, such as volume swept per fish, filtering efficiencies for various particle sizes, and fish respiration rates. Although this has been done, results from two recent investigations suggest that additional model complexity is required to realistically assess the impact of menhaden on Chesapeake Bay water quality. The unique position menhaden occupy in the Chesapeake Bay ecosystem food web dictates that future efforts must realistically account for, or simulate, physical and ecological dynamics that influence menhaden abundance and filtering capacity. For example, two goals of Chesapeake 2000 are: to continue efforts to achieve and maintain the 40 percent nutrient reduction goal agreed to in 1987; and, by 2010, to remove the Bay and the tidal portions of its tributaries from the list of impaired waters under the Clean Water Act. It is possible that future nutrient reductions may influence menhaden populations by influencing prey availability. Additionally, as the Chesapeake 2000 commitment to "develop ecosystem-based multispecies management plans for targeted species" emphasizes, fish populations respond dynamically to changes in fishing pressure as a result of non-linear food web interactions. Approaches used to assess the potential filtering impact of increased (or decreased) menhaden populations must account for these complexities.

An overview of Atlantic menhaden life history and predator-prey interactions will be presented along with recent research into the impact of factors such as harvest, nutrient input, and climate variability on the Atlantic menhaden population. Relevant information pertaining to current efforts to craft a Chesapeake Bay Fisheries Ecosystem Plan and construct a Chesapeake Bay Ecosystem Model will also be discussed. Because this workshop should address limitations of the currently available data for supporting future modeling efforts, an overview of existing Chesapeake Bay monitoring activities will also be briefly outlined.

Modeling the ecosystem level impacts of Menhaden (*Brevoortia tryannus*) in Chesapeake Bay.

Thomas Miller
Chesapeake Biological Laboratory
University of Maryland Center for Environmental Science
P.O. Box 38, Solomons, MD 20688
miller@cbl.umces.edu

Menhaden are an important and abundant member of the ichthyoplankton community in the Chesapeake Bay. They occupy a unique trophic niche. Although larvae are zooplanktivorous, from the late juvenile stage menhaden become filter-feeders removing both detrital and phytoplankton particles from the water column. Additionally, the grazing activity of menhaden converts nutrients in the phytoplankton and detrital particles, that would normally cycle quickly through the ecosystem, into fish tissue which cycles more slowly. Thus it has been suggested that menhaden have the potential to impact phytoplankton dynamics through two different modes: direct control through grazing, and indirect control by altering the dynamics of the nutrient pool. If either or both of these potential impacts are valid, then there is the potential that we can control water quality by regulating the pattern of removals in the commercial fishery by implementing quotas, size limits or seasonal closures. In this presentation I will review questions central to the potential role menhaden may play in regulating nutrient quality.

Menhaden diets have not been studied intensively. There are limited data on patterns of diet selectivity, or the foraging patterns of menhaden. However, the studies that have been published indicate that menhaden utilize branchial feeding baskets to retain phytoplankton-sized particles when water is passed over their gills. There is also clear evidence of a response in feeding to changes in swimming speed. These data have lead to the convention of modeling menhaden feeding as the product of the phytoplankton biomass in the water, the mouth gape of an actively feeding menhaden, the filtering efficiency and the swimming speed. These assumptions have allowed estimates of the potential per capita grazing rate of menhaden. However, there is little information on the response of menhaden to alternative prey fields. Of equal importance to quantifying feeding patterns of individual menhaden is the need to quantify the functional and numerical responses of menhaden to changes in phytoplankton abundance. There are limited data available to address these questions. Most studies have assumed a type I functional response, and no numerical response.

Understanding the seasonal and spatial dynamics of menhaden is vital if they are to be used to regulate water quality. Research has indicated that the population is limited by fall-time availability of habitat. However, even in these periods only 30% of the Bay volume was predicted as failing to support menhaden growth. Recruitment seemed to be less of a bottleneck, although coast-wide, recruitments are at near record lows. This suggests that summer time plankton abundances are not limiting menhaden populations, thereby questioning the potential regulatory impact they may have on phytoplankton production.

