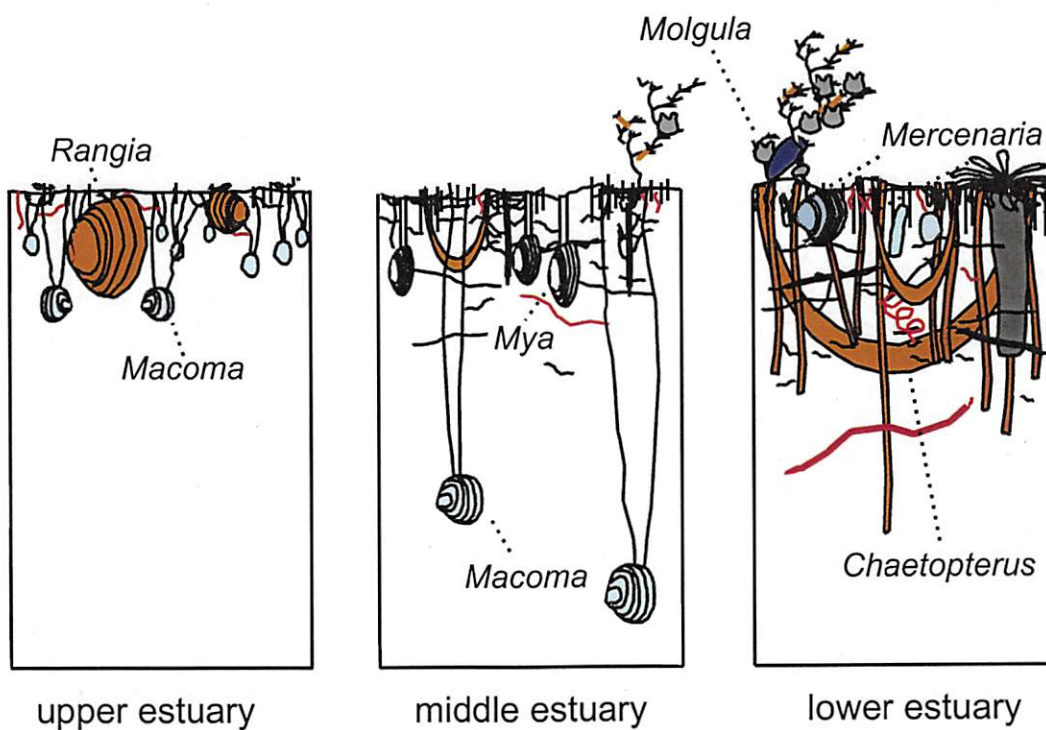


# Review of the Benthic Process Model with Recommendations for Future Modeling Efforts



**A Report from the  
Benthic Process Model Review Team**

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## **Executive Summary**

The Benthic Process Model Review Team, assembled by the Modeling Subcommittee during Fall 2000, reviewed the benthic model developed for the Chesapeake Bay Water Quality Model, a component of Chesapeake Bay Estuary Modeling Package. Review of the model presented in the technical report, *Development of a Suspension Feeding and Deposit Feeding Benthos Model for Chesapeake Bay* (USCE 0410) was guided by questions provided by the Modeling Subcommittee. The Review Team was further charged with advising the Modeling Subcommittee regarding the future directions in benthic process modeling that will be needed in order to satisfy the goals and objectives stated in the Chesapeake 2000 Agreement.

As stated by the Benthic Modeling Team during the model review process (Appendix B) “The present benthic model represents a first attempt to directly couple a complex eutrophication model with a simulation of benthic biomass. The original goals were to include a dynamic suspension feeding loss term to remove algal biomass, organic detritus, and inorganic suspended solids in an ecologically relevant manner, to compute a significant food component (both bivalve and annelid biomass) for higher trophic levels, and to simulate the impacts of hypoxia on benthic resources. The model was developed to be as generic as possible with few regionally-specified parameters or processes.” These are diverse and complex objectives. Several aspects of the present modeling approach are worthy of praise. Efforts were made to include state-of-the-art components within the bounds of logistical practicality. Many parts of the model are sophisticated and well researched. For example, representations of key benthic processes, such as filtration as a function of bioenergetics and environmental parameters, and interactions of deposit-feeders and diagenetic processes, are impressively advanced and bode well for the likely success of future improvements. The subsequent documentation of the model development process, followed by external review of the model and its assumptions, allowed identification of strengths and weaknesses and ensures that more confident choices can be made regarding future steps in model development.

In our analysis of the model framework we found systematic under- or over-prediction of the biomass of the two major functional groups in different regions of the bay. The present model tends to over-predict suspension-feeding biomass in the mid-to-lower bay, where bivalve biomass is low, and under-predicts or approximates suspension-feeding biomass in the upper bay and tributaries, where bivalve biomass is high. Furthermore, the model-data comparison for deposit feeders tends to be inversely correlated with that for suspension feeders. For both deposit and suspension feeders, the model tends to under-predict when observed biomass is high and over-predict when observed biomass is low. We considered how food availability, mortality terms, the exclusion of potentially important species or groups, and recruitment processes related to the observed trends.

In the body of this report we address the original questions posed by the Modeling Subcommittee and make a series of recommendations for model improvement. Although numerous issues have been identified, we recommend that initial efforts to improve the model focus on the following major issues:

- I. Ensure that particulate organic matter flux of to the benthos is correct** - The suspension feeder growth rate-predation balance in the present model formulation predicts that suspension feeding biomass is proportional to POC to the power 1.3. This formulation approximates the relationship between macrobenthic biomass and system averaged primary production determined for a variety of shallow water ecosystems, including upper and lower Chesapeake Bay. The direct tying of suspension-feeding biomass to POC causes the model response to be dictated largely by regional patterns in primary productivity. The model does not capture the large dynamic range (both in space and time) found in the observed bivalve biomass because the predicted POC, which forces the model, does not vary as strongly. As formulated, the model under-predicts suspension-feeding biomass in the upper bay and tributaries because POC input is not sufficiently higher there to entirely account for the higher observed suspension-feeding biomass.
- II. Modify the formulation for predation effects** - The present model uses a quadratic term to simulate predation effects on macrobenthic fauna. This approach appears to be most satisfactory when prey and their predators have similar rates of population growth. This is not likely the case for most macrobenthic prey-demersal predator relationships in the bay ecosystem. We recommend that an alternative formulation be employed, one that incorporates predator saturation at high prey density. We also recommend that consideration be given to adjusting the seasonal phasing (temperature-dependence) of prey growth and predator-induced mortality. Reformulation of the predation term and appropriate seasonal lagging will give macrobenthic species realistic predation refuges, which likely will result in higher standing stocks of macrobenthos in the model simulations.
- III. Include non-bivalve suspension feeders in the model** - The present model “overpredicts” suspension feeder biomass throughout the lower bay because infaunal bivalve suspension feeders are generally rare in that region. In reality, suspension feeders are abundant in the lower bay. The primary biomass contributor is the infaunal polychaete *Chaetopterus variopedatus*, as well as a variety of epifaunal species (tunicates, hydroids, bivalves). Existing data will allow us to begin to incorporate these groups and this should be a major focus of the next round of model development. Another significant concern is that the present approach uses annually averaged biomass to determine which species of suspension feeders are modeled. This approach is inherently biased towards identifying the longest-lived species, primarily the bivalves. Existing databases should be re-examined for infaunal groups that are important seasonal contributors to benthic productivity, but which may have been overlooked due to long-term biomass averaging. Likely candidates are amphipods, which are present throughout the system, as well as insects, which are most prevalent in tidal freshwater.

**IV. Develop a new framework for model development - Rapid progress on the challenging issue of linking benthic processes with hydrodynamic and water quality processes will be facilitated by the development of a framework that regularly brings together experts in the areas of benthic ecological processes, suspension feeder bioenergetics and ecosystem modeling.**

The 2000 Chesapeake Bay Agreement states the following goal: "By 2004, assess the effects of different population levels of filter feeders such as menhaden, oysters and clams on Bay water quality and habitat." Clearly, the existing model cannot be used readily to assess the effects of menhaden or other pelagic species on the bay's water quality. On the other hand it is not obvious to us how significantly better, more rapid progress for benthic suspension (filter) feeders would be made using a significantly different modeling strategy. The existing benthic process model has many positive features, designed to capture the feedbacks among benthic processes and water quality in the context of complex environmental and hydrodynamic processes operating within the Chesapeake Bay ecosystem. While modeling these interactions has proven difficult, the efforts to date have moved us forward and increased the utility of the Chesapeake Bay Estuary Modeling Package as a management tool. The questions raised by the initial efforts to incorporate benthic suspension and deposit feeder processes into the overall modeling scenario have sparked the interests and attention of both the scientific and management communities and forced all of us to seek greater understanding. We recommend continued efforts to refine the benthic process model based on the considerable insights gained over the last few years. To make the most progress in the shortest time frame, we further recommend that benthic ecologists, modelers and managers work together closely through the next phase of model development. We hope that all will benefit from the recommendations made in this report.

## Introduction

During Fall 2000, the Benthic Processes Model Review Team (hereafter, Review Team) began its review of the benthic model developed for the Chesapeake Bay Water Quality Model, a component of Chesapeake Bay Estuary Modeling Package. A primary objective for the Review Team was to review the model presented in the technical report, *Development of a Suspension Feeding and Deposit Feeding Benthos Model for Chesapeake Bay* (USCE0410), with some guiding questions provided by the Modeling Subcommittee (discussed below). The Review Team was further charged with advising the Modeling Subcommittee regarding the future directions in benthic modeling that will be needed to satisfy the goals and objectives stated in the Chesapeake 2000 Agreement, particularly the goal that pertains to the need to assess, by 2004, the effects of different population levels of filter feeders such as menhaden, oysters and clams on Bay water quality and habitat.

## Structure and History of the Review

A Review Team consisting of Linda Schaffner and Carl Friedrichs (both of Virginia Institute of Marine Science), and Dan Dauer (Old Dominion University) was formed during February 2000. These individuals have experience in the fields of benthic ecology, benthic processes and process modeling, but have had little to no previous involvement with the Modeling Subcommittee or its activities. The review process actively began during Fall 2000 following receipt of the technical report by members of the Review Team. After individually reviewing the report, Review Team members had their first meeting on 11 December 2000 and drafted initial comments and questions regarding the report (Review Team Questions and Comments, Appendix A). Linda Schaffner (VIMS) met with Lewis Linker (EPA), Carl Cerco (USACE-WES), Dominic Di Toro (HydroQual) and Mark Meyers (HydroQual) at the Bay Program Office on 8 January 2001 to discuss these questions and comments. Subsequently, the Modeling Team produced a written summary of the discussion and provided some of the additional information requested at the 8 January meeting (Appendix B). Review Team members Linda Schaffner (VIMS) and Carl Friedrichs (VIMS) met with Lewis Linker (EPA), (USACE-WES), Dominic Di Toro (HydroQual) and Jim Fitzpatrick (HydroQual) at the Bay Program office on 17 April 2001 to complete the discussion of questions and comments raised during the review process. This ongoing dialogue proved extremely useful in helping the Review Team members to better understand the strengths and limitations of the model and the historical decision-making processes that led to the current formulation. It also helped the modelers to better understand some of the biological/ecological concerns of the review team. In some cases this immediately led to new ideas of how to address areas of concern. Further discussions of the technical document and responses of the Modeling Team by members of the Review Team took place via e-mail between January and June 2001. An initial presentation of the findings of the Review Team was presented to the Modeling Subcommittee in July 2001. Subsequently, comments on the draft document were requested from benthic process experts of the Chesapeake Bay research community.

## Credits and Acknowledgements

Review Team members thank Lewis Linker (EPA), Carl Cerco (USACE-WES), Mark Meyers (formerly of HydroQual), Dominic DiToro (HydroQual) and Jim Fitzpatrick (HydroQual) for the useful dialogue maintained during the review process. After completion of the initial draft of the document, the authors sought comments from various benthic process experts of the bay community. This document has been improved based on comments received from Drs. Donald Boesch, Walter Boynton and Kenneth Tenore, all of the University of Maryland. We thank them for their time and insights.

