ABSTRACT

Title of Dissertation: EUTROPHICATION, HYPOXIA AND TROPHIC TRANSFER EFFICIENCY IN CHESAPEAKE BAY

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Coastal eutrophication is a global problem that has contributed to loss of estuarine habitats and potentially decreased fisheries production. Hypoxia is often observed in eutrophic estuaries where it can be an important cause of habitat loss. This study utilized a suite of empirical analyses to examine key linkages relating coastal eutrophication to hypoxia, trophic structure, and trophic transfer efficiency in Chesapeake Bay (CB), USA. A salt- and water-balance model, or "box" model, was developed to quantify large-scale physical transport for CB, an input to many subsequent analyses. Historical (1950-1999) dissolved oxygen (DO) data for CB showed that moderate hypoxia (DO<2.0 mg l^{-1}) increased ~3-fold, modulated by spring river flow. Severe hypoxia (DO<0.7 mg l^{-1}) occurred only in high flow years during 1950-1967, but was present annually since 1968.

Analysis using tree-structured regression showed that hypoxia was the most important factor determining patterns of macrobenthic biomass in Chesapeake Bay. Carbon budgets showed that, where habitat quality was poor, macrobenthic biomass was much less than could be supported by the organic carbon supply. In these cases, even dramatic reductions in carbon supply would not be expected to limit benthic production and by extension, trophic transfers to upper trophic levels via the benthos.

The effect of eutrophication and hypoxia on trophic structure and trophic transfer efficiency were examined by estimating trophic flow networks for three regions of CB during summer. In addition, a series of "rules" were described and used to infer the trophic flow network for a "restored" middle CB from historical data, comparative ecological relationships and mass balance constraints. Excessive carbon flow through bacteria was the most pronounced symptom of eutrophication in the modern mid Bay. The microbial food web transferred organic matter to trophic levels comparable to large piscivorous predators, maintaining average trophic transfer efficiency, even as the fraction of primary production transferred to top predators decreased. In the restored Bay, increased macrobenthic production shifted metabolic activity away from the microbial food web, increasing the potential trophic transfer to fish by 7-fold, even as total primary production decreased to 63% of the current average.

EUTROPHICATION, HYPOXIA AND TROPHIC TRANSFER EFFICIENCY IN CHESAPEAKE BAY

by

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DEDICATION

To Melissa and Lauren

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Chapter 1:

BACKGROUND AND INTRODUCTION

Coastal eutrophication is a global-scale problem that has contributed to loss of estuarine habitat and possibly to declines in important fish populations. Eutrophication has been strictly defined as an increase in the rate of supply of organic matter (Nixon 1995) and can result from either external inputs of organic matter, or more typically, from increased primary production. Eutrophication has sometimes been more broadly defined to include both the increase in organic matter supply and the myriad ecological changes that result (Cloern 2001). Here the stricter definition is preferred, while the associated ecological changes are termed "consequences of eutrophication" or "eutrophication effects."

One of the most alarming of these consequences of coastal eutrophication, and a major cause of habitat loss, is the growing incidence of hypoxia and anoxia (Diaz and Rosenburg 1995). Hypoxia is defined here in the broadest possible way as a condition of depressed dissolved oxygen (DO) concentration sufficient to cause any adverse ecological effect. The severety or intensity of hypoxia refers to the degree to which DO is depressed. Many sessile benthic or epibenthic species are well-adapted to moderately depressed DO levels, such as 2.0 mg l^{-1} (Diaz and Rosenburg 1995). Hypoxia-tolerant benthos can survive DO<2.0 mg l^{-1}, but severe hypoxia (i.e. DO<0.5 mg l^{-1}) or complete anoxia commonly eliminates all metazoan life (Diaz and Rosenburg 1995). Motile species such as fish and crabs can often (but not always) escape hypoxic habitats and are apparently less well adapted to hypoxia. Thus, subtle

behavioral effects can sometimes be observed at DO levels only slightly below saturation (Breitburg et al. 1997), while acute effects can occur at DO levels easily adequate for hypoxia-tolerant taxa. Aside from direct effects associated with exposure to hypoxia, biota may be adversely affected by the loss of use of the affected habitat and the prey that may have been present within it. The consequences may be increased if the degraded habitat was preferred because it provided refuge from predation, optimal temperature, or other benefits.

The possible loss of habitat and prey resources associated with hypoxia is a major reason that one may associate eutrophication and hypoxia with the potential for decreased fisheries production and yield. Another related mechanism, not emphasized in this study, is loss of vegetated habitats associated with eutrophication (Kemp et al. 1983). Lacking effects of this nature, there is no *a priori* basis for assuming that eutrophication will have any adverse effect on fisheries yield. Three hypothesized relationships between total organic input and combined fisheries yield illustrate some possibilities (Fig. 1-1). The type 'a' response entails a linear increase in secondary production with primary production, implying constant or nearly constant trophic efficiency. This may be the most commonly reported relationship in the literature. Nixon (1982) observed a positive relationship between primary production and fisheries yield, where primary production varied from ~50 gC m^{-2} y^{-1} to nearly 1000 gC m^{-2} y^{-1}. Iverson (1990) observed a very strong correlation (r^2=0.96) between phytoplankton production and fish plus squid yield in 10 open-ocean and coastal ecosystems with primary production between 50 and 250 gC m^{-2} y^{-1}. Finally, assuming total phosphorus is an indicator of the primary productivity of lakes, Hanson

and Leggett (1982) also found that fish yield in lakes was positively correlated with primary production. There is ample reason to believe that type 'b' and type 'c' functional relationships can and do occur (Fig. 1-1). The initial decrease in the slope of lines 'b' and 'c' indicate that beyond some level of primary production or organic input, one or more more of many possible alternative controls begin to become more important (Fig. 1-2). Examples include changes in food quality, limiting food supply at some other point in time (i.e. "bottlenecks"), availability of suitable habitat or substrate, and control by predators. A decrease in the slope of 'c' to less than zero (Fig. 1-1) implies that further increases in organic supply rate decrease the production potential of the ecosystem. The best documented examples of this type of response have been related to macrobenthic "succession" along a gradient in time or space of organic enrichment (Pearson and Rosenburg 1978). The species-abuundance-biomass (SAB) model of Pearson and Rosenburg (1978) describes the general nature of changes in these three properties of benthic communities with distance from a source of enrichment. Closest to the source, where enrichment is greatest, all three properties decline to zero, ostensibly due to oxygen stress.

Resolving eutrophication effects on fisheries production in whole systems may be hard to be resolve because fisheries production has sometimes, or perhaps more often than not, been degraded by overfishing before the most dramatic effects of eutrophication became evident (e.g. Jackson et al. 2001, but see Boesch et. al. 2001). Regardless of the primacy of fishing versus eutrophication effects on fisheries, fishing pressure can dramatically affect fish populations, giving managers good reason to account for, if not emphasize, population dynamics of targeted populations.

Nonetheless, there is growing recognition that fish populations and the fisheries they support must be managed in a way that accounts for the interconnectedness of living systems. This idea underlies the growing emphasis on "ecosystem-based fisheries management." In the same vein, it has often been implied, if not clearly stated, that protection and restoration of fisheries is an important objective of water quality and ecosystem restoration. A good example is the recently signed agreement to continue restoration of Chesapeake Bay, known as "Chesapeake 2000" (EPA 2000). This new emphasis increases the need for scientific models and data effectively characterizing linkages between primary production, water quality and secondary production.

The environmental history of Chesapeake Bay over the past 100 years has seen dramatic changes in both fisheries (e.g. Houde et al. 1999) and water quality (e.g. Harding and Perry 1997), and may be a classic illustration of the need for integrated analysis of ecological change. This dissertation research developed along those lines. Chapter 2 examines the underlying physical transport regime which is central to the ecology of estuaries in general and Chesapeake Bay in particular. The resulting estimates of physical transport characteristics, while useful in their own right, enter analyses in each of the subsequent chapters.

Chapter 3 examines the 50-year record of dissolved oxygen data for the Bay, establishing the extent of hypoxia today and the nature of its increase since 1950. Further, the physical and biological controls on hypoxia are examined, suggesting prospects for restoration.

Chapter 4 quantifies the deposition of organic matter resulting from the spring phytoplankton bloom, a major ecological feature of the Bay. This process has long been connected to the formation and maintenance of hypoxia in summer, as well as the sustenance of macrobenthic production. The relationship between freshwater inputs during spring and deposition of phytoplankton to sediments is explored and quantified, directly examining a process implicit in the river flow-hypoxia relationships identified in Chapter 3.

Chapter 5 focuses on the macrobenthic communities of the Chesapeake Bay. These communities may have changed more than any other in the Bay, first due to massive removal of oyster stocks by fishing and secondly by the two-fold insult of excessive sedimentation and hypoxia. The patterns of macrobenthic biomass in the Bay are explored in relation to habitat factors utilizing a novel tree-structured data analysis approach. Tree-structured data analysis is effective for uncovering hidden relationships in large data sets for which responses to a large number of explanatory variables are highly non-linear or discontinuous and where interactions among variables are complex. The application to Chesapeake Bay illustrates where and when hypoxia affects the benthos, as well as the effect of other properties such as sediment type. Chapter 5 also begins to explore the connections between primary and secondary production in Chesapeake Bay. A question first raised by simulation modeling results, namely whether decreased primary production could actually reduce secondary production in the benthos, is examined using a bioenergetic budgeting approach. These computations, as well as those from all previous chapters were utilized in Chapter 6.

Chapter 6 presents the results of a trophic network modeling activity which examines how, or if, secondary production in Chesapeake Bay could be sustained if primary production is reduced substantially through environmental management. Here questions related to trophic transfer efficiency, alternative carbon flow pathways, the effect of gelatinous zooplankton blooms, and bacterial domination of the ecosystem are brought together. Historical data, comparative ecological models, and mass balance arguments are combined to envision how carbon flow in a "restored" middle Chesapeake Bay might be different from today, and as importantly, how much fish production it might be able to sustain.

Chapter 7 serves to some extent as an epilogue to Chapter 6, examining the trophic level estimates derived from the trophic network models using analysis of stable nitrogen isotopes. Chapter 8 provides a brief synopsis of the major results of all the chapters and suggests future directions for related research.

In total, the results of this research connect nutrient-driven eutrophication effects, mediated by physical processes, to trophic transfer efficiency and potential fish production both today and in a restored Chesapeake Bay. The results suggest that nutrient loading rate reductions should lead to improved water quality, specifically a decrease in the extent and intensity of summer hypoxia and anoxia. These changes will result from a substantial decrease in phytoplankton production. Total organic input would likely decrease by a smaller fraction due to an offsetting increase in benthic primary production. Improved habitat quality should lead to increased biomass and production of macrobenthos in the mid Bay region. This and other ecological changes that can be expected should lead to decreased carbon flow through

both planktonic and benthic bacteria. Although it is suggested that the restored Bay will have lower levels of primary production than the modern Bay, more, not less, fish production could be supported by the restored Bay.

The objectives of ecosystem management and restoration (e.g. EPA 2000) require that ecosystem scientists begin to establish linkages across the trophic levels of the ecosystem and across the traditionally separate disciplines of science and management. Drawing on decades of research that makes such work possible, this dissertation makes a step in that direction.

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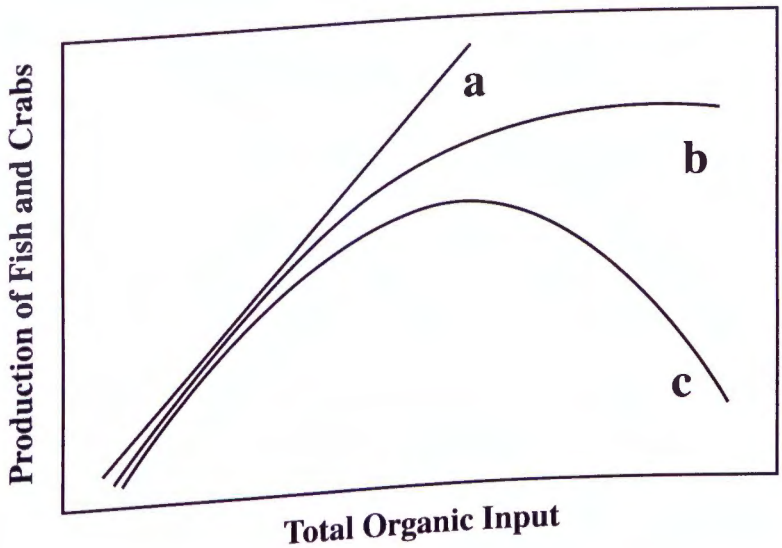

Fig. 1-1. Hypothesized functional relationships between total organic input (primary production+external inputs) and fisheries production. For a type 'a' response, fish production is a constant fraction of organic input. A type 'b' response involves saturating kinetics and would could be expected when secondary producers are unable to utilize additional inputs, but are not adversely affected by excess inputs. A type 'c' response indicates that excess organic inputs caus adverse ecological changes such as habitat degradation that decrease fish production.