San Francisco Bay Experience

Jan Thompson
U.S. Geological Survey
Jtompson@usgs.gov/ 650 329-4364

San Francisco Bay (SFB) is a low productivity, non-eutrophic system despite having large nutrient inputs. The major reasons for the low production in SFB are low light availability relative to the high rates of grazing in the system. The introduction of an exotic, suspension feeding bivalve (*Potamocorbula amurensis*) into the system in 1986, in conjunction with more than a decade of work on the phytoplankton dynamics of the system has allowed us to examine the effect of increased suspension feeding on the phytoplankton dynamics of the two major embayments in SFB. The contrast between the embayments is signficant as the phytoplankton biomass in the Northern Bay (NB) has declined and seasonal blooms have all but disappeared, whereas the phytoplankton biomass and blooms have not been altered in the Southern Bay (SB) despite the invasion by the same species.

Chlorophyll *a* concentrations did not increase above background levels for the first 10 years of the *P. amurensis* invasion in the NB. Estimated carbon consumption by the bivalve population (based on secondary production estimates) and water column turnover rates (based on estimated benthic grazing rates) confirm that the bivalve is capable of controlling the phytoplankton biomass in the manner observed. We have seen some food web responses to the reduction in phytoplankton biomass, including a decline in population densities of one copepod (*Eurytemora affinis*) and in a trophically important mysid shrimp. Most recently we have seen blooms during two years when the bivalve population declined in the shallow water during winter. These rejuvenated blooms are, compared to historic blooms, short (2 weeks instead of 16+ weeks), out of season (spring instead of summer and fall) and small in magnitude. This recent pattern of small blooms in NB is similar to the pattern we see in SB, for which the interactions of phytoplankton dynamics, nutrient concentrations, light limitation, and grazer dynamics have been more intensively examined in the field and with a series of numerical models. Conclusions from our joint field/modeling study in SB include the following: (1) Shallow water phytoplankton production is a primary factor in bloom development and thus modeling and measurement of shallow water grazing, nutrients, and light availability are critical in our understanding of bloom development. (2) Because blooms begin in the shallows and nutrients originate in the deep channel in this system it is necessary to accurately estimate lateral transport between channel and shallow water. (3) Benthic grazing rates can change very rapidly following recruitment of grazers, and monthly estimates of grazing rates is the minimum temporal scale. (4) Spatially intensive estimates of benthic grazing rates, nutrient concentrations, turbidity, and chlorophyll *a* concentrations are necessary during critical periods that can be established with model results. (5) Given the difficulty in estimating hydrodynamically and behaviorally accurate benthic grazing rates, ranges of benthic grazing rates that are applicable for the organisms (eg. assuming no concentration boundary layer (CBL), assuming maximum CBL, assuming maximum CBL but assuming not all animals feed all of the time) can be used in numerical models to determine the relative importance of benthic grazing in the system. (6) The models are particularly useful in looking at factors with very different time scales (eg. How does the short time scale change in light attenuation (hours) affect bloom development relative to the long-term (days to weeks) limitation of benthic grazing).

Defining the Filter-Feeding Commitment of the Bay Agreement

Robert E. Magnien
Maryland Department of Natural Resources
Tawes State Office Building., D-2
580 Taylor Ave. Annapolis, MD 21401
RMAGNIEN@dnr.state.md.us/ 410 260 8630

The Chesapeake Bay Agreement of 2000 calls for "**By 2004 assess the effects of different population levels of filter feeders such as menhaden, oysters and clams on Bay water quality and habitat**". The major Bay Program committees involved in satisfying this commitment and numerous managers and scientists from state and federal agencies as well as academia, were canvassed to help define the management objectives and scientific scope of this commitment.