## Summary of Findings

### *The Model Framework*

The current model allows for coupling of a filtration-based suspension feeder model and a deposit feeder/diagenesis model to the present eutrophication model in order to better simulate benthic effects on eutrophication processes, the role of benthic organisms in energy transfer to higher trophic levels and effects of hypoxia on benthic communities. Examination of model-data comparisons reveal systematic patterns of mis-match (Figure 1), some of which were noted in the body of the technical report, but which were not sufficiently emphasized in the report summary. Although small-scale variability of the observed benthos does complicate model-data comparison, clear regional patterns exist in the mis-match between observed and predicted biomass. Specifically, the present model tends to over-predict suspension-feeding biomass in the mid-to-lower bay, where bivalve biomass is low, and under-predict or approximate suspension-feeding biomass in the upper bay and tributaries, where bivalve biomass is high (Figure 1). Furthermore, the model-data comparison for deposit feeders tends to be inversely correlated with that for suspension feeders: the model tends to under-predict deposit-feeding biomass in the lower bay and over-predict deposit-feeding biomass in the upper bay. For both deposit and suspension feeders, the model tends to under-predict when observed biomass is high and over-predict when observed biomass is low. In other words, the dynamic range in the observed suspension-feeding bivalve biomass data is systematically larger than that found in the predictions.

Under-predictions of suspension-feeding biomass in the upper bay and tributaries and the generally subdued dynamic range of predicted biomass overall can be understood, at least in part, through an examination of the governing state equation for biomass. In all but the tidal freshwater regions for the suspension-feeding model, the dominant balance in the biomass state equation for both suspension and deposit feeders is between growth and predation. For the suspension-feeding model the balance is  $gS = \beta S^2$  where  $S$  is suspension feeder biomass,  $g$  is growth rate, and  $\beta$  is the predation rate. A similar relation holds for the deposition-feeding model. For the suspension-feeding case, substituting relations for growth rate yields:

$$S \approx (\text{constant}) \times (\text{O}_2 \text{ function}) \times (\text{TSS function}) \times (\text{POC}/\beta)^{1.3}$$

where POC is particulate organic carbon in the water column and the oxygen (O<sub>2</sub>) and total suspended solids (TSS) functions are logistic responses, which reduce biomass in response to decreased oxygen or increased suspended sediment concentration. The "constant" incorporates factors such as filtration rates and assimilation efficiencies, which are set to vary only weakly throughout the model domain. As stated in the technical report summary, "The benthos model is very sensitive to the food supply and to the severity and duration of hypoxia predicted by the water quality model." The above equation clearly indicates why.

Outside the minority of modeled cases where O<sub>2</sub> or TSS are important, the growth rate-predation balance predicts that suspension-feeding biomass will simply be proportional to POC to the power 1.3. This formulation approximates the relationship between macrobenthic biomass and system averaged primary production determined for a variety of shallow water ecosystems, including upper and lower Chesapeake Bay (Herman et al. 1999, Hagy 2001). The direct tying of suspension-feeding biomass to POC levels in the water column via the above relation causes the model response to be dictated ultimately by regional patterns in primary productivity or transport/delivery of phytoplankton to the benthos. The model cannot capture the large dynamic range (both in space and time) found in the observed bivalve biomass because the predicted POC, which forces the model, does not vary as strongly. The model under-predicts suspension-feeding biomass in the upper bay and tributaries because POC input is not sufficiently higher there to entirely account for the higher observed suspension-feeding biomass. This underscores the need to ensure that POC delivery from all potential sources (autochthonous and allochthonous) to the benthos is correctly parameterized.

The present model "overpredicts" suspension feeder biomass throughout the lower bay. The monitoring data used to calibrate the model shows that infaunal bivalve suspension feeders are generally rare in that part of the system. Thus, in initial review the model results are assumed to be incorrect. In reality, suspension feeders are abundant in the lower bay. The primary biomass contributor is the infaunal polychaete *Chaetopterus variopedatus*, as well as a variety of epifaunal species (tunicates, hydroids, bivalves) (Thompson and Schaffner 2000, Schaffner et al. 2001). The suspension feeder dominated benthic biomass of the lower bay is consistent with the level predicted for shallow water coastal ecosystems based on calculated levels of primary production (Herman et al. 1999, Thompson and Schaffner 2001, Hagy 2001).

The over-prediction of suspension-feeding bivalve biomass in the mid-bay is likely due to an inability of the model to properly represent the effects of hypoxia/anoxia in this region. This is partly a result of the inability of the underlying water quality model to fully reproduce the observed oxygen time-series and, therefore, some periods of severe hypoxia or anoxia.

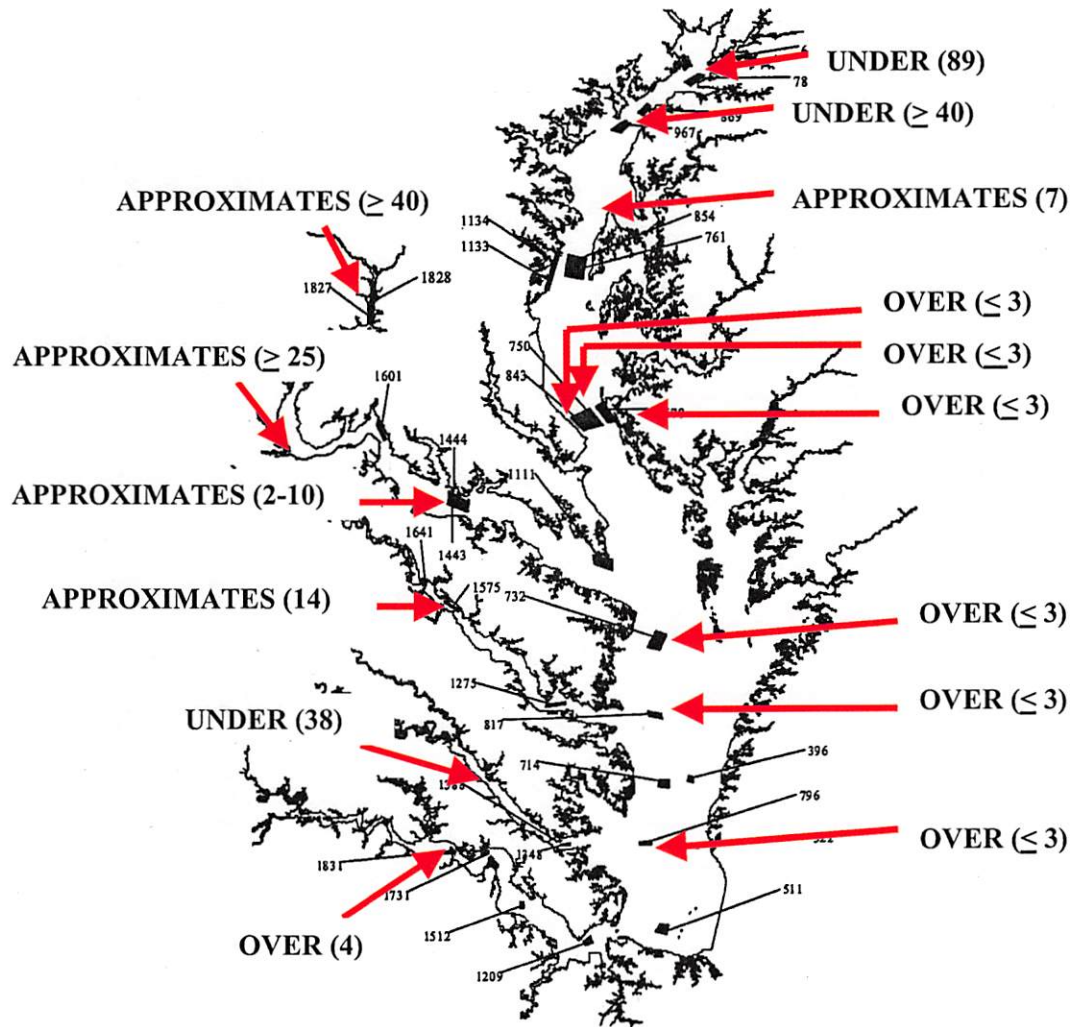


Figure 1. Comparison of model predictions for infaunal suspension feeding bivalves with biomass data collected by the Benthic Monitoring Programs of Maryland and Virginia. "UNDER" indicates that the model generally under-predicts biomass, "OVER" indicates that the model generally over-predicts biomass, and "APPROXIMATES" indicates that the model approximates the biomass observed in the monitoring program. Values in parentheses are average biomass values (g AFDW m<sup>-2</sup>) reported for the period 1984-1995 for fixed survey sites, as shown in Figure 2-4 of the technical report entitled *Development of a Suspension Feeding and Deposit Feeding Model for Chesapeake Bay*, Project No. USCE0410



The above discussion also highlights the limitations of the quadratic formulation for predation used in the present benthic model. As discussed below, predators do not become saturated at high densities of prey in the present benthic model. We suggest, however, that many of the benthic predators on macrofauna do not reproduce fast enough to fully capitalize on the abundance of prey. Additionally, benthic prey may have seasonal refuges from predators due to life history strategies and patterns of migration. A more appropriate predation relation would combine a quadratic dependence at low prey-to-predator densities with a linear or logistic relation at high densities. The above biomass equation reveals the ultimate sensitivity of the benthic model to the predation rate,  $\beta$ . In order to create high suspension-feeding biomass in tidal fresh water  $\beta$  was decreased by two orders of magnitude relative to the oligohaline/mesohaline. This indicates the use of the predation term in the model as a tuning parameter to bring the model results generally in line with the regional behavior of the inherently diverse benthos.

Most importantly, the above biomass equation highlights the one-size-fits-all approach used to date in modeling the benthos of the Chesapeake Bay. Future modeling should account for the region-specific presence of benthic species other than bivalves. A non-bivalve suspension feeder, the polychaete *Chaetopterus variopedatus*, dominates macrofaunal biomass and plays a key role in benthic-pelagic coupling processes in the lower bay. Even if they do not dominate the biomass standing stock of suspension feeders, high P/B species such as amphipods and insects may still play a disproportionate role in grazing the available POC as suspension or deposit feeders. In general, future modeling should anticipate more inclusion of regionally (i.e., ecosystem) specific behavior. This may seem like a step backward in that it may mean more localized "tuning." However, it is preferable to more highly tune appropriate model components than to lump critical model behavior into unconstrained catchall parameters like  $\beta$ . Admittedly, this suggested approach creates additional challenges when attempting to reproduce historically pristine conditions or model future scenarios with altered external forcings, since the species assemblages under such conditions are likely to be quite different. However, a more realistic modeling approach will also help identify laboratory and field research needed to better constrain ecosystem-specific behavior.

## **Responses to Specific Questions Posed by the Modeling Subcommittee**

### ***How can a more detailed representation of predation be added to the model?***

As presently formulated, the benthic model uses a quadratic term to simulate predation effects on macroinfauna. This approach appears to be most satisfactory when prey and their predators have similar rates of population growth, when the biomass of predators is expected to increase linearly with the biomass of their prey. An alternative formulation, especially one that incorporates predator saturation at high prey density, may better represent macrobenthic prey-demersal predator relationships in the bay system (Lipcius and Hines 1986).