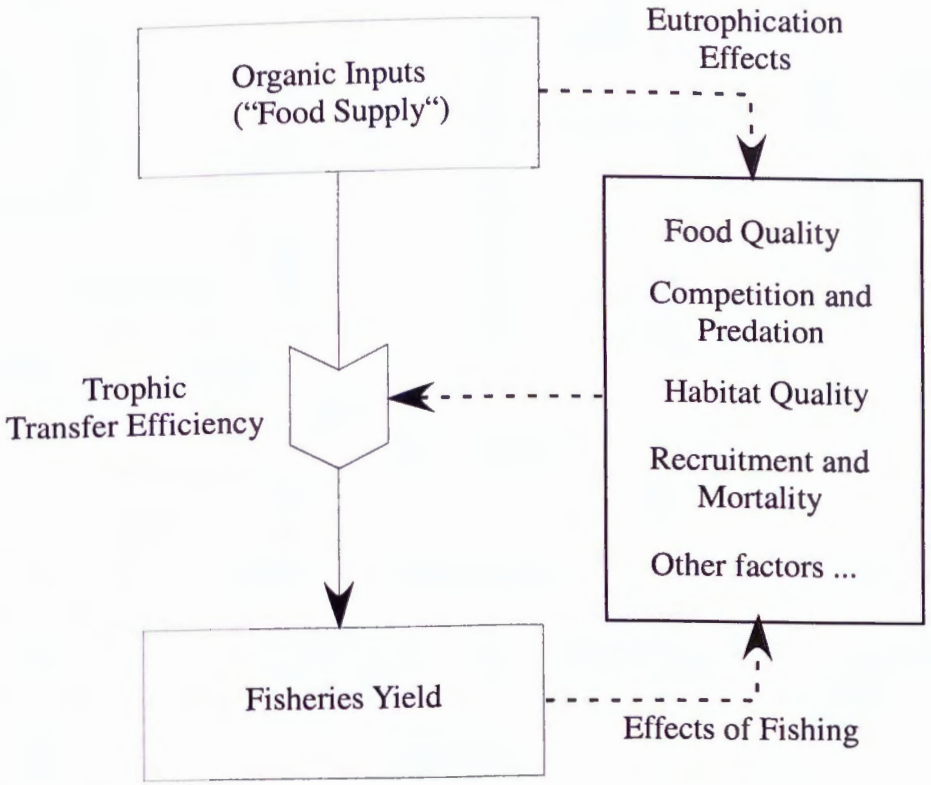

Figure 1-2. A conceptual diagram illustrating mediation of the transfer of organic carbon from inputs and primary producers to fisheries yields. Solid lines indicate carbon flow. Dashed lines indicate influence or "information" flow. The list of effects is not intended to be comprehensive.

Chapter 2:

A BOX MODEL APPROACH FOR ESTIMATING PHYSICAL TRANSPORTS AND EXCHANGES FOR THE CHESAPEAKE BAY

Abstract

A salt and water balance model, or "box" model, was developed to estimate the average hydraulic transport within Chesapeake Bay at a monthly time interval. The Chesapeake Bay system is a large complex of estuaries and river basins. Strong seasonal patterns in freshwater inputs lead to seasonal changes in salinity in the Bay itself, as well as its large tributary estuaries and fringing embayments. Therefore, implementing a box model for this system required that multiple freshwater sources and lateral salt exchanges be included in the model. The latter has not previously been considered in a box model. Estimated down-estuary transport was 1 to 3 times the discharge of the Susquehanna River into the oligohaline region of the Bay. In the mesohaline region, transport was 4 to 6 times the sum of up-stream freshwater inputs. In the polyhaline region of the Bay, down-estuary transport was 6 to 10 times total freshwater inputs. The distribution of vertical advection featured an area where seasonal downwelling occurs, in agreement with recent hydrodynamic modeling results and field observations. Vertical exchange velocity, a measure of non-advective vertical exchange, was lowest in the mesohaline region of the Bay, especially during summer when exchange velocity was 10-20 cm d^{-1} versus 60-90 cm d^{-1} in late fall. An index of water column stratification, based on the Brundt-Väisälä frequency, revealed a strong positive correlation between the average strength of water column stratification and the average spring discharge of the Susquehanna River (r^2=0.92).

Estimates of summer average vertical diffusion decreased with freshwater input and stratification, but other factors, potentially wind-driven lateral seiching, contributed significantly to vertical mixing. Landward advection into the mid Bay bottom layer increased with spring river flow, but this effect was attenuated in the up estuary direction.

This box model approach appears to be an effective and relatively simple tool for estimating time-averaged transport rates among regions of the Bay and between the surface and bottom layers, enabling many potential applications in ecology, environmental chemistry, and environmental management.

Introduction

Physical transport processes are a central feature of estuarine ecosystem dynamics. In fact, many biological and biogeochemical processes in estuaries would be difficult to understand except in the context of the physical transport regime. While the periodic ebb and flow of the tides is the most obvious feature of the circulation to the casual observer, much less obvious features may be as important. For example, net horizontal transport, whether the result of tidal dispersion or residual (sub-tidal) advection is responsible for transport of sediments, nutrients, organic matter, and plankton in both the up-estuary and down-estuary direction. In stratified estuaries, rates of cross-pycnocline exchange, whether via upwelling or turbulent diffusion, determine nutrient and oxygen transport across the pycnocline, affecting phytoplankton dynamics in the surface layer and the potential for hypoxia in the lower water column.

A variety of approaches are available for estimating transport within estuaries and for evaluating the possible role of physical transport in determining ecological or biogeochemical observations. These include mixing diagrams (e.g. Fisher et al. 1998), hydrodynamic simulation models (Johnson et al. 1991, Hood et al. 1999, Wang and Johnson 2000), direct current measurements and drifters (Valle-Levinson and Lwiza 1995, Janzen and Wong 1998), and box models (Pritchard 1969, Officer 1980, Hagy et al. 2000). Due to the potential for substantial changes in current regimes over short periods of time, as well as the high degree of spatial variability in current velocity (e.g. Elliott 1978), current meters are not likely to be an effective means of resolving average residual currents at the whole estuary scale. Hydrodynamic simulations provide the most mechanistic, spatial and temporal detail. However, this comes at the cost of enormous data requirements and computational complexity. Moreover, an additional consideration applies if the objective is to estimate sub-tidal vertical and horizontal current velocity and vertical diffusive transport at aggregated temporal and spatial scales. The high-frequency (i.e. minutes to hours) variations in tidal current velocities are the most certain predictions of hydrodynamic models, while residual current velocities are the least certain. This results from the fact that the tidal currents can largely be predicted by a barotropic model (i.e. vertically integrated), while the residual currents require a much more complicated baroclinic model. Accurate predictions of residual circulation therefore depend on careful calibration of diffusivity parameters until the model reasonably replicates observed salinity. Although this is a tractable problem, significant errors are possible and may be obscured by the otherwise impressive reproduction of tidal circulation. Careful work by skilled

investigators is needed to obtain good estimates. Therefore, another approach for estimating residual circulation, particularly a relatively simple approach, may also be useful.

Pritchard (1969) introduced box models as an approach for estimating residual circulation in estuaries using salinity as a natural conservative tracer of physical transport. Further elaborated upon by Officer (1980) and later by Hagy et al. (2000), the method involves dividing the estuary into a series of finite elements, or "boxes," which are assumed to be well-mixed. Two equations can be written for each box. One describes the balance of water flow into and out of the box, while the other describes the balance of salt transport into and out of the box. Provided that a few simplifying assumptions can be accepted (see "Methods"), a unique simultaneous solution to this system of linear equations can be obtained, providing estimates of the physical transport coefficients (Hagy et al. 2000). These estimates can then be readily utilized for ecological investigation. For example, Taft et al. (1978) used a box model based on the Officer (1980) methodology to infer the importance of ammonium recycling in the lower water column for the nitrogen requirements of the summer phytoplankton community in Chesapeake Bay.

Hagy et al. (2000) described two simple elaborations of the basic box modeling methodology (i.e. described by Officer 1980) that enabled these relatively simple models to reproduce surprisingly realistic features of the monthly average physical transport regime of Patuxent River, MD. Specifically, these elaborations involved relaxing two key model assumptions. Whereas Officer (1980) assumed that all freshwater entered the estuary at a single point, Hagy et al. (2000) generalized the

approach such that any quantified input of freshwater could be accommodated. The effect of this generalization on model estimates for Patuxent River estuary was not particularly large since Patuxent River is the only major freshwater source. However, the Susquehanna River accounts for only about 50% of freshwater inputs to Chesapeake Bay (Bue 1968), with the remainder coming from several other major tributary rivers. Thus, this was expected to be important for a Chesapeake Bay box model. The second, and perhaps more important, generalization described by Hagy et al. (2000) was the provision for seasonal changes in salinity. This proved to be very important for estimating residence times for Patuxent River estuary. Specifically, if salinity was increasing on a seasonal basis, a model neglecting the increase substantially overestimated residence time. The difference reflects the lack of direct correspondence at seasonal time scales between freshwater inflow and seawater inflow due to gravitational circulation. Since salinity also changes seasonally in Chesapeake Bay, this generalization is probably also important for a Chesapeake Bay box model.

This paper describes a 9-segment, 2-dimensional box model developed to estimate hydraulic transport in the mainstem of Chesapeake Bay. The model incorporates the features described by Hagy et al. (2000), plus additional elaboration that was included to improve applicability to Chesapeake Bay, a large, physically complex estuary adjoined by substantial tributary estuaries. The intended use of this model was to compute circulation in a manner sufficient to estimate regional and seasonal scale input-export budgets of major dissolved and particulate materials. These include, but are not limited to, organic carbon, dissolved oxygen, nitrogen, phosphorus, and silicate (Hagy 1996). The highest possible spatial and temporal

articulation was utilized to minimize the error that can result from overly aggregated models of this type (Webster et al. 2000).

Study Area

Chesapeake Bay (the Bay) is a large, partially-stratified, estuary. In addition, the Bay is part of a major complex of river basins and associated estuaries and embayments (Fig. 2-1). There are several features of the Bay and associated tributaries that are important for the construction of box models. The circulation is mostly two-layer, with net circulation flowing landward in the bottom layer and seaward in the surface later (Pritchard 1952). The depth of no net motion intersects the bottom in the oligohaline region of the estuary (Wang and Chao 1996). Landward of this point, there is a one-layer circulation with net seaward flow at all depths. In the polyhaline region of the Bay, there are stronger lateral (i.e. normal to main Bay axis) gradients in salinity and current velocity compared to elsewhere in the Bay (Pritchard 1952, Valle-Levinson and Lwiza 1995).

Over the length of the estuary, 7 major tributary estuaries discharge freshwater into Chesapeake Bay. These include the Susquehanna, Choptank, Patuxent, Potomac, Rappahannock, York and James Rivers (Fig. 2-1). As important is the fact that, as illustrated for Patuxent River by Hagy et al. (2000), these estuaries exchange salt with the mainstem Bay during seasonal cycles of salt accumulation and depletion. Several large embayments are also present, including Tangier Sound, Pocomoke Sound and Eastern Bay. While these do not have substantial sources of freshwater input compared to the major rivers, they do exchange salt. The combined volumes of the

mainstem Bay, major tributary rivers, and major embayments include 91% of the total volume of the Chesapeake Bay system. The remaining water volume is contained within many smaller embayments and tributary rivers (Cronin and Pritchard 1975).

Methods

This study uses the salt and water balance-based box model approach, originally proposed by Pritchard (1969), elaborated upon by Officer (1980), and further developed by Hagy et al. (2000). In applying a box model, the estuary is divided into a series of discrete regions or "boxes," each of which is assumed to be well-mixed. In the simplest example of a box model for an estuary, a quantified freshwater flow, Q_f, enters a well-mixed basin of volume, V (Fig. 2-2, upper panel). Estuarine water of known average salinity, s_{in}, flows out of the basin into the sea at rate Q, while the estuary exchanges water at rate E via non-advective dispersion with the coastal zone where the known salinity is s_{out} (Fig 2-2). For this simple case, the water balance equation is

$$\frac{dV}{dt} = Q_f - Q \qquad (1)$$

The change in estuarine water volume, V, over time is dV/dt, which, averaged over many tidal cycles, is assumed to be zero. Therefore, the seaward advection is simply equal to the freshwater input.