In seeking information to support management decisions, the Bay Program has often and successfully used the approach of developing 'management questions' that clarify and focus the collection and analysis of technical information to support a broad initiative. Discussion of this issue led to the development of the following management questions:

1.) Are filter-feeding organisms in the Chesapeake Bay and its tributaries capable of significantly improving water and habitat quality at present, historical, or potentially restorable population levels?
2.) If filter-feeding organisms ***are*** judged to be capable of significantly improving water and habitat quality, what are:
    a.) the key species and the range of population levels among the suite of important filter-feeders required to see positive impacts?
    b.) the important relationships with 'bottom-up' (e.g. nutrient/sediment inputs) controls that could influence the impact of filter-feeders?

In addition to helping to formulate the management questions, contributors also suggested that the following "effects" be evaluated:

1.) water clarity and resultant influence on SAV populations
2.) productivity, biomass (chlorophyll) and species composition of phytoplankton and zooplankton
3.) dissolved oxygen
4.) nutrient dynamics (recycling, denitrification, burial, etc.
5.) significance of the above to, and altered relationships among, recreationally and commercially important finfish and shellfish
6.) differences in effects nearshore vs. offshore and by salinity zone

All contributors favored an approach that would include a comprehensive suite of the significant filter-feeders in the Bay, not only the "oysters, clams and menhaden" specifically referred to in the Agreement.

Considering the scope of the questions, effects to be evaluated, and comprehensive suite of filter-feeders to be evaluated, conducting the scientific work needed would appear to be a formidable task. While most contributors favored a comprehensive evaluation, they also recognized that scientific understanding, time frames and budgets would set bounds on what could be evaluated by 2004. The challenge now is to identify the key analyses that will best address the management questions. A three page “white paper” with some additional background and detail is available on the filter-feeding workshop web site.

Filter Feeders in the Chesapeake Bay Environmental Model Package

Carl Cerco
Army Corp of Engineers
Carl.F.Cerco@erdc.usace.army.mil

The CBEMP

The Chesapeake Bay Environmental Model Package (CBEMP) was the first to combine a three-dimensional hydrodynamic model, an advanced model of eutrophication kinetics, and a fully-predictive sediment diagenesis model. The CBEMP has been used to provide guidance in the 1992 re-evaluation of load reductions, to reconstruct historic trends and origins of anoxia, and to guide management of Chesapeake Bay tributaries.

CE-QUAL-ICM

The water-column processes model within the CBEMP is CE-QUAL-ICM. This version of the model simulates a suite of 24 state variables and provides representation of the marine carbon, nitrogen, phosphorus, and silica cycles. CE-QUAL-ICM is accompanied by a fully-predictive sediment diagenesis model that provides computations of sediment oxygen demand and sediment-water nutrient fluxes. The model has the capability to represent primary production, phytoplankton functional groups and abundances, and grazing of phytoplankton by the microzooplankton and mesozooplankton functional groups. It represents multiple organic carbon pathways that include transfer to the pelagic food chain, decomposition in the water column, and settling and subsequent decomposition in the sediment.

Benthos

Benthos were incorporated in to the CBEMP during the “Tributary Refinements” phase of the modeling effort. Benthos are divided into two groups: deposit feeders and filter feeders. The deposit-feeding group represents benthos which live within bottom sediments and feed on deposited material. The filter-feeding group represents benthos which live at the sediment surface and feed by filtering overlying water.

Filter Feeders

Filter feeders are incorporated into the model through a submodel which interacts with the main model of the water column and the sediment diagenesis submodel. Benthos monitoring data were examined and a dominant species was identified for 25 regions of the bay. Three dominant species were sufficient to characterize the system: *Rangia cuneata*, *Macoma balthica*, and *Corbicula flumenea*.

Each was modeled with the same equation:

$$\frac{d\,FF}{dt} = If \bullet alph \bullet PC \bullet FF - r \bullet FF - bet \bullet FF^2$$

where FF = biomass; If = ingestion rate; alph = assimilation efficiency; PC = particulate carbon in water column; r = respiration; and bet = nonrespiratory mortality. Dominant species were differentiated through assignment of parameter values. In addition to temperature and DO, effects of suspended solids were considered in calculating ingestion, respiration, and mortality. Assimilation efficiencies were assigned to each form of particulate organic carbon in the water column.