Our rationale for suggesting the alternative formulation is as follows. The annelids constitute one of the two major functional groups modeled. They are primarily short-lived (weeks to months) to annual species, characterized by relatively rapid population growth rates. They typically exhibit multiple spawning events for individuals or multiple recruitment events for a population within a single year (Diaz 1984, Holland et al. 1987, Marsh and Tenore 1990, Seitz and Schaffner 1995, Thompson and Schaffner 2000). There are exceptions, such as the polychaete *Chaetopterus variopedatus*, which has a maximum life span of at least two years (Thompson and Schaffner 2000). The suspension-feeding bivalves fully span the range from highly opportunistic (e.g. *Mulinia lateralis*) to long-lived (e.g. *Mercenaria mercenaria*). In contrast, the most important benthic predators (crabs and fish) have life spans of years, slower growth rates than their invertebrate prey, and typically have only one recruitment event per year. An exception to this is small invertebrate predators of juvenile macrofauna, such as platyhelminths (flatworms) and small gastropods, which may exhibit relatively opportunistic life-history patterns. These small predators prey mostly on juvenile macrofauna, not adults, which play a much more important role in biomass accumulation and benthic functional processes.

Evidence from field and laboratory experiments indicates that predation on estuarine benthos can be intense, especially for the small, opportunistic species that live near the sediment-water interface (Virnstein 1977, Dauer et al. 1982b, Diaz and Schaffner 1990). But, larger benthos and those living deeply within the sediment have an effective refuge from predation (Blundon and Kennedy 1982, Lipcius and Hines 1986).

As summarized in the responses of the Modeling Team to Review Team questions discussed at the 8 January 2001 meeting (Appendix B):

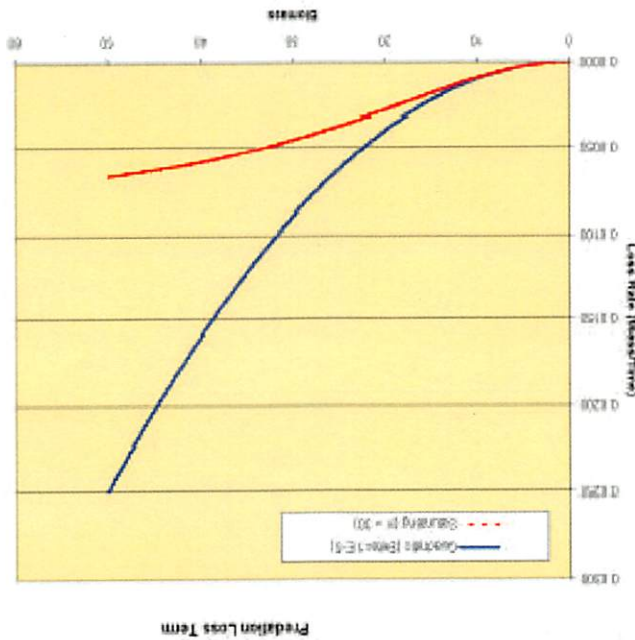
“In its simplest terms, the benthic model (for either deposit or suspension feeders) reflects net growth (assimilation minus respiration) and predation loss (neglecting for the moment hypoxic mortality):

$$\frac{dM}{dt} = \mu M - \beta M^2 \quad (1)$$

where  $M$  is the benthic biomass,  $\mu$  is the net specific growth rate, and  $\beta$  is the mortality rate. The second term on the right hand side is a quadratic closure term representing predation. Of course, the biomass of the predator is not modeled here. It is assumed, however, that predator biomass is linearly related to prey biomass, through the parameter  $\beta$ . This function is desirable mathematically, because it becomes dominant, relative to the net growth term, at high biomass, so that the prey or benthic biomass cannot grow excessively large.

This formulation is satisfactory where both predator and prey have similar time scales of population increase. However, in the case of invertebrate prey, with high intrinsic growth rates, and the potential for multiple spawns and recruitment events per year versus invertebrate or vertebrate predators (crabs and fish) with slower growth rates and single annual recruitment events, there is no room for saturation of the predation

Figure 2. Predation loss terms, showing the quadratic relationship used in the present model and a modified, saturating function for simulating saturation of predation loss. See Appendix B.



Both functions are graphed in Figure 2.

with a new parameter  $K_m$ , in units of benthic biomass which reflects saturation of predation at a specified level of prey biomass. At high benthic (prey) biomass,  $M^2 \gg K_m^2$  and the entire term simplifies to  $-\beta$ . This states that at large prey biomass, predation rate becomes independent of prey concentration (the rate is said to be “zeroth order”).”

$$Predation (M) = -\beta \frac{K_m^2 (K_m^2 - M^2)}{K_m^2 + M^2} \quad (2)$$

function. A modified formulation of the predation term was discussed, which could be tested in the present model framework:

**As discussed at the 8 January 2001 meeting, a more appropriate predation relationship would combine a quadratic dependence at low prey-to-predator densities with a linear or logistic relation at high densities. This will allow saturation of the predators, with predation rates independent of prey density, at high levels of prey biomass.**

The relative temperature-dependency of growth and predation in the model, as it affects the seasonality of predation pressure relative to periods of peak growth of macroinfauna, should also be re-evaluated in the next stage of model development. In the present formulation of the model, maximum predation-induced mortality is coincident with the period of maximum growth of the prey - in other words there are no significant lags. In contrast, our experience working in the bay indicates that prey often have a seasonal refuge from predation pressure. Many of the important demersal fish predators, such as spot and croaker, are not active in the bay system until late spring - early summer, with highest consumption of benthic invertebrate prey occurring during summer months (Holland et al. 1987, Marsh and Tenore 1990, Seitz 1996). It may also be the case that predation mortality declines more rapidly than prey growth rates in the fall, as many predators leave the system for the continental shelf. Thus, considerable growth (and production) of benthic prey may occur during the spring/early summer and late fall, when predation pressure is relatively low.

**In addition to the use of a predation term of the form described above, we recommend consideration be given to adjusting the seasonal phasing (temperature-dependence) of prey growth and predator-induced mortality. Appropriate lagging will give macrobenthic species seasonal predation-refuges, which will likely result in higher standing stocks of benthos in the model simulations.**

***Are there any species or groups that should be added to the model?***

The present benthic model simulates two functional groups of infauna: deposit-feeding annelid worms and suspension-feeding bivalves. While it is reasonable to assume that these two groups comprise much of the benthic macroinfaunal biomass in the Chesapeake Bay estuarine system, as they do in coastal ecosystems worldwide, the data supporting this assumption were not included in the technical report. Based on the inquiries of the Review Team, the Modeling Team subsequently demonstrated that these groups, on average, account for 76% of the total baywide benthic macroinfaunal biomass reported by the Benthic Monitoring Programs of Maryland and Virginia (Figure 3). Nonetheless, we continue to have concerns regarding how well the groups chosen fully reflect important functional roles of macrobenthos.

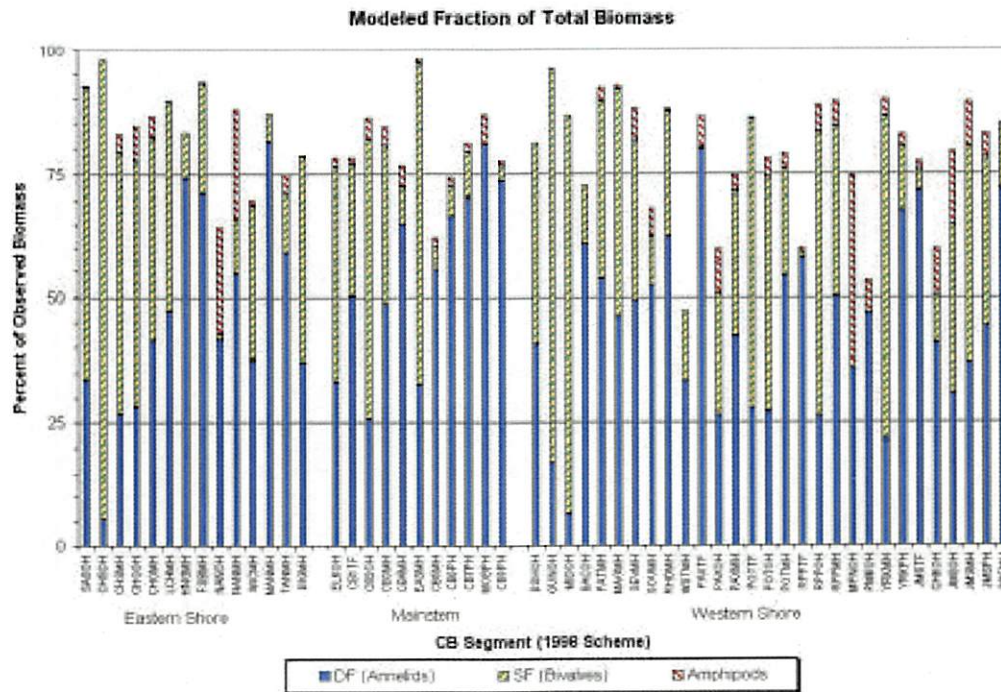


Figure 3. Dominant groups contributing to total observed benthic biomass. Deposit-feeding (DF) annelids and suspension-feeding (SF) bivalves are represented in the Chesapeake Bay benthic model. Data are shown by Chesapeake Bay Program Segment (1998) designation, as averages from the Benthic Monitoring Program for the period 1984-1997. See Appendix B.

Using long-term averages to determine the relative functional importance of benthic species has an inherent bias. Functional groups comprised of species characterized by life spans approaching or exceeding annual time scales (e.g. bivalves) are favored over functional groups or species characterized by high rates of population growth and production over short time frames (e.g. amphipods). Secondary production over a population cycle could be exactly the same, but in one scenario it might be spread over a year, while in another scenario it might be spread over an interval of a few weeks or months. This has significant implications for nutrient cycling and transfer of production to higher trophic levels. Macrofauna with strong seasonal pulses of production might be especially important in the mesohaline regions (e.g. middle bay), where seasonal hypoxia/anoxia limits the development of longer-lived species.

Based on available data, the easiest example to provide is the case of *Leptocheirus plumulosus*. This small, infaunal, suspension-feeding/surface deposit-feeding species is the dominant amphipod of the oligohaline to lower mesohaline reaches of the bay and its tributaries. The data presented in Figure 3 demonstrate that within these areas of the bay and tributaries, amphipods can account for 5% or more of the total infaunal biomass. *L. plumulosus* proliferates rapidly during the period of sedimentation of the spring bloom to densities of  $10^3$  to  $10^4$  individuals  $m^{-2}$ , and subsequently crashes due to food limitation and predation (Holland et al.



1987, Holland et al. 1988, Marsh and Tenore 1990). For the period July 1985 to June 1986, Holland et al. (1988) estimated secondary productivity of *L. plumulosus* to be as high as 10 g AFDW m<sup>-2</sup> yr<sup>-1</sup> at a station in the Chester River, MD. Marsh (1988) found that 60 % of the secondary production of *L. plumulosus* occurred during a four week spring period at stations in the lower Patuxent River.

We suggest that the present formulation of the model downplays the potentially important roles of highly productive, seasonally dominant macrobenthic taxa, especially when they are abundant in only one or two of the major salinity regimes.

**Existing databases, including the spatially extensive random samples from both states, should be re-examined for infaunal groups that are important seasonal contributors to benthic productivity and functional processes. While adequately sampled by the monitoring programs, these species may be overlooked for the modeling effort due to long-term biomass averaging. Likely candidates are amphipods, which could be present throughout the system, as well as insects, which are likely to be most prevalent in tidal freshwater.**

In the present model, only bivalve suspension feeders are simulated, but a wide variety of other suspension feeding taxa are found in the bay, sometimes at very high densities. In the lower mainstem bay, where bivalve suspension feeders are relatively rare, other suspension feeders, which range from sponges to tunicates, constitute a non-negligible fraction of the biomass in some regions (Schaffner 1990, Wright et al. 1997, Schaffner et al. 2001). For the most part, these taxa are poorly represented in the benthic monitoring program database because colonial epifauna are explicitly excluded from the benthic monitoring programs of both states. Furthermore, gear and methodological limitations can make adequate sampling of colonial forms difficult in programs using gear designed to sample infauna.