The salt balance equation is

$$V\frac{ds_{in}}{dt} = E(s_{out} - s_{in}) - Qs_{in} \qquad (2)$$

Substituting Q_f for Q based on the water balance equation, one can solve for E in terms of known values, giving

$$E = \frac{V\frac{ds_{in}}{dt} + Qs_{in}}{(s_{out} - s_{in})} \tag{3}$$

Although simple, this basic formulation is not entirely unrealistic, and can yield useful results (e.g. Gordon et al. 1996). For a horizontally and vertically articulated box model, the approach described by Hagy et al. (2000) applies. Namely, the water budget for a surface layer box "m" is

$$\frac{dV}{dt} = Q_{m-1} + Q_{vm} + Q_{fm} - Q_m \tag{4}$$

where Q_m is the seaward advection out of the box, Q_{m-1} is the seaward advection into the box, Q_{vm} is the vertical advection into the box, and Q_{fm} is the freshwater input to the box. The salt budget is

$$V_m\frac{ds_m}{dt} = Q_{m-1}s_{m-1} + Q_{vm}s'_m - Q_m s_m + E_{vm}(s'_m - s_m) + \tag{5}$$

$$\left[E_{m-1,m}(s_{m-1} - s_m) + E_{m,m+1}(s_{m+1} - s_m)\right]$$

where the Q terms are as above and V_m is the box volume, s_m is the average salinity in the box, s_{m-1} is the average salinity in the adjacent landward box, s_{m+1} is the average salinity in the adjacent seaward box, and s'_m is the average salinity in the bottom layer box in the same model segment. The terms $E_{m-1,m}$ and $E_{m,m+1}$ are the horizontal dispersive exchange with the adjacent landward and seaward boxes, respectively, while E_{vm} is the vertical non-advective exchange across the pycnocline. In order to obtain a fully determined linear system of equations, where a unique solution can be

obtained, it is necessary to have no more than two unknown terms per box. Hagy et al. (2000) reasoned using arguments based on the estimated mass-transfer Peclet number that, for Patuxent River estuary, horizontal salt-transport due to horizontal dispersion would be quantitatively insignificant compared to horizontal advection. The assumption was justified in the same way for Chesapeake Bay. Therefore, the bracketed terms in eq. (4) were neglected. Using the approach of Hagy et al. (2000), a closed form solution to the linear system of equation can be obtained by combining the salt and water balance equations. Namely, the water balance for the boundary between segment m and segment $m+1$ is

$$Q'_{m+1} = Q_{m-} \sum_{j=1}^{m} Q_{fj} \tag{6}$$

where $\sum_{j=1}^{m} Q_{fj}$ is the sum of all freshwater inputs landward of and including box m.

The corresponding salt balance equation is

$$\sum_{j=1}^{m} V_m \frac{ds_m}{dt} + \sum_{j=1}^{m} V'_m \frac{ds'_m}{dt} = Q'_{m+1} s'_{m+1} - Q_m s_m \tag{7}$$

where the summation terms refer to the combined change in salt storage in all surface layer and bottom layer boxes landward of segment m. Substituting the right hand side of eq. (6) for Q'_{m+1} in eq. (7) and solving for Q_m, one obtains

$$Q_m = \frac{\left(s'_{m+1} \left[\sum_{j=1}^{m} Q_{fj} + Q_r \right] + \left[\sum_{j=1}^{m} V_j \frac{ds_j}{dt} + \sum_{j=2}^{m} V'_j \frac{ds'_j}{dt} \right] \right)}{s'_{m+1} - s_m} \tag{8}$$

which is the same as eq. (7) in Hagy et al. (2000). The general similarity to eq. (3) should also be apparent, except that horizontal advection replaces horizontal diffusive exchange and aggregated freshwater input and salt storage replaces the single-box values. Solving eq. (8) for all Q_m, then substituting into eq. (6), one can compute landward advection at each segment. Substituting Q_m and Q'_m into eq. (4) gives upwelling advection. Finally, given all the estimates of advection, one can compute E_{vm} from eq. (5).

The box model divides Chesapeake Bay into 9 segments of unequal length (Fig. 2-1, Fig. 2-3. Table 2-1). The most landward segment includes only net seaward flows and is assumed to be vertically well mixed. All other model segments are vertically divided into a surface layer and a bottom layer, each assumed to be well mixed vertically and horizontally. Net advection in the surface layer is down-estuary, while the bottom layer has net up-estuary advection. Vertical advection (i.e. upwelling or downwelling) exchanges water between the layers. The transition from one to two layers occurs at the boundary between segment 1 and 2. In segment 1, landward-flowing water from the bottom layer of segment 2 mixes with freshwater from the Susquehanna River, then enters the seaward-directed flow from segment 1 to segment 2. This seaward flow enters only the surface layer box in segment 2. Freshwater inputs enter each surface layer box as determined by the water budget.

Additional terms were needed to account for changes in salt storage in the major tributary estuaries and in the larger embayments flanking the mainstem Bay (Fig. 2-1, Fig. 2-2). These water bodies exchange water and salt with the mainstem via tidal and other mechanisms. Most rivers have either a shallow sill (<10 m) or a vary

narrow, but slightly deeper, access channel (Fig. 2-1). An exception is the Potomac River, which has a wider and deeper access channel. However, this channel is only 12-15 m deep, similar to the pycnocline depth in the mainstem Bay. It was therefore assumed that salt and water exchanges with tributaries involve only the surface layer of the mainstem Bay, regardless of the transport regime at the tributary mouth. Therefore, these exchanges do not affect the water balance equations for the Bay model except as a net water outflow equal to the freshwater input to the tributary. Such freshwater inputs were already accommodated in the model formulation of Hagy et al. (2000). In contrast, salt exchanges with tributary rivers and embayments appear as additional salt storage terms added to eq. (5), giving

$$V_{tm}\frac{ds_{tm}}{dt}+V_m\frac{ds_m}{dt}=Q_{m-1}s_{m-1}+Q_{vm}s'_m-Q_m s_m+E_{vm}(s'_m-s_m)+ \qquad (9)$$

$$\left[E_{m-1,m}(s_{m-1}-s_m)+E_{m,m+1}(s_{m+1}-s_m)\right]$$

where V_{tm} is the volume of the tributaries or embayments adjacent to box m up to the limit of salt intrusion and ds_{tm}/dt is the change in the average salinity in that volume. These terms can also be collected as in eq (7) giving

$$\sum_{j=1}^{m}V_{tm}\frac{ds_{tm}}{dt}+\sum_{j=1}^{m}V_m\frac{ds_m}{dt}+\sum_{j=1}^{m}V'_m\frac{ds'_m}{dt}=Q'_{m+1}s'_{m+1}-Q_m s_m \qquad (10)$$

which can be combined with eq (6) to update eq. (8). The result is

$$Q_m=\frac{\left(s'_{m+1}\left[\sum_{j=1}^{m}Q_{fj}+Q_r\right]+\left[\sum_{j=1}^{m}V_j\frac{ds_j}{dt}+\sum_{j=2}^{m}V'_j\frac{ds'_j}{dt}+\sum_{j=1}^{m}V_{tm}\frac{ds_{tm}}{dt}\right]\right)}{s'_{m+1}-s_m} \qquad (11)$$

The tributary basins and embayments that were included in the model are Eastern Bay (embayment), Choptank River, Patuxent River, Potomac River, Rappahannock River, Tangier Sound (embayment), Pocomoke Sound (embayment), York River and James River (Table 2-3). The mainstem Bay accounts for 67% of the total volume of Chesapeake Bay and tributaries. The additional tributaries and embayments account for an additional 24%. Thus, 91% of the Chesapeake Bay system volume is included (Table 3). Smaller tributaries and embayments comprise the remaining 9% of the volume and were neglected.

Vertical non-advective exchanges (E_{vm}) can be calculated equivalently from either surface layer or bottom layer salt-balance equations once all the other exchanges are known. In this case, it was simpler to compute E_{vm} from the salt-balance equations for the bottom layer boxes. The equations were written to be conditional upon the sign of Q_{vm} due to the known occurrence of downwelling advection (i.e. $Q_{vm}<0$) in Chesapeake Bay in some places at some times of the year (Chao and Paluszkiewicz 1991). For the case where $Q_{vm}>0$ the salt balance equation can be solved for E_{vm} to obtain

$$E_{vm} = \frac{\left(-V'_m \frac{ds'_m}{dt} + Q'_{m+1} s'_{m+1} - Q_{vm} s'_m - Q'_m s'_m \right)}{s'_m - s_m} \qquad (12)$$

When $Q_{vm}<0$ (i.e. the downwelling case), the salt balance equations changed such that vertical advection becomes a source of salt to the bottom layer rather than a loss. The revised salt balance is

$$V'_m \frac{ds'_m}{dt} = Q'_{m+1} s'_{m+1} - Q_{vm} s_m - Q'_m s'_m - E_{vm}\left(s'_m - s_m\right) \qquad (13)$$

which can be solved for E_{vm} to obtain

$$E_{vm} = \frac{\left(-V'_m \frac{ds'_m}{dt} + Q'_{m+1} s'_{m+1} - Q_{vm} s_m - Q'_m s'_m \right)}{s'_m - s_m} \qquad (14)$$

Since the sign of Q_{vm} changes when downwelling replaces upwelling, it was unnecessary to change the sign for the Q_{vm} term in the salt balance equation (eq. 3). The only difference between eq. 12 and eq. 14 is that s_m replaces s'_m in the term representing the vertical advective salt flux due to the fact that downwelling water has the salt content of the surface layer water, while upwelling water has the salt content of bottom layer water.

Sources of Data and Computation of Inputs

Salinity data were obtained from the Chesapeake Bay Water Quality Monitoring Program, which collected water quality data at a series of 20 stations down the central axis of the Chesapeake Bay (Fig. 2-1, Table 2-2). Cruises were conducted on a bi-weekly basis, except in winter when cruises were conducted monthly. Sampling began in 1984 and is ongoing at present. The vertical resolution of the data is 1 m. Average salinity for the tributaries was computed using the available Chesapeake Bay Water Quality Monitoring Program data at stations indicated in Table 2-2. Both mainstem and tributary salinity data were interpolated to a grid transecting the estuary at a vertical resolution of one meter and a horizontal resolution of one nautical mile. Grid cells corresponded to tabulated cross-sectional volumes (Cronin

and Pritchard 1975), which were used to compute volume-weighted average salinity (Hagy et al. 2000).

The major tributary rivers are the dominant sources of freshwater to Chesapeake Bay (Table 2-3). These include (north to south) the Susquehanna, Choptank, Patuxent, Potomac, Rappahannock, York and James. These rivers are all gauged at their fall lines (Fig 2-1) and data discharge totals are available from the USGS. Data for 1984-1998 were obtained and averaged by month for this study. The York River includes the combined flows of the Mattaponi and Pamunkey Rivers. The tidal James River combines the James and Appomattox Rivers (Fig. 2-1). Together, the drainage basins of the gauges at the fall lines of these rivers comprise 130,798 km^2, or 78% of the 166,717 km^2 drainage area of Chesapeake Bay (EPA 1998, Table 2-3). Although there are many small watersheds that are gauged, none were significant in size and most have only short or incomplete flow records. Thus, ungauged portions of the watersheds of the major tributaries were estimated on the basis of the flow/area of the associated tributary. The ungauged areas of the watershed of the major tributaries totaled 16,992 km^2 (Table 2-3). Other ungauged areas were combined into four groups, the Eastern Shore in Pennsylvania, Delaware, Maryland and Virginia, the western shore in Pennsylvania and Maryland, the western shore in Virginia, and open water (Table 2-3). It was assumed that direct precipitation to the water surface was approximately balanced by evaporation. Therefore, open water was assumed to contribute no net freshwater input (Bue 1968, Hagy et al. 2000). The flow for the other areas was based on the flow/area from nearby gauged basins. The basins that were used for this purpose included the Choptank River (Eastern Shore), Patuxent

River (MD western shore), and Mattaponi River (VA western shore). These ungauged areas totaled 16,866 km^2. In total the water budget accounted for 99% of the entire watershed (Table 2-3). While estimates of flow for ungauged areas based on flow/area in nearby basins are not as certain as direct observations, errors would have to be large to significantly affect the results because such a large fraction of the discharge from the watershed (78%) is directly gauged.