Appendix D
Workshop Participants

Lowell Bahner
National Oceanic and Atmospheric
Administration
Chesapeake Bay Office
410 Severn Ave, Suite 107
Annapolis, MD 21403
(410) 267-5660
lowell.bahner@noaa.gov

Steve Bartell
The Cadmus Group, Inc.
78A Mitchell Road
Oak Ridge, TN 37830
(865) 425-0401
(865) 425-0482 (fax)
sbartell@cadmusgroup.com
smbartell@aol.com

Sasha Bishton
Chesapeake Research Consortium
Chesapeake Bay Program Office
410 Severn Avenue, Suite 109
Annapolis, MD 21403
(410) 267-5718
(410) 267-5777 (fax)
bishton.alexandra@epa.gov

Claire Buchanan
Interstate Commission on the Potomac
River Basin
6110 Executive Blvd., Suite 300,
Rockville, MD 20852
(301) 984-1908 x112
(301) 984-5841 (fax)
cbuchan@potomac-commission.org

Melissa Bugg
Chesapeake Research Consortium
645 Contees Wharf Road
Edgewater, MD 21037
(410) 798-1283
(410) 798-0816 (fax)
bugg@serc.si.edu

Denise Breitburg
Academy of Natural Sciences
Estuarine Research Center
10545 Mackall Rd.
St. Leonard, MD 20685
(410) 586-9711
(410) 586-9705 (fax)
Breit@acnatsci.org

Marie H. Bundy
Academy of Natural Sciences
Estuarine Research Center
10545 Mackall Rd.
St. Leonard, MD 20685
(410) 586-9710
(410) 586-9705 (fax)
bundy@acnatsci.org

Nancy H. Butowski
Maryland Department of Natural
Resources
Tawes State Office Bldg., B-2
580 Taylor Avenue
Annapolis, MD 21401
(410) 260-8268
(410) 260-8278 (fax)
nbutowski@dnr.state.md.us

Arthur J. Butt, PhD
VA Department of Environmental
Quality
Chesapeake Bay Office
PO Box 1009
Richmond, VA 23240
(804) 698-4314
(804) 698-4116 (fax)
ajbutt@deq.state.va.us

Carl Cerco
cerco@homer.wes.army.mil
cercoc@wes.army.mil

Richard Dame
Coastal Carolina University
Marine Science
PO Box 261954
Conway, SC 29528
(843) 349-2216
dame@coastal.edu

Daniel M. Dauer
Old Dominion University
Norfolk, VA. 23529
(757) 683-4709
(757) 683-5283 (fax)
ddauer@odu.edu

Frank Dawson
Maryland Department of Natural
Resources
Tawes State Office Building, E-2
580 Taylor Avenue
Annapolis, Maryland 21401
(410) 260-8795
(410) 260-8779 (fax)
FDAWSON@dnr.state.md.us

Joe Desfosse
Atlantic States Marine Fisheries
Commission
1444 "Eye" St., NW, 6th Floor
Washington, DC 20005
(202) 289-6400
(202) 289-6051 (fax)
jdesfoss@asmfc.org

Michael A. Fritz
U.S. Environmental Protection Agency
Chesapeake Bay Program Office
410 Severn Ave, Suite 109
Annapolis, MD 21403
(410) 267-5721
(410) 267-5777 (fax)
fritz.mike@epa.gov

Eileen Hofmann
Center for Coastal Physical
Oceanography
Crittenton Hall
Old Dominion University
Norfolk, VA 23529
(757) 683-5334
(757) 683-5550 (fax)
hofmann@ccpo.odu.edu

Raleigh Hood
University of Maryland
Center for Environmental Studies
Horn Point Laboratory
raleigh@hpl.umces.edu

William S. Hunley
Hampton Roads Sanitation District
P.O. Box 5911
Virginia Beach, VA 23471-0911
(757) 460-4252
(757) 460-2372 (fax)
WHunley@hrsd.dst.va.us