The composition and diversity of epifaunal assemblages of the lower mainstem bay and the lower York River have been documented in a series of papers (Dauer et al. 1982a, Fredette and Diaz 1986, Schaffner 1990, Wright et al. 1997, Sagasti et al. 2000, 2001, Schaffner et al. 2001). While there are no published estimates of standing stocks or secondary production for the dominant species, Linda Schaffner presented data on epifauna collected as part of a crab-dredging survey of the lower mainstem bay conducted during winter 1986 (Schaffner and Diaz 1988) at the Modeling Subcommittee Workshop on Living Resources held in Annapolis, MD in May 1999. She found that standing stocks of various suspension-feeding colonial taxa were on the order of 1 to 3 grams AFDW m<sup>-2</sup> for a single mid-winter survey period, with highest values observed at depths less than 9 m. This equals or exceeds the long-term average biomass estimates for infaunal suspension-feeding bivalves of the region and the maximum values are comparable to biomass estimates for deposit-feeding annelids in the lower bay mainstem.

Massive accumulations of epifauna (mostly hydroids and tunicates) often occur in the lower York (Wright et al. 1987, Schaffner et al. 2001, Schaffner et al. unpublished data for March, June and September 2001). These accumulations are in the form of mounds with spatial dimensions of 10s of centimeters to 10s of meters and spacings of meters to 10s of meters within patches. While the patchiness and composition of the accumulations makes them difficult to

sample with traditional grabs or box cores, their spatial distributions are easily mapped with side-scan sonar and the fauna composition is easily verified by dredging. Recruitment patterns of epifauna of the lower York River are highly seasonal, with continuous shifts in species dominance through the year (Sagasti et al. 2000). Available data indicate that growth rates of individual taxa can be extremely high over short time periods (Fredette and Diaz 1986, Sagasti et al. 2000).

**Epifaunal suspension feeders are important components of the benthos of the middle to lower estuary. They may be increasing in abundance as other, more desirable suspension feeders decline. Available data will allow us to make preliminary estimates of the biomass of this functional group. In the longer term, field-based investigations are needed to determine the seasonal abundance and growth rates of epifaunal suspension feeders.**

The benthic monitoring programs of both states rely on sampling gear and field methodologies that, while generally reliable and cost effective for sampling the infauna, are not sufficient to adequately sample all species. This is especially true for those species that are patchily distributed, large and/or deep dwelling, or highly fragile. For example, a recent series of investigations (Thompson Neubauer 2000, Thompson and Schaffner 2000, Thompson and Schaffner 2001) demonstrated that the infaunal polychaete (*Chaetopterus variopedatus*) is a dominant suspension feeder of subtidal regions of lower Chesapeake Bay. New recruits and early juveniles of this species are highly fragile and adults build U-shaped tubes that can reach 20 cm or more into the sediment, with tube openings separated by as much as 30 cm. Thompson and Schaffner (2001) reported average densities of approximately 100 individuals m<sup>-2</sup> and recruitment densities of more than 1000 individuals m<sup>-2</sup> over a 53 km<sup>2</sup> study region of the lower bay between the mouth of the York River and Cape Charles. Average annual secondary productivity over a two year period (1994-95) was 26 g C m<sup>-2</sup>, with periods of rapid growth and high production during the spring through summer months. Estimates of water filtration rates for *C. variopedatus* are comparable to rates measured for bivalves, analyses of chlorophyll and lipid biomarkers in worm guts and tissues demonstrate that labile phytoplankton is an important food source for the lower bay population, and worm biodeposits are relatively organic-rich (Thompson Neubauer 2000). When the biomass of *Chaetopterus variopedatus* is taken into account, macrofaunal biomass in lower Chesapeake Bay is at the level predicted based on a regression relationship between macrofaunal biomass and primary production for shallow water ecosystems (Herman et al. 1999, Hagy 2001).

**An infaunal polychaete, *Chaetopterus variopedatus*, is the dominant suspension feeder of lower Chesapeake Bay. Future modeling efforts for the lower bay region must include this keystone species.**

**A model formulation that includes the potential for interactions among the major infaunal and epifaunal suspension-feeding groups will be necessary to simulate changing environmental conditions as increasing efforts are made to restore water quality and oyster populations to the ecosystem.**

Another group of benthic organisms completely excluded from the present benthic model is the meiofauna. This taxonomically diverse group, dominated by copepods and nematodes, is functionally important in benthic processes in other coastal ecosystems globally (Valiela 1995, Alongi 1998). We also know that they are important prey items for some of the demersal fish predators, such as spot (*Leiostomus xanthurus*). In a study of feeding habits of juvenile spot collected from the lower Chesapeake Bay mainstem between May and November 1994, Horvath (1997) found that meiofauna and small macrofauna were dominant components of the diet. In studies by Stickney et al. (Savannah River and Ossabaw Sound, GA; 1975) and Hodson et al. (Cape Fear River Estuary, NC; 1981), harpacticoid copepods were found in juvenile spot stomachs more frequently than any other prey item (88% and 70%).

**While easily overlooked, there is evidence from other systems for the likely importance of meiofauna in benthic processes, especially the diagenesis of organic matter and support of higher trophic levels. Efforts should be made to estimate the contribution of this group to benthic processes in the Chesapeake Bay ecosystem.**

### ***How can the recruitment process be represented in the model?***

In the present model, recruitment is addressed only via the maintenance of a small refuge biomass within each model grid cell, from which new growth and the production of biomass following a period of anoxia or mortality due to predation and food limitation. This formulation has significant limitations. For example, recovery in the model may be timed differently than the natural recruitment process. In addition, the refugium approach can not simulate the natural “source-sink” dynamics of recruitment processes. The question of how best to incorporate the recruitment process into the benthic model can benefit from a review of what we know regarding benthic recruitment processes in the bay.

Recruitment of macrobenthos is a seasonal process in most temperate estuaries, cued by temperature and food availability. Many of the numerically dominant species of the oligohaline and mesohaline reaches of the bay and its tributaries exhibit peak recruitment during the spring, with a second smaller peak during the fall (Diaz 1984, Holland et al. 1987). In the polyhaline, where both short-lived “estuarine opportunists” and longer-lived species commonly co-occur, various species are recruiting throughout the spring, summer and fall. The short-lived species exhibit patterns of abundance similar to those observed at lower salinities, while the longer-lived species recruit primarily during summer and fall months (Diaz 1984, Zobrist 1988, Schaffner 1990, Seitz and Schaffner 1995, Thompson and Schaffner 2001).

For the oligo- to mesohaline waters of the Maryland Bay and its tributaries, Holland et al. (1987) found that salinity, acting on recruitment processes, was the major factor determining regional and long-term abundance patterns of macrobenthos in areas not affected by hypoxia/anoxia. In general, relationships between salinity and abundance were strongest following the spring period of recruitment. Dissolved oxygen levels strongly affected patterns of abundance in deeper areas of the bay. Predation on macrobenthos by fish and crabs affected the amplitude of annual recruitment pulses. Food limitation apparently determined the magnitude of summer macrobenthic mortality. Marsh and Tenore (1990) subsequently showed that “estuarine



opportunists,” such as the amphipod *Leptocheirus plumulosus* and polychaete *Streblospio benedicti*, complete an entire production cycle on material derived from the spring bloom. Primary production derived from the initial stages of the spring bloom (which may begin in late winter) is used initially to proliferate gametes. Larvae or neonates are then released and have the potential to be transported to distant sites for subsequent growth. Longer-lived polychaetes of the polyhaline regions of the bay (e.g. *Chaetopterus variopedatus* and *Loimia medusa*) and many of the bivalve species of the bay use the spring bloom to proliferate gametes, while the development of larvae and juveniles coincides the summer period of high primary productivity (Thompson and Schaffner 2001).

Given the results discussed above, recruitment and POM deposition are seen as critical, but not necessarily directly linked, processes affecting the distribution and abundance of many macrobenthos species of the Bay and its tributaries. POM deposition from the late winter/early spring phytoplankton bloom may affect the number or quality of gametes produced by overwintering adult macrobenthos. Spring hydrodynamics and salinity are expected to strongly govern the distribution of new recruits. Thus, the composition of macrobenthic communities and their resultant functional potential are expected to be partly uncoupled from POM deposition. Subsequent growth and survival of recruits will, however, be strongly tied to the availability of POM and predation, as is presently modeled.

Possible scenarios to incorporate recruitment into the existing benthic model were discussed at the 8 January 2001 meeting between the Review Team and the Modeling Team. The Modeling Team indicated that full simulation of larval development, transport and survival imposes computational burdens that at present cannot be included in the water quality-benthos model. Given the need to reflect the types of processes discussed above, an alternative approach was discussed that would involve tracking a biomass fraction “shed” from reproductive adults as “spawn.” A portion of that biomass then “recruits” to the benthos at appropriate times/locations determined by factors simulated in the hydrodynamic and water quality models (e.g. circulation processes, salinity and temperature). As an added note, we suggest that it is appropriate to allow for growth of adult biomass (to simulate development of gametes/increases in fecundity), prior to the simulated period of spawning. This overall approach would begin to capture aspects of the source-sink dynamics that likely influence macrobenthic recruitment dynamics, especially in deeper parts of the bay where adult biomass does not accumulate due to DO stress.

**We recommend reformulating the model to allow for simulation of recruitment processes, via the shedding and subsequent recruitment of a portion of the biomass accrued by adults prior to the period of spawning.**

***Should the model add representation of age or size groups, e.g. larvae, juveniles, adults?***

High per capita growth rates characteristic of larvae and juveniles, coupled with high settlement densities, means that early life history stages can make significant contributions to overall production for many estuarine invertebrates. In a study of population dynamics and secondary production of the infaunal polychaete *Loimia medusa* in the lower York River, Seitz

and Schaffner (1995) demonstrated that rapidly growing juveniles accounted for 36% of the annual secondary productivity for this species, which has a life span of approximately one year. Thompson and Schaffner (2001) found that production in lower Chesapeake Bay by juveniles of *Chaetopterus variopedatus* accounted for 17% and 105% of total production in 1994 and 1995, respectively, representing low and high recruitment years. In a study of the spring recruitment dynamics of dominant macrobenthic invertebrates for the period 15 March to 12 June 1985, conducted at a series of stations along a depth gradient of the lower York River, Zobrist (1988) found that new recruits and juveniles dominated community abundance patterns. For the most abundant polychaetes, a suite of relatively small “estuarine opportunists” including *Asabellides oculata*, *Streblospio benedicti*, *Eteone heteropoda*, and *Mediomastus ambiseta*, 75 to 93% of the total individuals captured during the study period were retained on either 125 or 250  $\mu\text{m}$  mesh screens, with the remainder retained on 500  $\mu\text{m}$  mesh screen. In contrast, most individuals of the bivalve *Mulinia lateralis* were sufficiently large at recruitment to be captured on a 500  $\mu\text{m}$  screen. In an ongoing study of benthic recruitment dynamics of the York and Patuxent River estuaries, new recruits of the bivalves *Macoma balthica* and *Macoma mitchelli* are being retained on 125 and 250  $\mu\text{m}$  mesh screens, while larger juveniles are retained on the 500  $\mu\text{m}$  mesh screen (Schaffner and Hinchey unpublished). From recent laboratory studies we know that neonate and early juvenile *Leptocheirus plumulosus* are retained on 250  $\mu\text{m}$  mesh screen, while late stage juveniles and adult size classes are retained on 500  $\mu\text{m}$  mesh screen (Schaffner in progress).

The sampling protocols for the benthic monitoring programs of both states call for the use of a 500  $\mu\text{m}$  screen to effectively retain adult macrobenthic organisms and separate them from the sediment matrix in which they reside. Based on the available data, it is clear that this protocol results in underestimates of the abundance of most species due to loss of juvenile stages. This means that abundance and growth will likely be significantly underestimated during the spring period of heavy recruitment, and perhaps during the summer and fall.