At the large scale of this analysis, human diversions of freshwater for purposes such as municipal or industrial use would have to be very large to be of any significance in the overall water budget. Moreover, because of the size of Chesapeake Bay, withdrawals are balanced by returns to nearby areas of the estuary (Bue 1968). In the case of smaller estuaries such as Tomales Bay (Smith et al. 1991) and Patuxent River (Hagy et al. 2000), these alterations must receive careful attention. A possible exception is the estimated 27 $m^3 s^{-1}$ diversion of freshwater from the Chesapeake Bay to the Delaware Bay due to net transport through the Chesapeake and Delaware Canal (Bue 1968, Wang and Johnson 1999). This flow was subtracted from the freshwater inputs to segment 1.

Scale-Independent Transport Estimates

Each of the estimated bulk transport estimates (e.g. units = $m^3 s^{-1}$) generated by box models can be expressed as a scaled quantity that can be more readily interpreted and compared to other data. In particular, such scaled quantities are useful for comparing estimates for different regions of the Bay. For example, the estimated advection (Q_m; $m^3 s^{-1}$) divided by the average cross sectional area (m^2) of the model

segment yields a quantity that approximates the spatially averaged residual (i.e. net non-tidal) current velocity (m s^{-1}) over the cross section. Similarly, the upwelling transport (Q_{vm}) divided by the pycnocline area estimates spatially averaged upwelling velocity. Vertical non-advective exchange (E_{vm}), scaled by the pycnocline area (i.e. E_{vm}/A), gives a quantity termed the non-advective exchange velocity. Multiplying by the height of the pycnocline region gives an estimate of vertical eddy diffusivity (D_z). This conversion can be illustrated by writing the analogous expressions for the salt flux across the pycnocline in terms of both the box model coefficient, vertical diffusivity, and a discrete approximation based on vertical diffusivity. This is

$$E_{vm}(s'_m - s_m) = AD_z \frac{\partial s}{\partial z} \approx AD_z \frac{(s'_m - s_m)}{\Delta z} \qquad (15)$$

where A = the pycnocline area and Δz = the mean height between box centers. Rearranging gives the conversion from the non-advective exchange coefficient to diffusivity, or $D_z = \frac{\Delta z E_{vm}}{A}$. In the mesohaline Chesapeake, the mean distance from surface and bottom layer box centers (Δz) is ~9 m. Table 4 provides the physical dimensions of the boxes needed to compute physical transport rates in these alternative units.

Validation Data Sets

Two data sets were used to provide independent validation of box model results. The Chesapeake Bay Observing System (www.cbos.org) is an array of permanent moorings located in Chesapeake Bay that provide telemetered physical

oceanographic measurements both in real time and archived data sets. A multi-year record of surface layer (2.5 m) and bottom layer (18.5 m) current velocity collected at a frequency of 12 hr^{-1} was obtained and used to compute average residual current velocity in that region of the mid Bay.

The other validation data set was obtained from the National Science Foundation-Funded Chesapeake Bay Land-Margin Ecosystem Research Program, which collected physical oceanographic data along transects of the mainstem Chesapeake Bay at extremely high spatial resolution (8 Hz) using a towed, undulating CTD device (SCANFISH). Temperature and salinity data collected by SCANFISH along a transect between the Potomac and Rappahannock Rivers were used to compute and map the Brundt-Väisälä frequency (N^2), a measure of water column stability, which can be computed from the vertical density gradient via

$$N^2 = g \cdot \frac{1}{\sigma} \cdot \frac{\partial \sigma}{\partial z} \qquad (16)$$

where g is the gravitational constant (9.81 m s^{-2}) and σ is the density of water (kg m^{-3}; Massel 1999). This quantity, N, is a "frequency" because in eq. 16 the units of mass (kg) and distance (m) cancel, leaving only units of inverse time, namely s^{-1} or Hertz (Hz). A reason that high buoyancy frequency indicates high water column stability is analogous to the dependence of the pitch (frequency) of a plucked violin string on the tensioning of the string.

Interannual Variability and the Effect of Freshwater Inflow

The effect of seasonal to annual scale changes in freshwater discharge rates on physical transport regimes was examined using both the box models and a model-free (i.e. does not depend on the box model) measure of vertical water column structure (i.e. stratification strength). For the former, physical transport rates were computed for each of the 156 months during the period 1986-1998 using the box model. Rather than using seasonal average inputs, the box model computation utilized the observed monthly data. Seasonal average rates of horizontal advection and vertical diffusion were compared to freshwater inflow rates using regression.

For the latter, it was necessary to develop an index of stratification appropriate for the seasonal/whole-system scale of interest. The index was based on the Brundt-Väisälä frequency, which is a measure of water column stability as described above (Massel 1999). In this case, the vertical density gradient, $\partial\sigma/\partial z$, was calculated at a 1-m depth interval using a 2-m moving window. Maximum N^2 (units: s^{-2}) typically occurs within the pycnocline, and with lower values within the surface and bottom mixed layers (Fig. 2-4). The strength of the pycnocline was quantified as the maximum value of N^2 (Fig. 2-4), hereafter referred to using the notation "max(N^2)." For each sampling date between 1984 and 1999, max(N^2) was calculated at 1.85 km (1 NM) intervals down the entire axis of the Bay. An index of stratification strength for summer in the mid-Chesapeake Bay was obtained by averaging all observations of max(N^2) between 102 and 222 km from the Bay mouth for April-September, the period encompassing the beginning of oxygen depletion in spring and ending with the re-oxygenation of the lower mixed layer in fall (Chapter 3).

Results and Discussion

Water Budget

The computed 1986-1998 average freshwater input to Chesapeake Bay was 2,215 $m^3 s^{-1}$, of which the Susquehanna flow accounted for 48% (Table 2-5a). All other inputs were combined by model segment. Thus, segment 6, which includes the Potomac River, accounted for 22% of the total input. Segment 9, which includes the James and Appomattox Rivers, accounted for 14% of the total. Combined inputs between the Susquehanna River and the Potomac River accounted for only 5.2% of the total freshwater input.

The estimated freshwater inputs can be aggregated to compare with the estimates of the United States Geological Survey, which uses the method of Bue (1968) to calculate monthly streamflow inputs above 5 cross sections of Chesapeake Bay. The present estimates were in very close agreement with the USGS estimates, departing by less than 4% at each of 5 reference points during 1996 and 1997, the two years for which direct comparisons were made. The extremely close agreement between the USGS estimates and this study reflect the fact that large areas of the Chesapeake Bay watershed are gauged and that watershed areas needed to estimate the remaining areas have been tabulated and published.

Seaward Advection

Down-estuary advection increased in the seaward direction, reflecting the inclusion of the upwelling flows from the bottom layer into the seaward flows. This

can be expressed as a multiple of the total landward freshwater inputs (R_t), giving an indication of the magnitude of the landward transport in the bottom layer (Table 2-5b, Fig. 2-5). This multiple increased from $1.5R_t$ at 240 km (Patapsco R.) to a value between $3R_t$ and $7R_t$ at the Bay mouth (Fig. 2-5). Expressed as a multiple of the Susquehanna River flow only (R), advection varied between $1.5R$ at 240 km to a seasonally varying range of $4.5R$ to $11R$ near the Bay mouth (Table 2-5b). The seasonal pattern in this multiple does not reflect a seasonal intensification of gravitational circulation, as was found for the Patuxent River (Hagy et al. 2000). In this case, it simply reflects persistence of the gravitational circulation despite the seasonal decrease in river flow (Table 2-5b). The magnitude of up-estuary advection in each segment is not reported, but can be easily computed from seaward advection minus the cumulative freshwater inputs (Table 5a,b), satisfying the water balance expressed in eq. 6.

Average net non-tidal current velocities along the main axis of the estuary were estimated by dividing the advective transport rate by the respective surface layer or bottom layer cross-sectional area. Although the advective transport rates increased down-Bay (Table 2-5b), the residual current velocities were relatively constant due to the increasing cross-sectional area of the estuary. Estimated net non-tidal current velocity in the surface layer averaged 4.8 cm s^{-1} in the upper Bay (box 1) with higher velocity (8-9 cm s^{-1}) associated with spring freshwater discharge. In the mid-Bay (box 5) average net non-tidal current velocity was 3.7 cm s^{-1} with peak velocity (~5 cm s^{-1}) in late spring and a seasonal minimum (2 cm s^{-1}) in July. Using these velocities and the length of each model segment, the estimated transit time in the surface layer from

the Susquehanna River to the Atlantic Ocean varied between a minimum of 57 days in March and a maximum of 141 days in August.

The mid-Bay net seaward velocity was smaller than average velocities estimated using a current meter located at 2.5 m depth on the mid-Bay Chesapeake Bay Observing System (CBOS) buoy. The current meter measured an average velocity of 5-8 cm s^{-1} compared to 2-5 cm s^{-1} from the box model (Fig. 2-6). The higher rates observed by the CBOS buoy most likely reflect higher current velocities in the mid-channel relative to the cross-section average, the latter of which the box model estimates. Net non-tidal landward current velocity in the bottom layer averaged 7.7 cm s^{-1} in the mid-Bay with higher velocity (10-11 cm s^{-1}) in winter-spring and lower velocity in summer (4 cm s^{-1}). These rates compared much better to the CBOS current meter estimates, which are for a current meter at 18.5 m depth (Fig. 2-6). The box model estimates agreed especially well with the current meter data during July-October, while the box model estimates were higher earlier in the year. The closer agreement may reflect lower lateral variation in current velocity in the narrower lower layer channel, which would tend to reduce differences between the mid-channel estimate and the cross-sectional average. Interestingly, agreement in the bottom layer implies that the box model is correct in the surface layer as well provided that the freshwater inputs are reasonably correct (see eq. 6). In general, the agreement that was observed between the box model and current meter data was very encouraging.

Vertical Advection

Upwelling occurs along the entire salinity gradient of the Bay during most of the year. Since the pycnocline area varies among the model segments, the volumetric rate of upwelling (Table 2-5c) was scaled by the pycnocline cross-sectional area (Table 2-4) to estimate average upwelling velocity (Fig. 2-7). North of the Choptank River (180 km), upwelling velocity reached seasonally maximal rates during October through April, coincident with peak river discharge. Peak velocity was approximately 90-100 cm d^{-1}. During summer, upwelling was slower, 17-40 cm d^{-1}. In the mesohaline Bay, between the Rappahannock River and the Choptank River, seasonal variations in upwelling were small and average upwelling was generally lower, about 24 cm d^{-1}. Further to the south, in the region near the mouth of the Potomac River (120 km), upwelling was more intense, ~40-70 cm d^{-1}. A small component of this additional upwelling could be attributable to upwelling in the Potomac River, although it does not seem likely that this is sufficient to account for the difference in upwelling between segment 6 and segment 5 (Fig. 2-7). Interestingly, the box model estimated weak downwelling (0 to -20 cm d^{-1}) in segment 7 during October-April. During the remainder of the year, there was only weak upwelling (<10 cm d^{-1}).

Both the region of enhanced upwelling near the Potomac River and the region of weak upwelling or downwelling may be related to effects of the shoaling of the central channel of the Chesapeake Bay in segment 7 between the Potomac and Rappahannock Rivers (Fig. 2-1). During periods of high river flow, the surface layer outflow is topographically impeded, leading to downwelling landward of the shoal. In response, enhanced upwelling is expected landward from the downwelling region

(Chao and Paluszkiewicz 1991). Chao and Paluszkiewicz (1991) investigated this so-called region of "hydraulic control" theoretically via model simulations. Direct observations also suggest the presence of this feature. A near-synoptic profile of the Brundt-Väisälä frequency in the region during a high river flow period in April 1998 showed that the pycnocline is displaced downward landward of the shoal, then rebounds further landward (Fig. 2-8). Although the scale of this feature is smaller than suggested by the upwelling and downwelling patterns in Fig. 2-7, the difference may be related to the spatial resolution of the box model. Thus, the locations of the regions of upwelling and downwelling in Fig 2-7 are only approximate.

Vertical Non-Advective Exchange

Upward diffusion of salt across the pycnocline occurs along the salinity gradient of Chesapeake Bay and causes the bottom layer salinity to decline in the landward direction. During spring, vertical exchange was lowest (~20-60 cm d^{-1}) in the lower mesohaline Bay, near the mouth of the Potomac River. Minimum non-advective exchange velocity was observed during May through October between the Potomac River and Eastern Bay (Fig. 2-9). Values were typically 10-20 cm d^{-1}. Summertime vertical exchange velocity was higher in the upper Bay (~70-90 cm d^{-1}) and much higher (~90-130 cm d^{-1}) in the lower Bay. In fall, exchange velocity in the middle Bay approximately doubled in September compared to August, then doubled again in October. Thus, fall non-advective exchange was ~60-90 cm d^{-1} in the middle Bay. Fall exchange in the lower Bay was comparable to spring, while in the upper Bay, higher exchange was observed in the fall, ~ 110 cm d^{-1}.