Stephen J. Jordan
MD Department of Natural Resources
Sarbanes Cooperative Oxford
Laboratory
904 S. Morris St.
Oxford, MD 21654
(410) 226-0078
sjordan@dnr.state.md.us

David G. Kimmel
University of Maryland
Center for Environmental Science
Horn Point Laboratory
2020 Horns Point Road
P.O. Box 775
Cambridge, MD 21613
(410) 221-8477
(410) 221-8490 (fax)
dkimmel@hpl.umces.edu

Celere Leonard
Chesapeake Research Consortium
Chesapeake Bay Program Office
410 Severn Avenue, Suite 107
Annapolis, MD 21403
(410) 267-5675
(410) 267-5777 (fax)
celere.leonard@noaa.gov

Lewis Linker
U.S. Environmental Protection Agency
Chesapeake Bay Program Office
410 Severn Avenue
Annapolis, MD 21403
(410) 267-5741
(410) 267-5777 (fax)
linker.lewis@epa.gov

Robert Magnien
MD Department of Natural Resources
Tawes State Office Building, D-2
580 Taylor Avenue
Annapolis, MD 21401
(410) 260-8630
(410) 260-8640 (fax)
RMAGNIEN@dnr.state.md.us

Roberta L. Marinelli
University of Maryland
Center for Environmental Science
Chesapeake Biological Laboratory
P.O. Box 38
Solomons, MD 20688
(410) 326-7201(office)
(410) 326-7393 (lab)
(410) 326-7378 (fax)
marinelli@cbl.umces.edu

Thomas Miller
University of Maryland
Center for Environmental Studies
Chesapeake Biological Laboratory
P.O. Box 38
Solomons, MD 20688
(410) 326-7276
(410) 326-7318 (fax)
miller@cbl.umces.edu

Roger Newell
University of Maryland
Center for Environmental Studies
Horn Point Laboratory
PO Box 775,
Cambridge, MD 21613
(410) 221-8410
(410) 221-8490 (fax)
newell@hpl.umces.edu

Derek Orner
NOAA
Chesapeake Bay Office
410 Severn Avenue, Suite 107A
Annapolis, MD 21403
(410) 267-5676
(410) 267-5666 (fax)
derek.orner@noaa.gov

James J. Pletl
Hampton Roads Sanitation District
P.O. Box 5911
Virginia Beach, VA 23471-0911
(757) 460-4246
(757) 460-2372 (fax)
JPletl@hrsd.dst.va.us

Mike Roman
University of Maryland
Center for Environmental Studies
Horn Point Laboratory
PO Box 775
Cambridge. MD 21613
(410) 221-8425
roman@hpl.umces.edu

Linda C. Schaffner
Virginia Institute of Marine Science
The College of William and Mary
Gloucester Point, VA 23062
(804) 684-7366
(804) 684-7293 (fax)
linda@vims.edu

David H. Secor
University of Maryland
Center for Environmental Studies
Chesapeake Biological Laboratory
PO Box 38
Solomons, MD 20688
(410) 326-7229
(410) 326-7318 (fax)
secor@cbl.umces.edu

Kevin Sellner
Chesapeake Research Consortium
645 Contees Wharf Road
Edgewater, MD 21037
(410) 798-1283
(410) 798-0816 (fax)
sellner@serc.si.edu

Laurie Sorabella
Virginia Institute of Marine Science
PO Box 1346
Gloucester Point, VA 23062
(804) 684-7481
(804) 684-7752 (fax)
laurie@vims.edu

Debbie Steinberg
Virginia Institute of Marine Science
P.O. Box 1346
Gloucester Point, VA 23062
(804) 684-7838
(804) 684-7293 (fax)
debbies@vims.edu

Jan Thompson
U.S. Geological Survey
(650) 329-4364
jthompso@usgs.gov

Robert Wood
University of Maryland
Center for Environmental Studies
Chesapeake Biological Laboratory
Bwood@cbl.umces