**Efforts should be made to use existing data to estimate the potential contribution of new recruits and juveniles to macrobenthic biomass, and to determine how these size classes contribute to critical biological processes such as respiration and excretion, growth and filtration, recognizing that these effects will likely be most apparent following periods of recruitment. The results of these efforts should be used to guide future decisions regarding the need for additional sampling or a shift in the modeling approach.**

***Are there any important processes or functions missing from the model?***

***Are there any other suggested revisions to the model?***

The seasonal dynamics of benthic processes and their linkages with water column processes and predation were not emphasized in the technical report. Thus, we were unable to fully assess the seasonal aspects of model performance versus “real world” dynamics. Benthic community dynamics have been particularly well documented for the mesohaline reaches of Chesapeake Bay (Boesch et al. 1976a, 1976b, Boesch 1977, Holland 1985, Holland et al. 1987, Marsh 1988, Marsh and Tenore 1990). These investigators have shown that the period of late winter to early summer is a critically important time of benthic recruitment and production in the

oligo- and mesohaline reaches of the bay. Because it is also a time of high freshwater inputs, high nutrient loading, high standing stocks of phytoplankton, and the onset of hypoxia/anoxia, understanding temporal variations in benthic-pelagic linkages is critical.

**We recommend that a future modeling scenario include a detailed examination of temporal dynamics, especially at seasonal and interannual scales, of the mesohaline benthic communities of the bay.**

Some of our concerns regarding effects of salinity on recruitment processes have been mentioned in an earlier section. Implicit in the discussion is the idea that “biology matters” -- that individual species have preferred salinity ranges for optimal function. As presently formulated, the benthic process model does not directly parameterize salinity effects on processes such as respiration, feeding and growth. Instead, equations representing “adapted” organisms are applied for each major salinity regime. It is difficult to assess how well this approach simulates growth during periods when the salinity regime is lower or highly variable relative to “average” conditions.

**A re-consideration of how to simulate the seasonal effects of salinity on benthic processes is warranted. In particular, we need to know to what degree respiration, filtration and growth of individuals within each major salinity regime are influenced by the seasonally low or variable salinity regimes common in the upper bay and tributaries.**

Relationships between DO and benthic processes also deserve further consideration. In the current model, a single level of hypoxia tolerance is set for each major faunal group, with the suspension-feeding bivalves being considered relatively more tolerant than the deposit-feeding annelids. Our assessment is that the existing literature does not support these assumptions. Hypoxia tolerance does show broad patterns among taxonomic groups, with polychaetes, mollusks, platyhelminths and cnidarians being relatively tolerant, while crustaceans and vertebrates are considered relatively intolerant (Mangum and van Winkel 1973, Diaz and Rosenberg 1995). Nevertheless, tolerance of hypoxia can vary as much among species in a single taxonomic group as among species in different groups (McMahon and Russell 1978, Sagasti et al. 2001, Schaffner personal observation). And, there are clear differences in the ability of macrobenthos to survive when oxygen is low versus when oxygen is effectively absent and sulfides are present (Llansó 1991, Diaz and Rosenberg 1995, Sagasti et al. 2000, 2001).

The frequency and duration of hypoxia/anoxia are critical factors for the structure and function of estuarine benthic communities (Diaz and Rosenberg 1995, Sagasti et al. 2000, 2001). In the York River estuary, where hypoxia is common but anoxia is rare during the summer months, Neubauer (1993) found that there were no clear relationships between macrofauna abundance or productivity and cyclic hypoxia. He concluded that euryhaline opportunists, the dominant infauna of the region, are well adapted to tolerate the stress of the cyclic low dissolved oxygen events, which typically last a week in this region of the estuary. Similarly, Sagasti et al. (2000, 2001) documented thriving assemblages of epifauna in the same areas of the lower York and found that the most of the epifaunal species abundant during summer months tolerated hypoxic events of a week or more. Mobile benthic predators are more sensitive to hypoxic events than their relatively sessile prey species (Sagasti et al. 2001). But, large mobile predators,

such as fish and crabs, exhibit escape responses at about 2 mg L<sup>-1</sup> and may, thereby, effectively avoid areas of hypoxia/anoxia (Pihl et al. 1991, Nestlerode and Diaz 1998). Absent or rare in these areas are species intolerant of low oxygen.

Successful estuarine species must maintain high fitness despite physiological stress. They do this through behavioral, compensatory and resistance adaptations of individuals, and life history/recruitment dynamics at the population level, augmented by high growth rates fueled by high nutrient/food availability. Thus, recruitment dynamics, growth rates (as affected by hypoxia-induced stress) and predation-induced mortality interact to determine community composition (Sagasti et al. 2000, 2001). The result is complex relationships among environmental stressors and between the stressors and ecosystem function. These sorts of interactions are likely to be especially important determinants of benthic processes in the areas that fringe the deep, anoxia-prone channels, and they may also be critical in governing any eventual recovery of the deep channels should near-bottom oxygen levels increase to values approaching 2 mg L<sup>-1</sup>.

**The present model does not simulate complex interactions among critical processes such as recruitment, growth, hypoxia-induced mortality and predation-induced mortality, which are essential for understanding how benthic communities will respond to improving oxygen levels associated with bay restoration efforts. To address this issue will require incorporation of new and existing data on recruitment dynamics, hypoxia-induced effects on growth and filtration rates of individuals as balanced by high levels of food-availability, and the interactions between hypoxia and predation rates.**

***Is an individual-based model that combines the present eutrophication model with a bioenergetics model and a population model feasible?***

***By 2004, we are expected to make an assessment of the ecological effect of filter feeders on the bay. Is the present model "on track" to make this assessment?***

***What would an "ideal" model of benthos in the bay look like?***

These questions are related in the sense that they require us to make an assessment of how far the present model is from an "ideal" model of the benthos, one that would allow us to confidently simulate some or all of the highly interactive components of the bay ecosystem. In a recent article entitled *Modeling for Estuarine Synthesis*, Eileen Hofmann (2000) noted, "...Most biological models represent compromises between what is known and what can be done. However, the key issue is that models be formulated with a level of complexity that is suitable to address the scientific question being asked." With respect to the goals of the just-completed modeling effort that led to the present review, it has been stated, "The present benthic model represents a first attempt to directly couple a complex eutrophication model with a simulation of benthic biomass. The original goals were to include a dynamic suspension feeding loss term to remove algal biomass, organic detritus, and inorganic suspended solids in an ecologically relevant manner, to compute a significant food component (both bivalve and annelid biomass)

for higher trophic levels, and to simulate the impacts of hypoxia on benthic resources (Modeling Team Responses to 8 January meeting).”

Clearly, these are rather ambitious and complex objectives and the present model represents a significant effort to simulate important processes and process interactions in a highly complex and dynamic ecosystem. The present level of model complexity may not be sufficient to address some of the questions currently being asked. This does not mean, however, that we should move to an individual-based model at this point if doing so would add additional complications, and distract from the more urgent need to better represent larger-scale interactions. We recommend that the immediate goal of the Modeling Team be to improve the present model based on the recommendations made above. Some of the recommendations we have made should be relatively easily accomplished within the context of the existing model, although others may require new approaches and, perhaps, new models. In order to continue rapid progress on these challenging issues during the next phase of model development, we strongly recommend that a framework for bringing together experts in the areas of benthic ecological processes, suspension feeder bioenergetics, and modeling be maintained.

## Literature Cited

- Alongi, D. M. 1998. Coastal Ecosystem Processes. CRC Press.
- Blundon, J.A. and V. S. Kennedy. 1982. Refuges for infaunal bivalves from the blue crab, *Callinectes sapidus* (Rathbun), predation in Chesapeake Bay. *Jour. Exp. Mar. Biol. Ecol.* 65: 67-81.
- Boesch, D.F., M.L. Wass and R.W. Virnstein. 1976a. The dynamics of estuarine benthic communities. P. 176-196 in M. Wiley (ed.), *Estuarine Processes*, Vol. I., Academic Press.
- Boesch, D.F., R.J. Diaz and R.W. Virnstein. 1976b. Effects of tropical storm Agnes on soft-bottom macrobenthic communities of the James and York estuaries and the lower Chesapeake Bay. *Ches. Sci.* 17: 246-259.
- Boesch, D. F. 1977. A new look at the zonation of benthos along the estuarine gradient, p. 245-266. In B. C. Coull (ed.). *Ecology of Marine Benthos*. University of South Carolina Press, Columbia.
- Dauer, D.M., G. Tourtellotte and R. Ewing. 1982a. Oyster shells and artificial worm tubes: the role of refuges in structuring benthic communities of the lower Chesapeake Bay. *Int. Revue ges. Hydrobiol.* 67: 661-677.
- Dauer, D.M., R. Ewing, G. Tourtellotte and W. Harlan. 1982b. Predation, resource limitation and the structure of benthic infaunal communities of the Lower Chesapeake Bay. *Int. Revue ges. Hydrobiol.* 67: 477-489.
- Diaz, R.J. 1984. Short term dynamics of the dominant annelids in a polyhaline temperate estuary. *Hydrobiologia* 115: 153-158.
- Diaz, R. J. and R. Rosenberg. 1995. Marine benthic hypoxia: a review of its ecological effects and the behavioural responses of benthic macrofauna. *Oceanography and Marine Biology Annual Review* 33:245-303.
- Diaz, R. J. and L. C. Schaffner. 1990. The functional role of estuarine benthos, p. 25-56. In M. Haire and E. C. Krome (eds.), *Perspectives on the Chesapeake Bay, 1990. Advances in Estuarine Sciences*. Chesapeake Research Consortium, Gloucester Point, Virginia. Rpt. No. CBP/TRS41/90.
- Fredette, T.J. and R.J. Diaz. 1986. Secondary production of *Gammarus mucronatus* Say (Amphipoda:Gammaridae) in warm, temperate estuarine habitats, York River, Virginia. *J. Crustacean Biol.* 6: 729-741.
- Hagy, J. 2001. Patterns of macrobenthic biomass and community bioenergetics in Chesapeake Bay during summer in relation to habitat quality and organic carbon supply. Chapter 4 of Dissertation, University of Maryland, Center for Environmental Studies.
- Herman, P.M.J., J.J. Middelburg, J. Van De Koppel and C.H.R. Heip. 1999. Ecology of estuarine macrobenthos. *Advances in Ecological Research* 29: 195-240.
- Hodson, R.G., J.O. Hackman and C.R. Bennett. 1981. Food habits of young spot in nursery areas of the Cape Fear River estuary, North Carolina. *Trans. Amer. Fish. Soc.* 110: 495-501.
- Hofmann, E.H. 2000. Modeling for estuarine synthesis. p. 129-148 in J. E. Hobbie (ed.) *Estuarine Science, A Synthetic Approach to Research and Practice*. Island Press.
- Holland, A.F. 1985. Long-term variation of macrobenthos in a mesohaline region of Chesapeake Bay. *Estuaries* 8: 93-113.