Compared to Patuxent River, vertical non-advective exchange velocity in Chesapeake Bay was relatively greater. For example, in the middle region of both estuaries, where non-advective exchange during summer was minimal, Patuxent River had exchange velocity ~5 cm d^{-1} (result derived from Hagy et al. 2000). Chesapeake Bay had values ~ 10-20 cm d^{-1}. Near the estuarine turbidity maximum of each estuary, exchange velocity was ~ 27 cm d^{-1} for Patuxent River versus 65-120 cm d^{-1} in Chesapeake Bay. However, because Chesapeake Bay has a greater average depth than Patuxent River, the turnover time for the lower layer volume based on the non-advective exchange alone was higher in Chesapeake Bay. During summer in the middle reach of Chesapeake Bay, this turnover time was ~50 days, approximately 5 times the turnover time for Patuxent River (~8-10 days), perhaps contributing to the greater severity of hypoxia and anoxia in Chesapeake Bay compared to Patuxent River (Hagy and Boynton 2000).

The average summertime non-advective exchange velocities (E_{vm}/A) for the mesohaline Bay, 10-20 cm d^{-1}, are equivalent to vertical diffusivities (D_z) of 0.10-0.21 cm^2 s^{-1} (eq. 5), a value similar to or slightly lower than previously reported estimates for Chesapeake Bay (Kemp et al. 1992).

Physical Transport Variability Associated with Freshwater Inflow

It has been previously suggested that spring average river flow affects summer water column stratification and vertical mixing by depressing average salinity throughout the Bay (Boicourt 1992). The horizontal salinity gradient between the estuary and the adjacent coastal water thereby serves as a "buoyancy reserve" from

which vertical salinity structure can be regenerated following any mixing event through gravitational circulation (Boicourt 1992). This basic model was supported by the results of this study. Summer water column stratification during 1984-1999, quantified using an index based on the Brundt-Väisälä frequency, was strongly related to Susquehanna River flow averaged over the period January-May (r^2=0.90; $p<0.01$; Fig. 2-10), increasing about 50% over the range of river flow. In contrast, other less integrative measures of river flow (i.e. individual months, two-month periods, etc.) were inferior predictors of stratification. Regardless of river flow, summer stratification in the mid Chesapeake Bay is strong. For example, the average squared buoyancy frequency (N^2) in Chesapeake Bay is about 10^{-2} s^{-2}, 500 times greater than the comparable value for the Atlantic Ocean (Massel 1999 reported a period of 4 minutes, or $(1/240)^2 = 7\times10^{-5}$ s^{-2}).

Vertical diffusivity (D_z) is expected to be inversely related to water column stability, a result supported here with qualification (Fig. 2-10). April-September median D_z for the middle segment of the mesohaline Bay (segment 5) varied between 0.24 cm^2 s^{-1} in 1992 and 0.09 cm^2 s^{-1} in 1998. The seasonal median was used to obtain a good indication of central tendency due to the presence of one or more extreme values in most years. In general, median D_z varied such that higher values were associated with low river flow (Fig. 9, lower panel). However, there was substantial uncertainty within this overall pattern. To quantify the relationship, while not allowing any single observation excessive leverage (in the statistical sense, see Sokal and Rohlf 1995, pg. 531), and without arbitrarily excluding any observations, the relationships between D_z and max(N^2) and D_z and January-May average river flow

were quantified using iteratively-reweighted regression (SAS Institute 1990). For 1986-1998, April-September median D_z varied was related to max(N^2) via

$$D_z = 0.26 - 11.8 \max\left(N^2\right) \quad (17)$$

(s.e. of slope = 6.5) and to January-May average Susquehanna River flow ($m^3\ s^{-1}$) via

$$D_z = 0.20 - 3.3(10^{-5})Q \quad (18)$$

(s.e. slope = 1.9 10^{-5}). According to the latter model, the expected D_z at low, average and high river flow is ~0.17, 0.15 and 0.12, respectively, a range of 40% relative to the minimum. This is slightly less variability than was observed for max(N^2) over the same range of spring river flow. Both models explained only ~22% of the variability in D_z and gave admittedly imprecise estimates of D_z, indicating that factors affected D_z in addition to water column stratification in the central channel of the Bay. This could include wind- and tide-driven seiching events (Breitburg 1990, Sanford et al. 1990, Boicourt 1992). The salt exchange resulting from such events would be integrated in the box-model based measures of vertical exchange, even though the effect on stratification in the central channel of the Bay might be minimal. Interestingly, residuals in the lower panel of Fig. 2-10 were related to departures from the relationships between hypoxia and river flow (e.g. 1992, 1995, 1998, Chapter 3). Negative residuals for 1995 and 1998 (Fig. 2-10) were related to unexpectly high hypoxic volume (Chapter 3), while positive residuals for 1992 and 1996 were associated with lower than expected hypoxia (Chapter 3).

While it has long been recognized that interannual changes in river flow could affect vertical mixing in Chesapeake Bay, the effect of river flow on horizontal advection is both more obvious intuitively and less clear in reality. On the one hand,

river flow contributes directly to seaward advection, and should be correlated, as implied by Fig. 2-5. On the other hand, seasonal variations in the flow multiples (Q/Q_r, i.e. $2R$, $3R$, $4R$ in Fig. 4) are associated with the seasonal pattern of freshwater input such that in spring, where river flow is high, the multiple is low. In summer and fall, when river flow is low, the multiple is high (Fig. 4). This mitigates against the simple effect of freshwater inflow on R. The same effect appears to operate interannually (Fig. 2-11), except that the increase in river flow overwhelms the decreasing multiple such that landward advection did in fact increase with freshwater inflow. At low average spring river flow (1000 $m^3 s^{-1}$), landward advection into the mid Bay during summer was 3.3-fold greater than spring average freshwater input, however this decreased to 1.9R at high flow (Fig. 2-11). Summer average landward advection into the mid Bay ($m^3 s^{-1}$) was predicted by

$$Q_7' = 2386 \pm 511 + 0.94 \pm 0.3 Q_r \qquad (19)$$

where Q_r is the January-May average Susquehanna River flow ($m^3 s^{-1}$, r^2=0.68, $p<0.05$). Further up-estuary, the multiple was lower (similar to Fig. 2-5) and there was no clear relationship between spring average freshwater inflow and landward advection.

Conclusions

The results suggest that this relatively simple box model is an effective tool for estimating net transport in Chesapeake Bay at seasonal time scales. Given the complexities of implementing a hydrodynamic circulation model for this purpose alone, or for interpreting the results of such a simulation, this approach may be a

useful alternative for ecologists and other environmental scientists seeking to evaluate large-scale transport issues for this system. In addition, as has been described to some extent here, comparisons among estuaries are possible, indicating how differences in physical transport could affect ecological processes in those ecosystems. Many such applications are possible. For example, it is possible to develop regionally and seasonally resolved oxygen budgets for the lower water column (see Chapter 2). These transport estimates could also be used to examine nutrient, carbon, or even dissolved toxicant transport within the estuary. Some of these applications have been approached in the past using similar methodologies (e.g. Taft et al. 1978, Officer et al. 1984). However, the model presented here utilized important improvements to the box model as well as a much more extensive water quality and freshwater input record.

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Table 2-1. The boundaries of the box model segments in channel kilometers from the mouth of the Bay and the depth of the pycnocline dividing the surface and bottom layers.

Segment Number	South Boundary (km)	North Boundary (km)	Pycnocline Depth (m)
9	1	19	6
8	19	46	7
7	46	93	8
6	93	139	12
5	139	185	12
4	185	222	12
3	222	241	7
2	241	259	5
1	259	287	N/A

Table 2-2. The volume of mainstem Chesapeake Bay and the tributaries and embayments with which lateral salt exchanges occur and the stations used to estimate mean salinity throughout the Chesapeake Bay estuarine system.

Basin	Volume (10^6 m^3)	% of Total	CBMP Stations[1]
Chesapeake Bay	51,027	67.0	CB1.1, CB2.1, CB3.1, CB3.2, CB3.3C, CB4.1C, CB4.2C, CB4.3C, CB4.4, CB5.1, CB5.2, CB5.2, CB5.3, CB5.4, CB.5.5, CB6.1 CB6.2, CB6.3, CB6.4, CB7.3, CB7.4
Eastern Bay	721	0.9	EE1.1
Choptank River	1,324	1.7	EE2.1
Patuxent River	430	0.6	TF1.5, TF1.6, TF1.7, RET1.1, LE1.1, LE1.2, LE1.3, LE1.4, CB5.1W
Potomac River	7,141	9.4	TF4.2, TF2.0, TF2.1, TF2.2, TF2.3, TF2.4, RET2.2, RET2.4, LE2.2, LE2.3
Rappahannock River	1,640	2.2	TF3.2, TF3.3, RET3.1, RET3.2, LE3.1, LE3.2, LE3.4, LE3.6
Tangier Sound	3,169	4.2	EE3.4, EE3.5
Pocomoke Sound	848	1.1	EE3.3
York River	917	1.2	TF4.2, RET4.1, RET4.3, LE4.1, LE4.2, LE4.3, WE4.2
James River	2,166	2.8	TF5.6, RET5.2, LE5.1, LE5.2, LE5.3, LE5.4, LE5.5
Total, Tributaries and Embayments	18,356	24	
Total Volume	69,383	91	

[1] Chesapeake Bay Water Quality Monitoring Program stations from which data was used to calculate the salinity of the respective water body.

Table 2-3. The fall line gauges, USGS ID and drainage area upstream of the fall line gauging station on the major tributaries of Chesapeake Bay. Freshwater flows enter the segment or segments indicated.

Basin	USGS ID	Gauged Drainage Area (km^2)	Ungauged Drainage Area (km^2)	Box Model Segment
Major Tributary Watersheds:				
Choptank River near Greensboro, MD	01491000	293	n/a[1]	5
Potomac River near Washington, DC	01646500	29,940	6,699	6
Patuxent River near Bowie, MD	01594440	901	550	5
Susquehanna River at Conowingo, MD	01578310	70,189		1
Rappahannock River near Fredericksburg, VA	01668000	4,134	2,462	7
Pamunkey River near Hanover, VA	01673000	2,800		
Mattaponi River near Beulahville, VA[2]	01674500	1,557		
York River (Mattaponi+Pamunkey)		*4,357*	2,323	8
Appomattox River near Matoaca, VA	02041650	3,481		
James River near Richmond, VA	02037500	17,503		
James River (James+Appomattox)		*20,984*	4,958	9
SUB-TOTAL		130,798	16,992	
Smaller Watershed Areas				
PA/DE/MD Eastern Shore[3,4]			9,086	1,3-7
VA Eastern Shore[3,4]			831	7
PA/MD Western Shore[3,5]			3,059	2,3,4
VA Western Shore[3,6]			1,812	6-9
Open Water			2,078	
SUB-TOTAL			16,866	
TOTAL AREA		130,798	33,858	

[1] Below fall line areas of the Choptank River were included within the PA/DE/MD Eastern Shore.
[2] The Mattaponi gauges did not function during late 1987 through early 1989. Monthly average flow of the Mattaponi during that period was estimated via a regression model (r^2>0.9) from the monthly average flow of the Pamunkey River.
[3] Areas determined from Phase IV Chesapeake Bay Watershed Model segments (EPA 1998; Hopkins et al. (2000).
[4] Flow/area based on gauged portion of Choptank River (USGS gauge 01491000).
[5] Flow/area based on gauged portion of Patuxent River (USGS gauge 01594440)
[6] Flow/area based on gauged portion of Mattaponi River (USGS gauge 01594440)

Table 2-4. The dimensions, including the length, pycnocline area, cross-sectional area (cross-sec), and volume of the surface layer (SL) and bottom layer (BL) boxes in segments 1 through 9 of the box model.

	Box 1	Box 2	Box 3	Box 4	Box 5	Box 6	Box 7	Box 8	Box 9
Length[1]	28	18	29	37	46	46	47	27	18
Surface Area[2]	217	255	169	489	655	1025	1425	782	454
Pycnocline Area[2]		80	92	144	249	278	904	510	289
Cross-Sec, SL[3]	28	60	52	107	123	185	212	178	139
Cross-Sec, BL[3]		13	31	27	35	37	85	83	57
Volume, SL[4]	773	1077	995	3961	5675	8502	9977	4796	2500
Volume, BL[4]		242	593	988	1612	1684	4015	2246	1018

[1] units=km; [2] units=km^2; [3] units=10^3 m^2; [4] units=10^6 m^3

Table 2-5. Box model estimates of the long-term (1986-1998) average monthly physical transport ($m^3 s^{-1}$) for Chesapeake Bay. Estimates include (a) Freshwater inputs to each model segment, (b) seaward advection in the surface layer of each segment, (c) upwelling in each two layer segment, and (d) non-advective vertical exchange in each two layer segment. All transport rates have units of $m^3 s^{-1}$.

(a.)

Month	Q_{f0}	Q_{f1}	Q_{f2}	Q_{f3}	Q_{f4}	Q_{f5}	Q_{f6}	Q_{f7}	Q_{f8}	Q_{f9}	Total
Jan	1300	28	38	25	21	78	722	184	133	482	3011
Feb	1269	36	35	28	23	84	731	181	158	493	3038
Mar	1923	55	49	37	31	113	1075	237	179	620	4318
Apr	2167	28	37	25	21	78	799	169	144	501	3969
May	1298	18	35	21	18	67	675	147	98	380	2757
Jun	681	1	23	13	12	42	317	98	53	252	1490
Jul	501	-12	17	7	7	25	199	60	36	156	996
Aug	389	-11	15	8	7	25	179	48	27	109	797
Sep	389	-17	15	6	6	20	219	63	31	178	909
Oct	612	-13	18	7	7	25	203	65	36	161	1121
Nov	1020	-9	26	10	10	34	310	95	56	206	1758
Dec	1257	10	32	18	16	57	487	130	99	311	2418
Average	1067	9	28	17	15	54	493	123	88	321	2215
% input	48	0.4	1.3	0.8	0.7	2	22	6	4	14	

(b.)

Month	Qf_0	Q_1	Q_2	Q_3	Q_4	Q_5	Q_6	Q_7	Q_8	Q_9
Jan	1300	1647	2529	3623	5235	6002	9207	8075	8504	16915
Feb	1269	1625	2525	3625	5091	5431	8520	6611	7373	14032
Mar	1923	2222	3040	4183	5975	6644	9837	9190	10417	21008
Apr	2167	2447	3064	3850	5342	6132	8987	9026	9145	15880
May	1298	1529	2081	2617	3544	4179	7288	8403	8598	13430
Jun	681	814	1293	1612	2197	2881	5116	5974	6671	11680
Jul	501	673	1070	1261	1921	2488	4274	4693	5481	9301
Aug	389	590	1020	1212	1938	2657	4592	5305	5808	9475
Sep	389	604	1180	1518	2220	3035	5362	6487	6922	13348
Oct	612	884	1499	2168	2812	3454	5254	5593	5539	9966
Nov	1020	1284	1989	2941	4569	5159	6822	5969	6276	11656
Dec	1257	1533	2415	3471	5109	5955	8633	8213	7738	15970
Average	1067	1321	1975	2673	3829	4501	6991	6962	7373	13555
Ratios:[1]										
$Q_m \Big/ \sum_{m=0}^{m} Q_{fm}$	1.0	1.2	1.8	2.4	3.4	3.8	4.2	3.9	3.9	6.1
Q_m / Q_{f0}	1.0	1.2	1.9	2.5	3.6	4.2	6.6	6.5	6.9	12.7

[1] calculated from the annual average.

(c.)

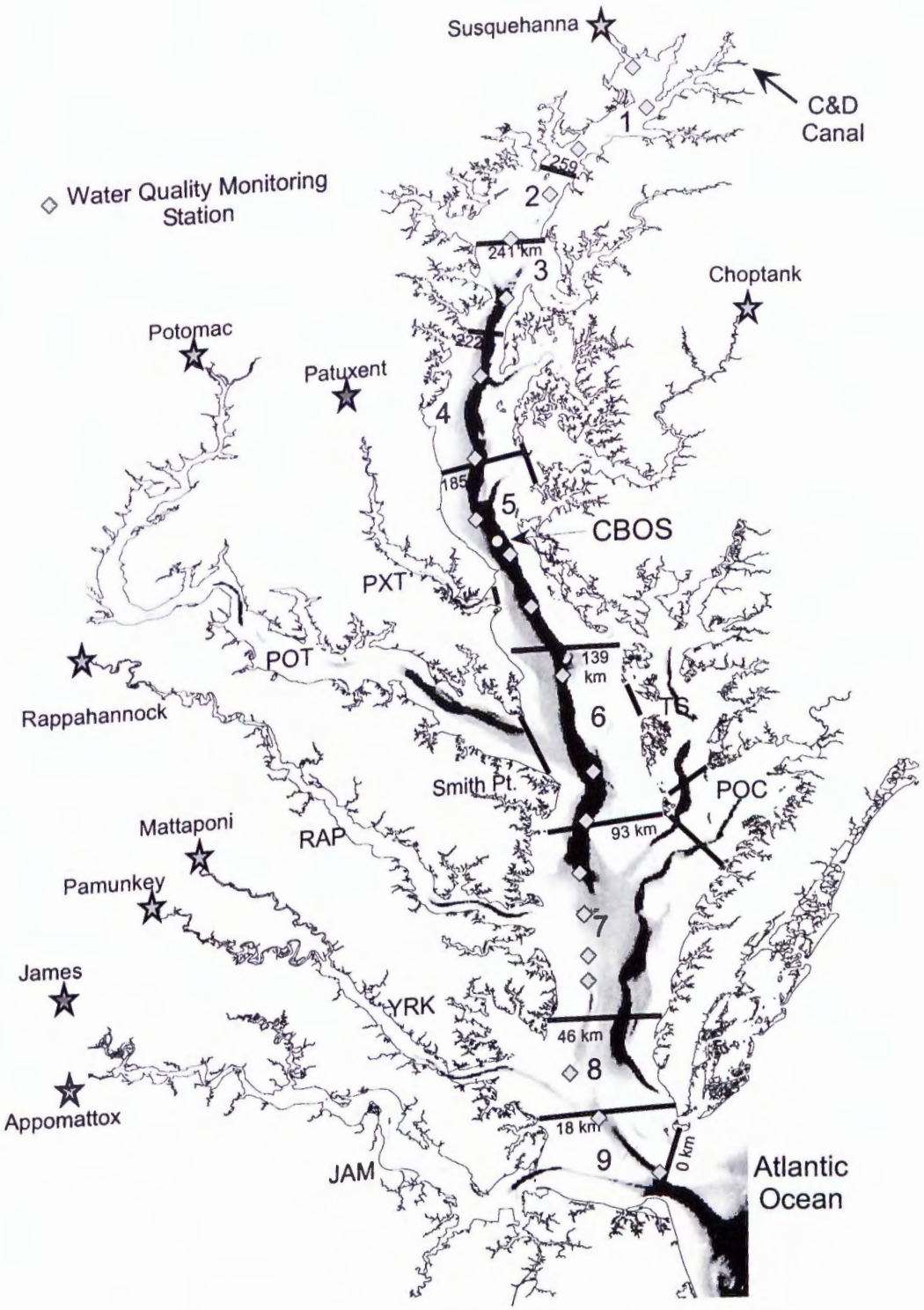
Month	Q_{v2}	Q_{v3}	Q_{v4}	Q_{v5}	Q_{v6}	Q_{v7}	Q_{v8}	Q_{v9}
Jan	844	1068	1592	689	2482	-1315	296	7929
Feb	865	1073	1442	256	2359	-2090	604	6167
Mar	768	1106	1761	557	2118	-884	1049	9971
Apr	580	761	1471	713	2055	-129	-26	6235
May	516	515	908	569	2433	968	97	4452
Jun	456	306	574	642	1918	761	644	4757
Jul	380	184	652	542	1587	359	752	3664
Aug	414	184	719	694	1756	665	475	3558
Sep	561	333	696	796	2107	1062	404	6248
Oct	597	662	637	618	1596	275	-91	4266
Nov	679	943	1618	556	1353	-949	251	5174
Dec	851	1037	1623	788	2191	-549	-574	7921

(d.)

Month	E_{v2}	E_{v3}	E_{v4}	E_{v5}	E_{v6}	E_{v7}	E_{v8}	E_{v9}
Jan	641	849	984	1398	1054	6740	13642	10620
Feb	818	1109	863	1107	802	3298	7816	8647
Mar	619	875	1073	1193	2341	5801	8089	8173
Apr	801	757	766	692	1267	6865	8820	5038
May	670	619	401	430	454	4423	8090	5037
Jun	728	724	392	451	630	3807	7580	3752
Jul	765	475	194	415	253	3226	5389	3285
Aug	915	520	-31*	397	224	3617	5916	3778
Sep	1148	892	310	804	1170	5430	11750	6694
Oct	1036	929	1236	1333	1982	7688	11059	6643
Nov	944	927	1468	2081	3288	9394	15775	8879
Dec	681	609	799	1562	2375	11448	31371	15948

* This estimate has been included for completeness, but is invalid and cannot be interpreted. Most likely, E_{v4} for August was small, but comparable to adjacent months.

Fig. 2-1. A map of Chesapeake Bay showing the bathymetry (<10, 10-15m, >15m), the boundaries of the segments of the box model, the embayments that were included in the salt budget (e.g. TS, YRK), and the fall lines for which freshwater inputs data were obtained (denoted by ☆) Tangier (TS) and Pocomoke Sounds (POC) were assumed to exchange primarily with box 7 because the deep channel runs in the North South direction into Box 7. The passes between the islands to box 6 are much narrower and shallower. Distances indicated on the segment boundaries are channel kilometers from the Bay mouth. The location of the mid-Bay Chesapeake Bay Observing System (CBOS) buoy, from which current meter readings were obtained is also indicated.


Susquehanna
C&D Canal
Water Quality Monitoring Station
259
241 km
222
185
139 km
93 km
46 km
18 km
0 km
1
2
3
4
5
6
7
8
9
Choptank
Potomac
Patuxent
CBOS
PXT
POT
TF
POC
Rappahannock
Smith Pt.
Mattaponi
RAP
Pamunkey
James
YRK
Appomattox
JAM
Atlantic Ocean