- Holland, A.F., A.T. Shaughnessy and M.H. Hiegel. 1987. Long-term variation in mesohaline Chesapeake Bay macrobenthos: spatial and temporal patterns. *Estuaries* 10: 227-245.
- Holland, A.F., A.T. Shaughnessy, L.C. Scott, V.A. Dickens, J.A. Ranasinghe and J.K. Summers. 1988. Progress Report: Long-term benthic monitoring and assessment program for the Maryland Portion of Chesapeake Bay (July 1986 – October 1987). Maryland Power Plant Research Program, PPRP-LTB/EST-88-1.
- Horvath, M. A. 1997. Effects of spot (*Leiostomus xanthurus*) induced bioturbation and suspension on the transport and fate of sediments and a particle-associated organic contaminant. M.S. thesis, School of Marine Science, College of William and Mary, Gloucester Point, VA.
- Llansó, R. J. 1991. Tolerance of low dissolved oxygen and hydrogen sulfide by the polychaete *Streblospio benedicti* (Webster). *Jour. Exp. Mar. Biol. Ecol.* 153: 165-178.
- Lipcius, R.N. and A.H. Hines. 1986. Variable functional responses of a marine predator in dissimilar homogeneous microhabitats. *Ecology* 67: 1361-1371.
- Mangum, C.P. and W. van Winkle. 1973. Responses of aquatic invertebrates to declining oxygen conditions. *Am. Zool.* 13: 529-541.
- Marsh, A.G. 1988. Seasonal dynamics of a mesohaline, soft-bottom, benthic community: secondary production, sedimentation, predation and nutrition. Ph.D. dissertation, University of Maryland.
- Marsh, A.G. and K.R. Tenore. 1990. The role of nutrition in regulating the population dynamics of opportunistic surface deposit feeders in a mesohaline community. *Limnol. Oceanogr.* 35: 710-724.
- Nestlerode, J.A. and R.J. Diaz. 1998. Effects of periodic environmental hypoxia on predation of a tethered polychaete, *Glycera americana*: implications for trophic dynamics. *Mar. Ecol. Prog. Ser.* 172: 185-195.
- McMahon, R.F. and W.D. Russell-Hunter. 1978. Respiratory responses to low oxygen stress in marine littoral and sublittoral snails. *Physiol. Zool.* 51: 408-424.
- Neubauer, R.J. 1993. The relationship between dominant macrobenthos and cyclical hypoxia in the lower York River. M.S. thesis, School of Marine Science, College of William and Mary, Gloucester Point, VA.
- Pihl, L., S. P. Baden, R. J. Diaz. 1991. Effects of periodic hypoxia on distribution of demersal fish and crustaceans. *Marine Biology* 108:349-360.
- Sagasti, A., L. C. Schaffner and J. E. Duffy. 2000. Epifaunal communities thrive in an estuary with hypoxic episodes. *Estuaries* 23: 474-488
- Sagasti, A., L. C. Schaffner and J. E. Duffy. 2001. Effects of periodic hypoxia on mortality, feeding and predation in an estuarine epifaunal community. *Journal of Experimental Marine Biology and Ecology* 258: 257-283.
- Schaffner, L. C. 1990. Small-scale organism distributions and patterns of species diversity: evidence for positive interactions in an estuarine benthic community. *Marine Ecology Progress Series* 61:107-117.

- Schaffner, L. C. and R. J. Diaz. 1988. Abundance and distribution patterns of the blue crab, *Callinectes sapidus*, in the lower Chesapeake Bay during the winter 1985-86. *Estuaries* 1:68-72.
- Schaffner, L. C., T. M. Dellapenna, E. K. Hinchey, C. T. Friedrichs, M. L. Thompson, M. E. Smith, and S. A. Kuehl. 2001. Physical energy regimes, sea-bed dynamics and organism-sediment interactions along an estuarine gradient. In J.Y. Aller, S.A. Woodin, and R.C. Aller (eds.), *Organism-sediment interactions*. pp 159-181 University of South Carolina Press.
- Seitz, R.D. 1996. The role of epibenthic predators in structuring marine soft-bottom communities along an estuarine gradient. Ph.D. dissertation, School of Marine Science, The College of William and Mary, Gloucester Point, VA.
- Seitz, R. D. and L. C. Schaffner. 1995. Population ecology and secondary production of the polychaete *Loimia medusa* (Terebellidae). *Mar. Biol.* 121: 701-711.
- Stickney, R.R., G. L. Taylor and D.B. White. 1975. Food habits of five species of young southeastern United State estuarine Sciaenidae. *Ches. Sci.* 16: 104-114.
- Thompson Neubauer, M. L. 2000. Demographics, production and benthic-pelagic coupling by the suspension feeding polychaete *Chaetopterus pergamentaceus* in the lower Chesapeake Bay. Ph.D. dissertation, School of Marine Science, The College of William and Mary, Gloucester Point, VA.
- Thompson, M. L. and L. C. Schaffner. 2000. Local demographics of the polychaete *Chaetopterus pergamentaceus* within the lower Chesapeake Bay and relationships to environmental gradients. *Bull. Mar. Sci.* 67: 209-219.
- Thompson, M. L. and L. C. Schaffner. 2001. Population biology and secondary production of the suspension feeding polychaete *Chaetopterus cf. variopedatus*: implications for benthic-pelagic coupling in lower Chesapeake Bay. *Limnology and Oceanography* 46: 1899-1907.
- Valiela, I. 1995. *Marine Ecological Processes*, Springer.
- Wright, L. D., D. B. Prior, C. H. Hobbs, R. J. Byrne, J. D. Boon, L. C. Schaffner, and M. O. Green. 1987. Spatial variability of bottom types in the Lower Chesapeake Bay and adjoining estuaries and inner shelf. *Estuarine, Coastal and Shelf Science* 24:765-784.
- Wright, L. D., L. C. Schaffner, and J. P.-Y. Maa. 1997. Biological mediation of bottom boundary layer processes and sediment suspension in the lower Chesapeake Bay. *Marine Geology* 141:27-50.
- Zobrist, E.C. 1988. The influence of post-settlement mortality on recruitment patterns in a soft-bottom habitat. M.S. thesis, School of Marine Science, College of William and Mary, Gloucester Point, VA.



## Appendix A.

### Benthic Model Review Team Questions and Comments on the Draft Technical Report

The Benthic Process Model review team (Dauer, Friedrichs, Schaffner - chair) met at ODU on December 11, 2000. Prior to this meeting each member of the group reviewed the document entitled "Development of a suspension feeding and deposit feeding model for Chesapeake Bay", U. S. Army Corps of Engineers, Project No. USCE0410, July 2000. Below is a summary of issues/questions raised at this meeting:

#### Groups modeled:

1. What percentage of total infaunal biomass is captured by the two functional groups modeled (deposit feeding annelids/polychaetes, suspension feeding bivalves) for the various segments modeled?
2. Based on available data, what percentage of suspension feeding biomass is likely to be infaunal versus epifaunal? Does it matter that epifauna such as *Molgula manhattensis* are not included in data sets used for the present model?
3. What are the implications of excluding suspension feeder groups characterized by somewhat lower biomass (relative to bivalves), but high production (high P/B) – e.g. the amphipod *Leptocheirus plumulosus*, which is abundant in the oligohaline?
4. What percentage of production is linked to new recruits and juveniles that typically pass through a 500  $\mu\text{m}$  screen?

#### Dissolved Oxygen:

1. Why don't the available data show a relationship between DO and biomass?
2. Based on the literature, what are the expected relationships between environmental DO levels and hypoxia tolerance for macrofauna?
3. As mortality due to DO increases, does the suspension feeding model simulate a "shrinking" of individuals due to the relationship between total biomass and individual size? In reality, aren't large individuals generally the most resistant to DO stress? How does this shrinking of individuals affect model outputs?

**Predation:**

1. Why is predation modeled as a quadratic function? Is this approach supported by the literature on predation effects on benthic macrofauna abundance/biomass? The quadratic approach seems to make predation an ad-hoc catch-all to keep the model stable under conditions of high production. As a result, the model predicts a lowest-order balance between growth and predation much of the time. Is this appropriate?
2. What was the calibration process used to determine species-specific rates of predation?
3. How do predation and growth phase with respect to temperature dependency? Plotting up graphs with single annual cycles (rather than long time series) would make it possible to delineate these relationships.

**Respiration:**

1. Don't some groups of inverts enhance their irrigation/filtration rates (to increase flux of O<sub>2</sub>) in mild hypoxia before shutting down?
2. Why does r<sub>20</sub> change by an order of magnitude from tidal freshwater to oligohaline/mesohaline?

**Sensitivity analyses:**

1. Have you done a sensitivity analysis? For example, the model seems to be extremely sensitive to range of values applied for the parameter  $\beta_{20}$ .
2. What about an inverse analysis approach? In other words, have you experimented to see what parameter values would be needed to force the model to match the data better?

**Stations used for modeling:**

1. How do the estimates of biomass for various segments change for fixed versus probability-based sampling strategies? e.g. fixed stations are channel only in VA, non-channel in MD.
2. Should the probability-based estimates of biomass be included in the model?

### **Suspension Feeder Model:**

1. Why do data values “line up” in figures such as 3-4, 3-5 and 3-6?
2. Are the derived biomass/abundance and individual weight/total biomass relationships influenced by the original methods used to obtain biomass (conversions rather than actual weights for MD data set)?
3. Why did you “recast” the turbidity function of Powell?
4. Particle filtration is not 100% efficient, so why assume that it is?
5. How do you know that suspension feeders don’t impact/utilize zooplankton biomass?
6. What are the three algal groups modeled? What is basis for assuming an 80% assimilation efficiency for algal C?
7. Why does  $\beta_{20}$  change by two orders of magnitude from tidal freshwater to oligohaline/mesohaline for suspension feeders? e.g. low  $\beta$  in TFW leads to high biomass, higher  $\beta$  in MH leads to lower biomass.

### **Deposit Feeder Model**

1. Is the Thomann (1994) reference available?
2. What references support the assumption that individual feeding rate decreases with increasing sediment organic carbon?
3. What is basis for the base predation rate used in model? Predation rate is high and, as a result, it generally balances growth. Is this realistic?
4. What is basis for the carbon assimilation efficiencies used in model?

### **General issues and questions:**

- 1) Based on the published literature on the Chesapeake Bay ecosystem and other estuaries/coastal systems:
  - a) What major factors control community composition of macrofauna?

- b) How important is the recruitment process expected to be for determining subsequent patterns of species composition, abundance and biomass? What major factors control recruitment?
  - c) Does the relative importance of food limitation vs. predation vs. DO change along the salinity gradient ?
  - d) Are there other important factors/processes that are expected to limit composition and productivity?
- 2) How is the benthos model likely to be influenced by the underestimate of production in the water column component of the model?
  - 3) Is there a POM resuspension component in the model?
  - 4) Does the model capture the spring “bloom” and subsequent early summer “bust” of deposit feeding annelids (which is known to occur prior to significant predation and in absence of DO stress) in the mesohaline reaches of the bay?
  - 5) How does the formulation of this model compare with other modeling approaches being used? What is the history of the model’s development?

**General editorial comments:**

1. The report needs to be proof-read. There are numerous inconsistencies, particularly with respect to station names/locations in text versus figures.
2. Did you model annelids or polychaetes (changes through text)?
3. It is assumed that the reader is very familiar with other components of the bay model.
4. The derivations of some model components are explained in great detail (e.g. filtration model), while other aspects are barely explained. Assumptions are made without citing appropriate references and there is little discussion of other models from which derivations may have been drawn.
5. A number of figures have symbols that are not explained in the caption or accompanying text.
6. Long time series plots make it difficult to assess temporal phasing of variables over annual time scales.
7. Plots of biomass vs DO for each functional group or major species would make it easier to visualize relationships or lack thereof.

## **Appendix B.**

### **Benthic Modeling Team Response to Benthic Processes Review Team Questions**

Meeting of January 8, 2001

Attending: Lewis Linker/EPA, Carl Cerco/USACE-WES, Linda Schaffner/VIMS, Dominic Di Toro/HydroQual, Mark Meyers/HydroQual

#### **Introduction**

The Benthic Processes Review Team was assembled by the Modeling Subcommittee to review the present benthic model developed for the Chesapeake Bay Water Quality Model, a component of Chesapeake Bay Estuary Modeling Package. The Review Team was further charged with determining the directions in benthic modeling that will be needed in order to satisfy the goals and objectives stated in the Chesapeake 2000 Agreement. The first action item for the team was to review the report, "Development of a Suspension Feeding and Deposit Feeding Benthos Model for Chesapeake Bay", with some guiding questions provided by the Modeling Subcommittee (Attachment A).