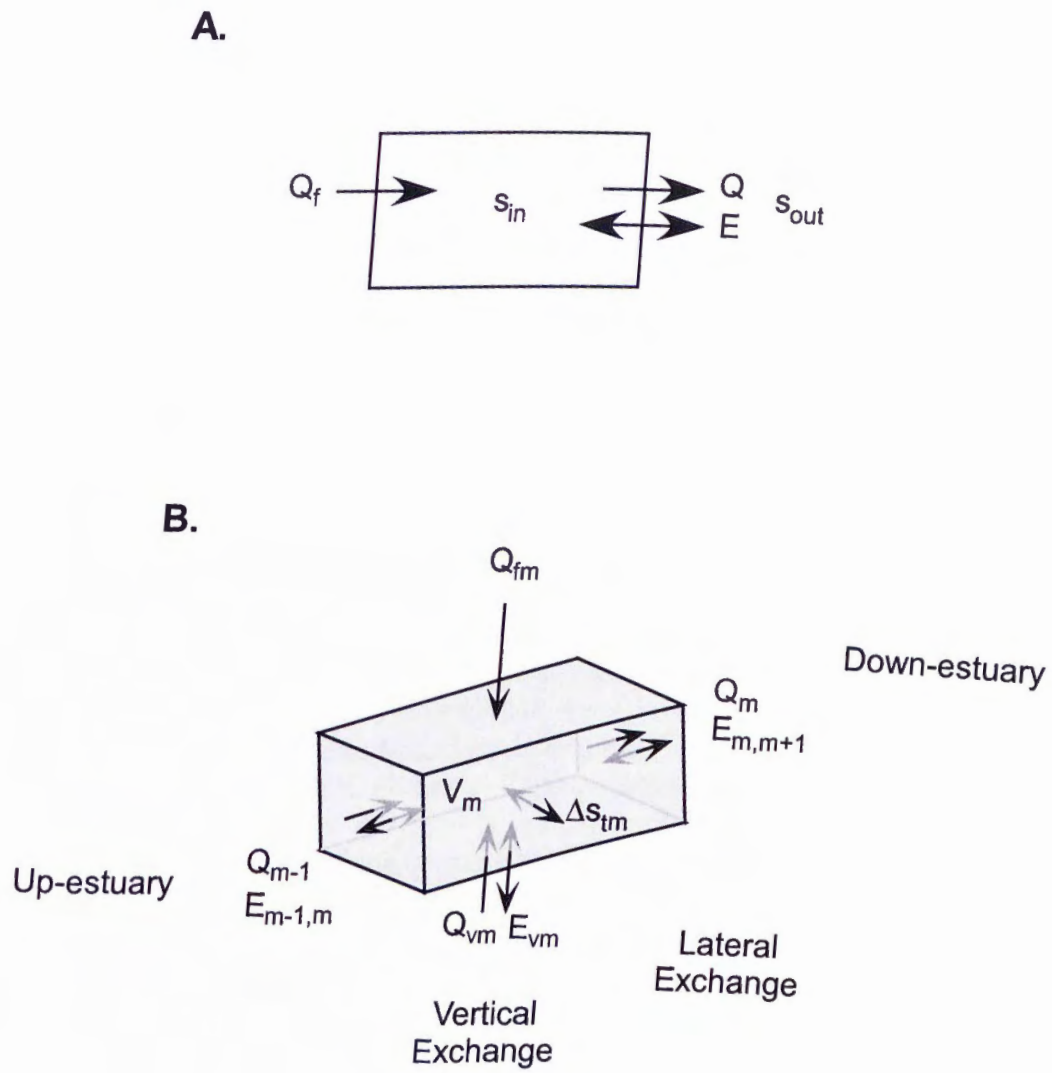
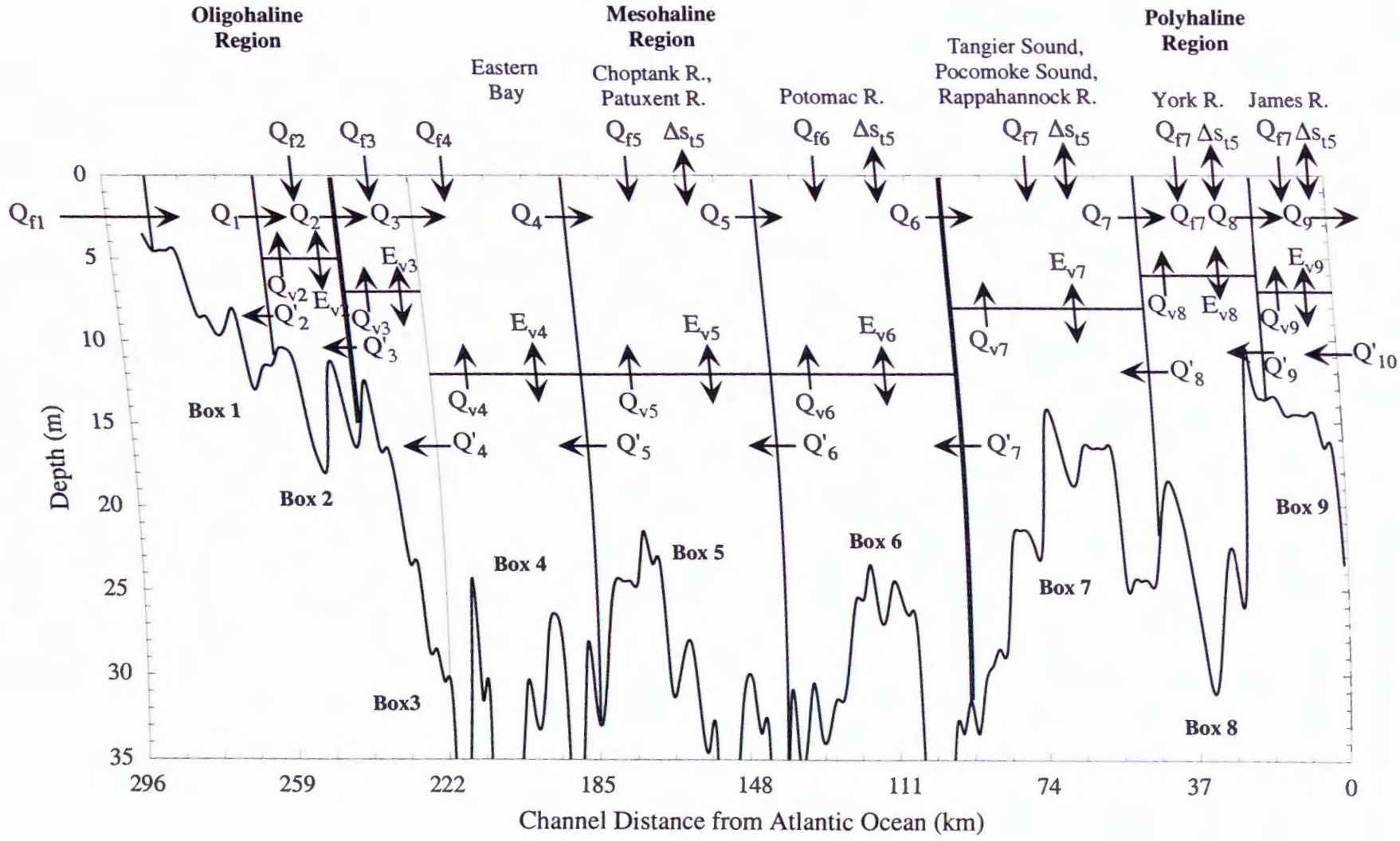


Fig. 2-2. (A) The simplest possible box model for an estuary, where Q_f is freshwater input, Q is advection out, and E is dispersive exchange at the seaward margin. (B) An illustration of the possible physical exchanges for a surface layer box (box "m") in a vertically structured, branching model such as the Chesapeake Bay box model. The exchanges correspond to terms in eq. (9). For all the model segments, $E_{m,m+1}$ and $E_{m-1,m}$ were assumed to be negligible. For bottom layer boxes, Q_{fm} and ΔS_m are not present and the horizontal advection terms are directed up-estuary.

Fig. 2-3. A schematic diagram of box model for Chesapeake Bay, drawn overlying the maximum depth profile of the estuary. The approximate boundaries of the major salinity zones of the estuary are shown as heavy lines. Bi-directional arrows indicate salt exchanges, while uni-directional arrows indicate advective flows. Exchanges involving Eastern Bay, Tangier Sound and Pocomoke Sound are lateral salt exchanges. Exchanges with the Choptank, Patuxent, Potomac, Rappahannock, York, and James Rivers involve salt exchanges and exports of fresh water into the indicated regions. Freshwater inputs to box 1 through 3 include only diffuse freshwater inputs from small watersheds.


Oligohaline Region
Mesohaline Region
Polyhaline Region
Eastern Bay
Choptank R., Patuxent R.
Potomac R.
Tangier Sound, Pocomoke Sound, Rappahannock R.
York R.
James R.
Depth (m)
Channel Distance from Atlantic Ocean (km)
Box 1
Box 2
Box3
Box 4
Box 5
Box 6
Box 7
Box 8
Box 9

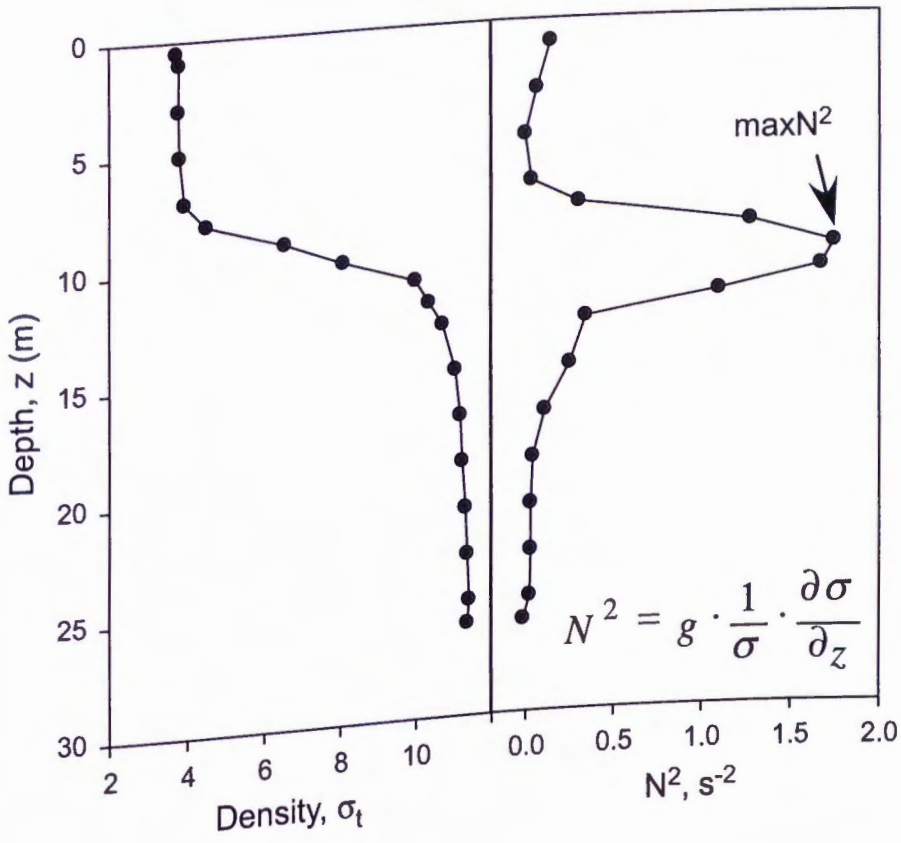


Fig. 2-4. An illustration of the definition of max(N^2), a measure of pycnocline strength based on the squared Brundt-Väisälä frequency (N^2). The data are from the Chesapeake Bay Water Quality Monitoring Program and were collected at a station in the mid Chesapeake Bay (CB4.3C) on July 7, 1998. In the formula for N^2, g is the gravitational acceleration (Massel 1999).

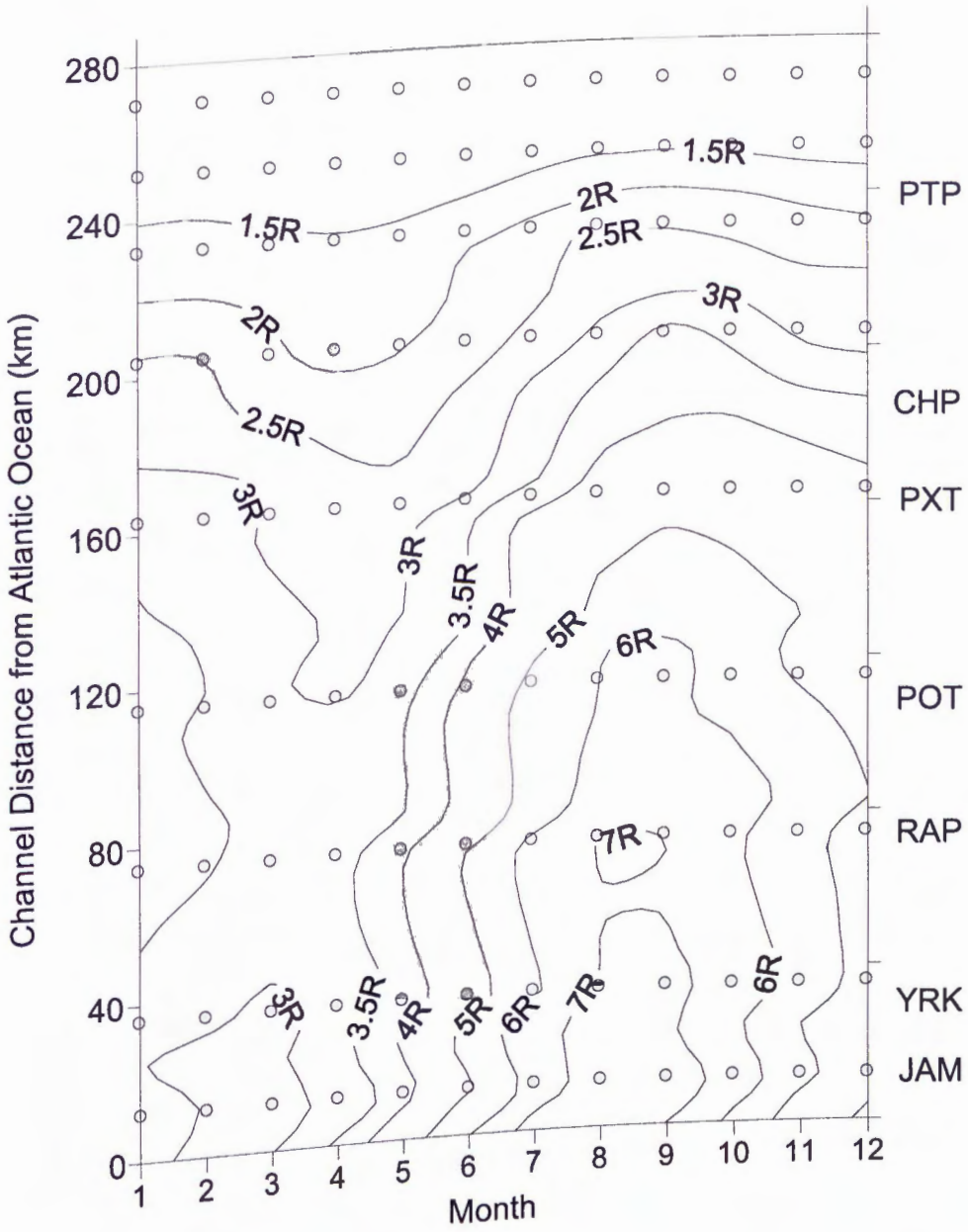


Fig. 2-5. Monthly average down-estuary advection computed using the box model and expressed as a multiple of the total landward freshwater input (R). Contours show the change in relative advection along the length of the estuary and through the seasons of the year. Shaded circles indicate the time/location combinations obtained from the box model and used to generate the contours. Codes on the right indicate the locations of major tributaries. JAM=James R., York=York R., Rap=Rappahannock R., POT=Potomac R., PXT=Patuxent R., CHP=Choptank R., PTP=Patapsco R.