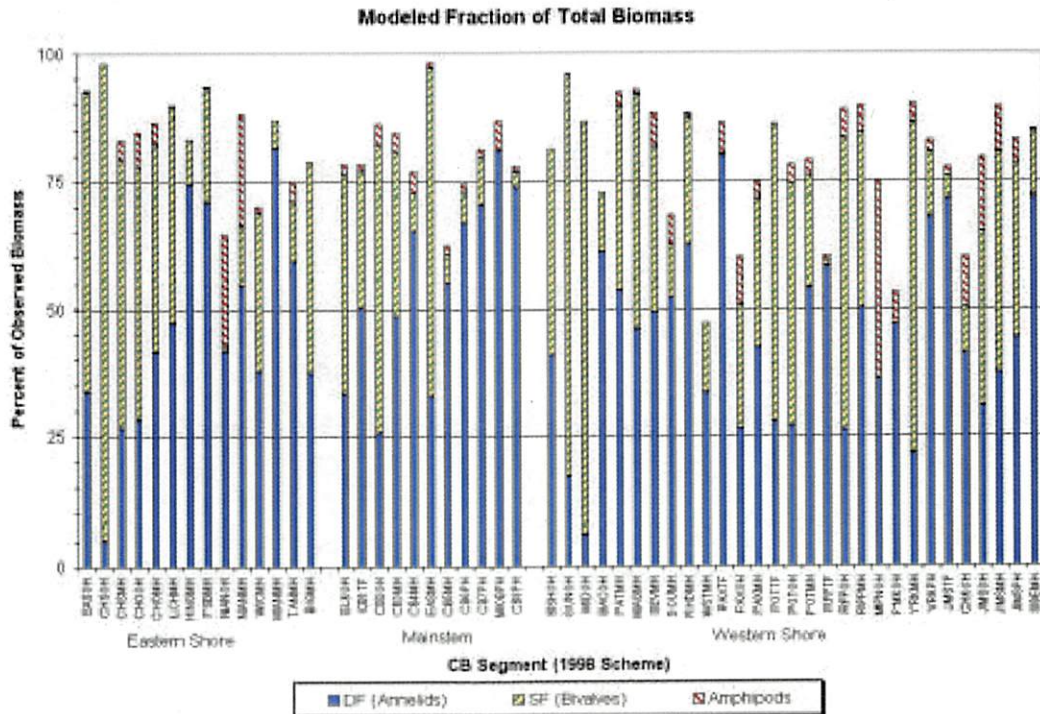
The Review Team consists of Linda Schaffner (Virginia Institute of Marine Science), Carl Friedrichs (VIMS), and Dan Dauer (Old Dominion University). After individually reviewing the report, the team met on December 11, 2000 to draft comments (Attachment B).

The present meeting reviewed these comments and further discussed the present modeling framework. Questions and comments identified in the team's initial meeting were reviewed. The team will present its final comments at the April 2001 Modeling Subcommittee Quarterly Review Meeting.

#### **Specific Issues Discussed**

##### **Groups Modeled**

The original benthos model report (HydroQual, 2000) did not discuss the percentage of total observed benthic biomass as seen in the Benthic Monitoring Program database that is reflected in the modeled deposit-feeding and suspension feeding groups. The present benthic biomass model simulates two functional groups: deposit-feeding annelid worms and suspension-feeding bivalves. Based on an analysis of the observed biomass data from 14 years of benthic monitoring (see Appendix A), these two groups combine, on average, to account for 76% percent of the total baywide benthic biomass (Figure 1). This percentage of biomass is consistent across regions of the bay: averaging 79, 78, and 74%, for Eastern Shore, Mainstem, and Western Shore segments, respectively (Figure 1). Also, as stated in the benthos Model report (HydroQual, 2000), bivalves tended to dominate the benthic fauna in the northern portion of the bay, while



**Figure 1.** Dominant groups contributing to total observed benthic biomass. Deposit-feeding (DF) annelids and suspension-feeding (SF) bivalves are represented in the Chesapeake Bay benthic model. Data are shown by Chesapeake Bay Program Segment (1998) designation, as averages from the Benthic Monitoring Program for the period 1984-1997. deposit-feeding annelids dominate in the southern, mesohaline to polyhaline portion of the bay (Figure 1).

The present model did not attempt to simulate suspension feeding epibenthic amphipods (*Leptocheirus* in fresh to oligohaline waters; *Gammarus* in meso- to polyhaline waters). According to the Benthic Review Team, these organisms are reasonably well-sampled in the Benthic Monitoring Program. They have high production to biomass ratios (P:B), suggesting that they may process significant amounts of organic matter. A review of the Benthic Monitoring Program database showed that approximately 7.5% (301 of 4026) of the cores containing amphipods with measured biomass had values of  $> 1.0 \text{ g AFDW m}^{-2}$ . The maximum observed amphipod biomass was  $12.0 \text{ g AFDW m}^{-2}$  at station LE4.1 (the lower York River) in March 1987. In this particular core, the total biomass of  $41.6 \text{ g AFDW m}^{-2}$  was distributed as follows: suspension feeding bivalves, 24%; deposit feeding annelids, 6.8%; amphipods, 29%; other, 40%. Other individual cores with high values ( $> 4 \text{ g AFDW m}^{-2}$ ) were found in the James, Potomac, Patuxent, and Choptank Rivers, as well as in Baltimore Harbor and in the northern

Mainstem Bay near Poole's Island. Averaged over time, amphipods comprise a significant component of the biomass in certain oligohaline habitats (Figure 1; Nanticoke, Patuxent, Mattaponi, York, Chickahominy, and James Rivers). However, averaged over time and space, amphipods represented less than 5% of baywide benthic biomass. This should not discount, however, the impact on algal production and biomass that amphipods might exert on local spatial and seasonal temporal scales.

Similarly, the present model did not explicitly model suspension feeding polychaete worms. According to the Benthic Review Team, the polychaete *Chaetopterus* is a dominant suspension feeding in the lower (Virginian) mainstem of Chesapeake Bay, reaching biomass levels of 10-30 g AFDW m<sup>-2</sup>. Assimilation efficiency of TSS (organic+inorganic) is ca. 25%. Based on estimates of its productivity, it may require 30-100% of the lower bay's primary production. Based on lipid bio-marker studies, 33-50% of its diet should be fresh algal biomass.

While the model did not simulate a suspension feeding worm, the suspension feeding bivalve component was active in the lower bay. Under Base Case water quality model conditions, the model over-simulated suspension feeding biomass (as bivalves), but under-simulated deposit-feeding annelid biomass. While this mis-calibration may suggest a fundamental problem with the benthos submodel, the under-estimation of deposit-feeding annelid biomass may also be associated with estimates of water column primary production provided by the water quality model that drive the benthos submodel. At the present time, the water quality model is undergoing revisions with respect to its computation and calibration of primary production. After these revisions are completed, the flux of organic matter to the lower bay bottom and its consumption by benthic fauna will have to be re-examined.

Another aspect of benthic ecology pointed out by the Benthic Review Team is the role of epibenthic suspension feeders. These organisms, such as hydroids and tunicates (e.g., *Mogula*), are poorly sampled by the Benthic Monitoring Program, but may be significant processors of organic matter (with high filtration rates and high biomass turnover). Total epibenthic biomass can reach 6 g DW m<sup>-2</sup>. Hydroid reefs attract additional suspension feeding epifauna, such as amphipods and bryozoans. Biomass is maintained through winter months, suggesting that this component can make rapid use of late winter-early spring algal blooms. Typical hard-substrate-associated fauna such as *Mogula* may be abundant in otherwise soft bottoms by attaching to sea fragments. However, patchiness of epifauna greatly exceeds that of infauna, confounding estimates of relative importance, the ability to adequately assess biomass and trends, or the ability to model the effects of such organisms.

The present benthic model has a very generalized ecological structure, dividing the fauna into a deposit feeding worm and a suspension feeding bivalve. The latter was further refined into three dominant species, so that the individual size dependence on filtration and other physiological rates could be captured with some fidelity. Based on the analysis of benthic biomass, this framework appears to be applicable across much of the bay. However, it may not accommodate specific regions of the bay where other benthic fauna and ecological processes

may be dominant. If there is significant benthic biomass in these locations that is not reflected in the simulation of deposit-feeding annelids and suspension feeding bivalves, then the fate of primary production that passes through the benthic food chain will be underestimated, again in these specific locations. If epibenthic suspension feeding activity is strong during the late winter-early spring algal bloom and if a significant fraction of winter spring algal biomass is removed by the benthos, then the model may not resolve well the spatial and temporal flux of particulate matter to the bottom in locations where epibenthos are abundant. The significance of as-yet unmodeled benthic fauna for both water quality and living resource issues and to what extent the present model structure can be parameterized to incorporate such unresolved benthic processes are important open questions for both modelers and the benthic experts.

### **Recruitment**

Recruitment is addressed in the present model only as the maintenance of a small refuge biomass within each model grid cell, from which new production and biomass accrue following a period of anoxia. There are no other seasonally signals or exogenous inputs.

Benthic recruitment is seasonal and salinity cued. Recruitment success is in part determined by larval survival and hydrology (affecting short-term salinity and food). Adult biomass varies with spawning. As a simple step to address recruitment, it may be possible to track biomass shed from reproductive adults as spawn, and deposit a fraction of that biomass at appropriate times and locations triggered by factors simulated in the hydrodynamic and water quality models. Full simulation of larval development, transport, and survival imposes a computational burden that at present cannot be included in the water quality-benthos model.

### **Predation**

In its simplest terms, the benthic model (for either deposit or suspension feeders) reflects net growth (assimilation minus respiration) and predation loss (neglecting for the moment hypoxic mortality):

$$\frac{dM}{dt} = \mu M - \beta M^2 \quad (1)$$

where  $M$  is the benthic biomass,  $\mu$  is the net specific growth rate, and  $\beta$  is the mortality rate. The second term on the right hand side is a quadratic closure term representing predation. Of course, the biomass of the predator is not modeled here. It is assumed, however, that predator biomass is linearly related to prey biomass, through the parameter  $\beta$ . This function is desirable mathematically, because it becomes dominant, relative to the net growth term, at high biomass, so that the prey or benthic biomass cannot grow excessively large.

This formulation is satisfactory where both predator and prey have similar time scales of population increase. However, in the case of invertebrate prey, with high intrinsic growth rates,



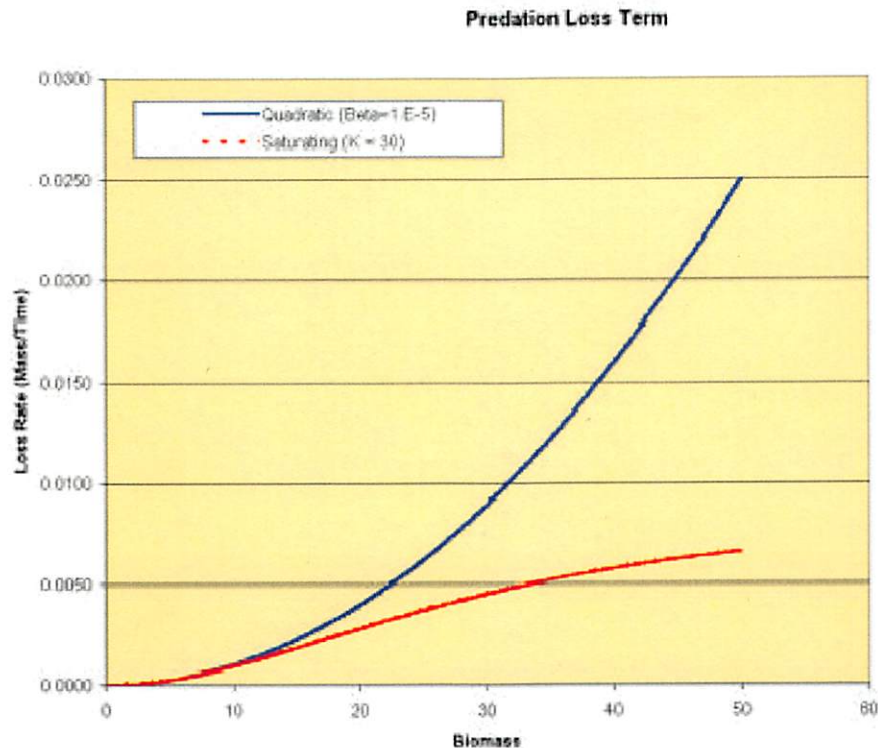
and the potential for multiple spawns and recruitment events per year versus invertebrate or vertebrate predators (crabs and fish) with slower growth rates and single annual recruitment events, there is no room for saturation of the predation function. A modified formulation of the predation term was discussed, which could be tested in the present model framework:

$$\text{Predation } (M) = -\beta \frac{K_m^2}{(K_m^2 - M^2)} M^2 \quad (2)$$

with a new parameter  $K_m$ , in units of benthic biomass which reflects saturation of predation at a specified level of prey biomass. At high benthic (prey) biomass,  $M^2 \gg K_m^2$  and the entire term simplifies to  $-\beta$ . This states that at large prey biomass, predation rate becomes independent of prey concentration (the rate is said to be “zeroth order”). Both functions are graphed in Figure 2.

## Conclusions

The present benthic model represents a first attempt to directly couple a complex eutrophication model with a simulation of benthic biomass. The original goals were to include a



**Figure 2.** Predation loss terms, showing the quadratic relationship used in the present model and a modified, saturating function for simulating saturation of predation loss.

dynamic suspension feeding loss term to remove algal biomass, organic detritus, and inorganic suspended solids in an ecologically relevant manner, to compute a significant food component (both bivalve and annelid biomass) for higher trophic levels, and to simulate the impacts of hypoxia on benthic resources. The model was developed to be as generic as possible with few regionally-specified parameters or processes.

The two groups, deposit feeding annelids and suspension feeding bivalves, included in the simulation comprise approximately 75% of the total observed benthic biomass in Chesapeake Bay and its tributaries. In certain regions, significant contributions to benthic biomass by other groups, notably amphipods, important in trophic interactions may be missed.

The model does not address other potentially significant benthic suspension feeders, such as epibenthic hydroids and tunicates. However, patchiness of the epibenthos is even more severe than that of the infauna presently documented by the long-term Benthic Monitoring Program. Assessing the relative functional roles and trophic importance of these epibenthic suspension feeders will require further consultations between the modelers and the benthic ecology experts.

The predation loss functions in the present model are very general, varying only with temperature, prey biomass, and dissolved oxygen concentration. Modification of the loss function as suggested above and inclusion of other factors (e.g., regional-specific parameters, salinity-based functions, or more specific seasonality) may be needed.

Similarly, the present model has no ecologically relevant recruitment function. Elaboration of recruitment for the presently modeled functional groups may aid in improving the spatial and temporal predictions of benthic biomass. Again, further guidance from benthic ecology experts will be needed to adequately address this.

The present water quality model is undergoing changes with respect to its simulation of primary production. Once those changes are reasonably completed, a new look at the couplings of primary production, organic matter flux to the benthos, and the utilization of that organic matter by the benthos should be undertaken to further define the present model's successes and weaknesses.

**Attachment A of Appendix B**  
**Analysis of Benthic Biomass from the Chesapeake Bay Benthic Monitoring Program**  
**(BENTHIC MONITORING PROGRAM) Database**

A copy of the BENTHIC MONITORING PROGRAM database was obtained from Jaqueline Johnson, the Living Resources Data Manager at the USEPA Chesapeake Bay Program Office (410-267-5729). This is a relational database stored in Microsoft Access (v. 97). The transmitted database file was dated August 30, 1999. This version contained several historical data sets as well as BENTHIC MONITORING PROGRAM data through 1998. For the present analysis, only BENTHIC MONITORING PROGRAM data were used, spanning the years 1984-1997. The 1998 BENTHIC MONITORING PROGRAM were not used because individual stations were not assigned to Chesapeake Bay Program monitoring segments (using the latest 1998 version of the segmentation scheme). The segmentation scheme divides the mainstem and individual embayments and tributaries into ecologically relevant salinity zones (tidal fresh, oligohaline, mesohaline, and polyhaline zones) and was found to be useful in summarizing patterns in the benthos. The BENTHIC MONITORING PROGRAM database also contains strata information for the randomized station design portion of the program. However, this stratification of the individual stations tends to aggregate many of the stations on much larger spatial scales, crossing relevant salinity zones that would be useful in discerning zonation of benthic fauna.

In the database, benthic biomass is listed for each core by the smallest practical taxonomic level. Biomass is recorded as grams ash-free dry weight (g AFDW) per core. The database contains gear size and conversion factor information for each core so that these values can be expressed on a per-square-meter basis. While all species are referenced using a standard Interagency Taxonomic Identification (ITIS) taxonomic serial number (TSN), these identifiers are also cross-referenced to the older National Oceanographic Data Center (NODC) hierarchical taxonomic codes. The NODC codes were used in this analysis to aggregate data to higher taxonomic levels, such as Bivalvia, Annelida, and Amphipoda. In addition, a Feeding Guild table is included in the database which assigns feeding designations (e.g., Suspension, Deep Deposit, Interface) to dominate taxa and groups (see Weisberg et. al., 1997). For this data analysis, "deposit feeding" annelids were considered to be all annelids not designated as suspension feeders, thus lumping together deep deposit, interface, omnivore/carnivore, and unassigned categories. Likewise, "suspension feeding" bivalves were considered to include designated suspension as well as interface feeders (a dominant bivalve, *Macoma baltica* has been observed to switch between interfacial and suspension feeding modes).

Total biomass as well as the biomass of desired groups of benthic fauna were determined for each core where there was measured biomass. Fractions of total biomass represented by categories of benthic fauna were also computed per core. Biomass and biomass fractions were averaged by station and date (a unique sampling event); some stations had replicate cores, others had only one core, depending on the particular sampling program. Further averaging was then performed over the period of interest (1984-1997) and with respect to the 1998 Chesapeake Bay

Monitoring Program Segmentation Scheme (Table 1). For some sampling events, biomass was estimated based on individual taxonomic morphometrics (e.g., length-weight, polychaete head-width versus length). These values were not used in the present analysis; only those biomass records which were flagged as "actual", meaning truly weighed, were used. In this way, variability in biomass within individual taxonomic groups as a result of uncertainties in regression relationships or morphometric measurements, did not confound the present analysis of functional group versus total benthic biomass.

<b>Table 1. Chesapeake Bay Program Segmentation Scheme (1998).</b>	
<b>CBSEG_1998</b>	<b>DESCRIPTION</b>
APPTF	APPOMATTOX RIVER-TIDAL FRESH REGION
BACOH	BACK RIVER-OLIGOHALINE REGION
BIGMH	BIG ANNEMESSEX RIVER-MESOHALINE REGION
BOHOH	BOHEMIA RIVER-OLIGOHALINE REGION
BSHOH	BUSH RIVER-OLIGOHALINE REGION
C&DOH	C&D CANAL-OLIGOHALINE REGION
CB1TF	CHESAPEAKE BAY-TIDAL FRESH REGION
CB2OH	CHESAPEAKE BAY-OLIGOHALINE REGION
CB3MH	CHESAPEAKE BAY-MESOHALINE REGION
CB4MH	CHESAPEAKE BAY-MESOHALINE REGION
CB5MH	CHESAPEAKE BAY-MESOHALINE REGION
CB6PH	CHESAPEAKE BAY-POLYHALINE REGION
CB7PH	CHESAPEAKE BAY-POLYHALINE REGION
CB8PH	CHESAPEAKE BAY-POLYHALINE REGION
CHKOH	CHICKAHOMINY RIVER-OLIGOHALINE REGION
CHOMH1	CHOPTANK RIVER-MESOHALINE REGION 1
CHOMH2	CHOPTANK RIVER-MESOHALINE REGION 2
CHOOH	CHOPTANK RIVER-OLIGOHALINE REGION
CHOTF	CHOPTANK RIVER-TIDAL FRESH REGION
CHSMH	CHESTER RIVER-MESOHALINE REGION
CHSOH	CHESTER RIVER-OLIGOHALINE REGION

CHSTF	CHESTER RIVER-TIDAL FRESH REGION
CRMH	CORROTOMAN RIVER-MESOHALINE REGION
EASMH	EASTERN BAY-MESOHALINE REGION
EBMH	EAST BRANCH ELIZABETH RIVER-MESOHALINE REGION
ELMH	ELIZABETH RIVER-MESOHALINE REGION
ELPH	ELIZABETH RIVER-POLYHALINE REGION
ELKH	ELK RIVER-OLIGOHALINE REGION
FSBMH	FISHING BAY-MESOHALINE REGION
GUNOH	GUNPOWDER RIVER-OLIGOHALINE REGION
HNGMH	HONGA RIVER-MESOHALINE REGION
JMSMH	JAMES RIVER-MESOHALINE REGION
JMSOH	JAMES RIVER-OLIGOHALINE REGION
JMSPH	JAMES RIVER-POLYHALINE REGION
JMSTF	JAMES RIVER-TIDAL FRESH REGION
LAFMH	LAFAYETTE RIVER-MESOHALINE REGION
LCHMH	LITTLE CHOFTANK RIVER-MESOHALINE REGION
LYNPH	LYNNHAVEN RIVER-POLYHALINE REGION
MAGMH	MAGOTHY RIVER-MESOHALINE REGION
MANMH	MANOKIN RIVER-MESOHALINE REGION
MATTF	MATTAWOMAN CREEK-TIDAL FRESH REGION
MIDOH	MIDDLE RIVER-OLIGOHALINE REGION
MOBPH	MOBIACK BAY-POLYHALINE REGION
MPNOH	MATTAPONI RIVER-OLIGOHALINE REGION
MPNTF	MATTAPONI RIVER-TIDAL FRESH REGION
NANMH	NANTCOKE RIVER-MESOHALINE REGION
NANOH	NANTCOKE RIVER-OLIGOHALINE REGION
NANTF	NANTCOKE RIVER-TIDAL FRESH REGION
NORTF	NORTHEAST RIVER-TIDAL FRESH REGION

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PATMH	PATAPSCO RIVER-MESOHALINE REGION
PAXMH	PATUXENT RIVER-MESOHALINE REGION
PAXOH	PATUXENT RIVER-OLIGOHALINE REGION
PAXTF	PATUXENT RIVER-TIDAL FRESH REGION
PIAMH	PIANKATANK RIVER-MESOHALINE REGION
PISTF	PISCATAWAY CREEK-TIDAL FRESH REGION
PMKOH	PAMUNKEY RIVER-OLIGOHALINE REGION
PMKTF	PAMUNKEY RIVER-TIDAL FRESH REGION
POCMH	POCOMOKE RIVER-MESOHALINE REGION
POCOH	POCOMOKE RIVER-OLIGOHALINE REGION
POCTF	POCOMOKE RIVER-TIDAL FRESH REGION
POTMH	POTOMAC RIVER-MESOHALINE REGION
POTOH	POTOMAC RIVER-OLIGOHALINE REGION
POTTF	POTOMAC RIVER-TIDAL FRESH REGION
RHDMH	RHODE RIVER-MESOHALINE REGION
RPPMH	RAPPAHANNOCK RIVER-MESOHALINE REGION
RPPOH	RAPPAHANNOCK RIVER-OLIGOHALINE REGION
RPPTF	RAPPAHANNOCK RIVER-TIDAL FRESH REGION
SASOH	SASSAFRAS RIVER-OLIGOHALINE REGION
SBEHM	SOUTH BRANCH ELIZABETH RIVER-MESOHALINE REGION
SEVMH	SEVERN RIVER-MESOHALINE REGION
SOMMH	SOUTH RIVER-MESOHALINE REGION
TANMH	TANGIER SOUND-MESOHALINE REGION
WBEMH	WEST BRANCH ELIZABETH RIVER-MESOHALINE REGION
WBRTF	WESTERN BRANCH-TIDAL FRESH REGION
WICMH	WICOMICO RIVER-MESOHALINE REGION
WSTMH	WEST RIVER-MESOHALINE REGION
YRKMH	YORK RIVER-MESOHALINE REGION

Appendix B

Appendix B

YORK RIVER-POLYHALINE REGION	YRKPH
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