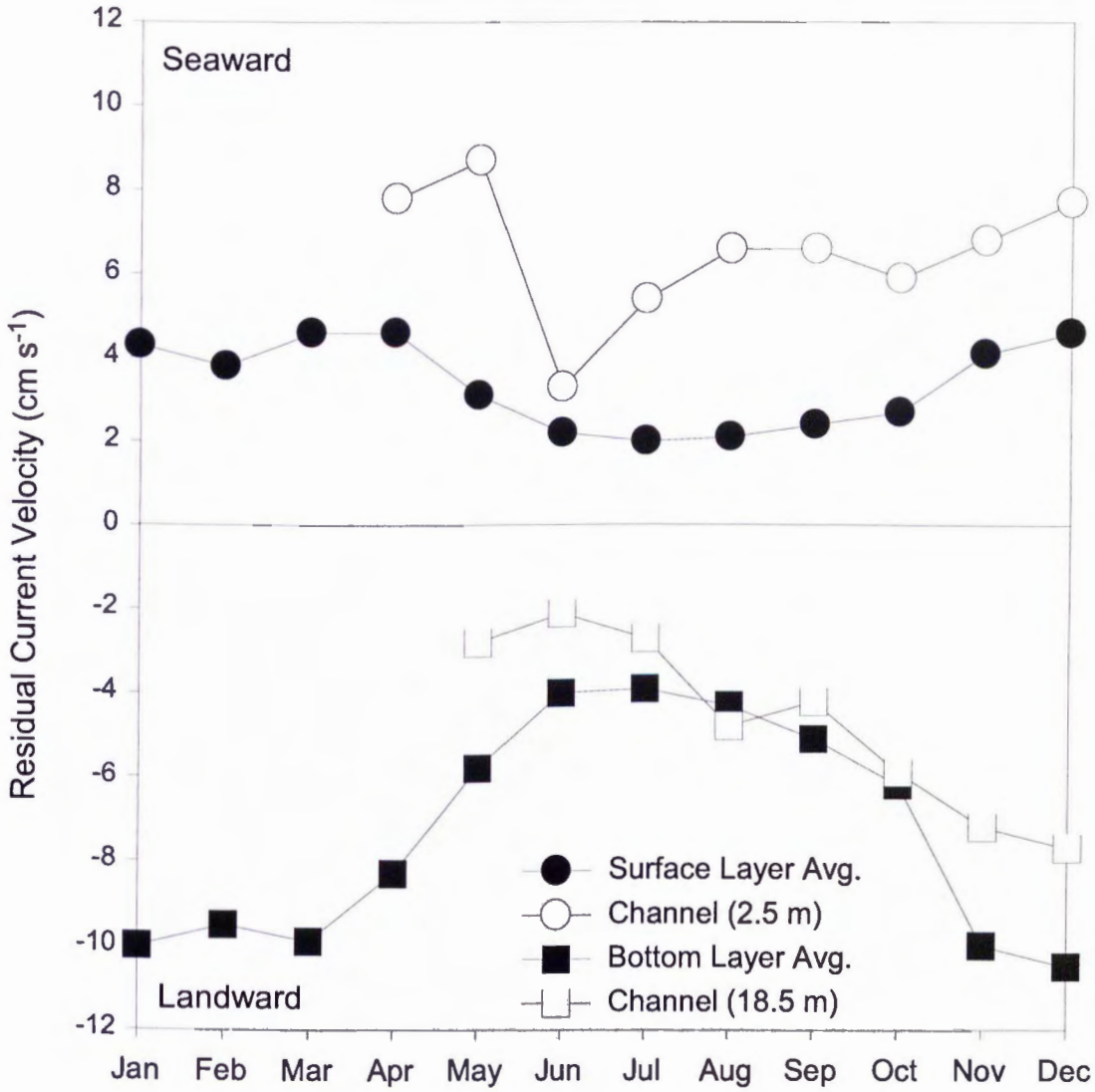


Fig. 2-6. A comparison of cross-section average current velocity computed by the box model for surface layer and bottom layer in segment 5 with residual current velocity obtained by averaging 1995-1999 current meter data at the mid-Bay mid-channel buoy of the Chesapeake Bay Observing System (CBOS, W. Boicourt, unpublished data). Current meters were located at 2.5 m and 18.5 m depth and recorded the current velocity at approx. 5 minute intervals.

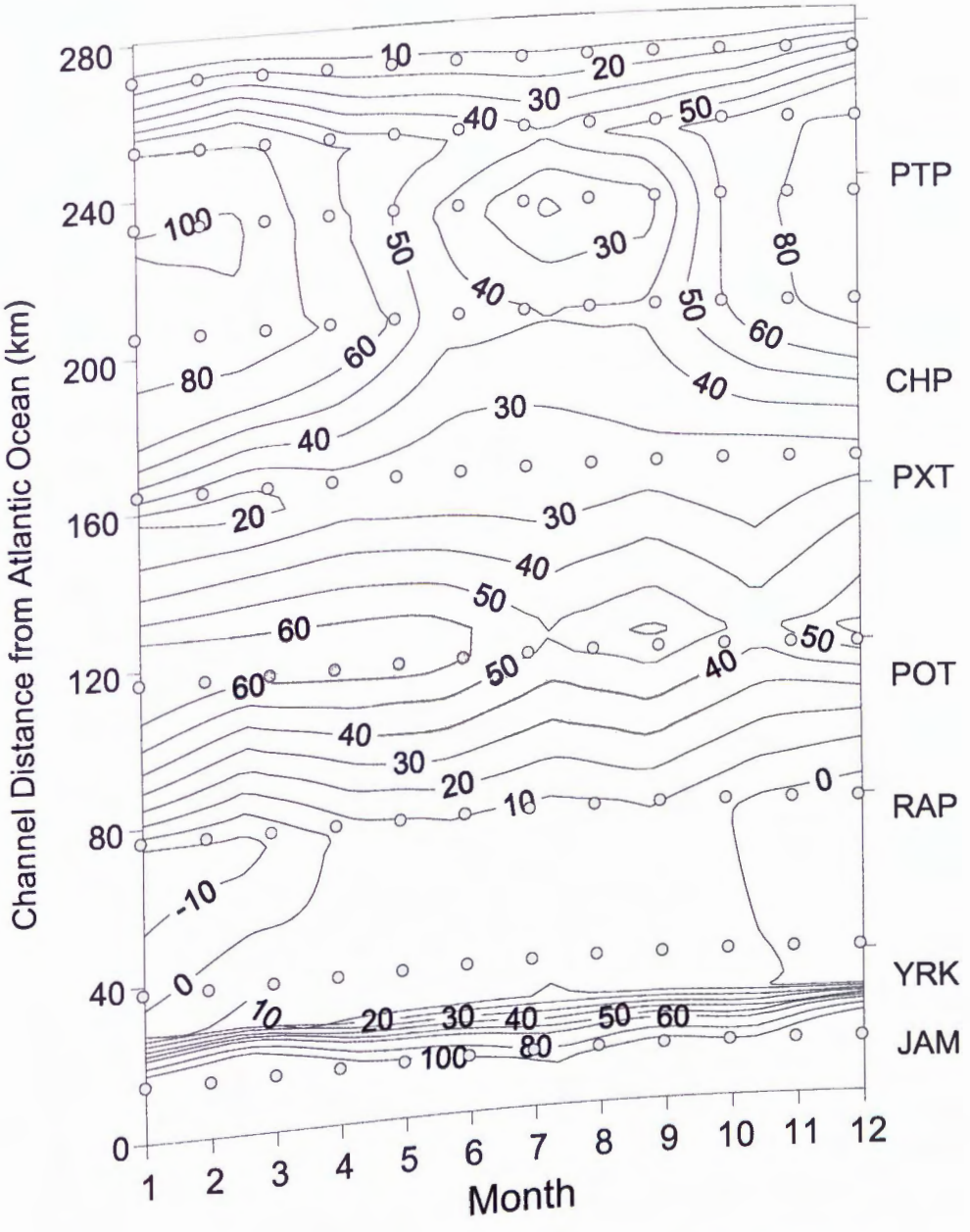


Fig. 2-7. Seasonal and spatial patterns in average upwelling current velocity (cm d^{-1}) in Chesapeake Bay as computed by the box model. Shaded circles indicate the time/location combinations obtained from the box model and used to generate the contours. Codes on the right refer to the locations of the major tributary rivers, and are described on Fig. 2-5. Modest negative values during November-April near 80 km (between Rappahannock River and Potomac River) indicate downwelling of surface water into the lower layer.

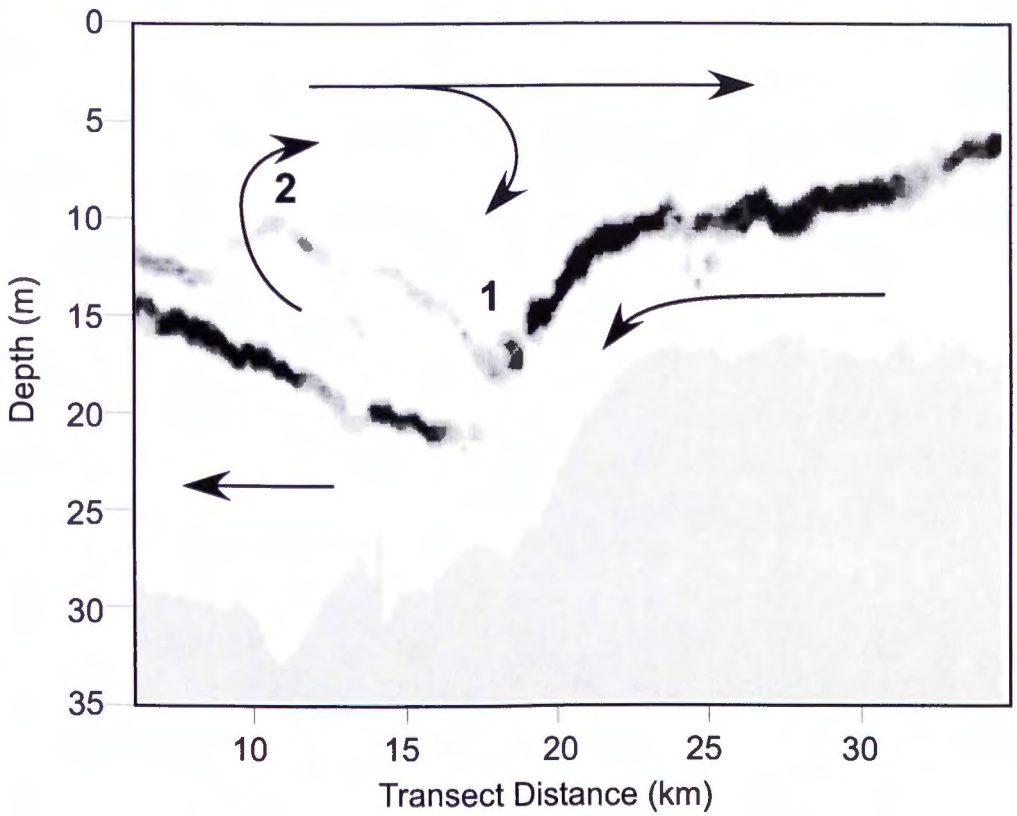


Fig.2-8. A profile of the Brundt-Väisälä frequency in the region of Chesapeake Bay just to the south of the Potomac River, collected in April 1998 by the Chesapeake Bay LMER (TIES) program using a towed undulating CTD device. Darker colors indicate increased density gradients, indicating the boundaries between water masses. The downwelling region is indicated by "1" while the enhanced upwelling region is indicated by "2."

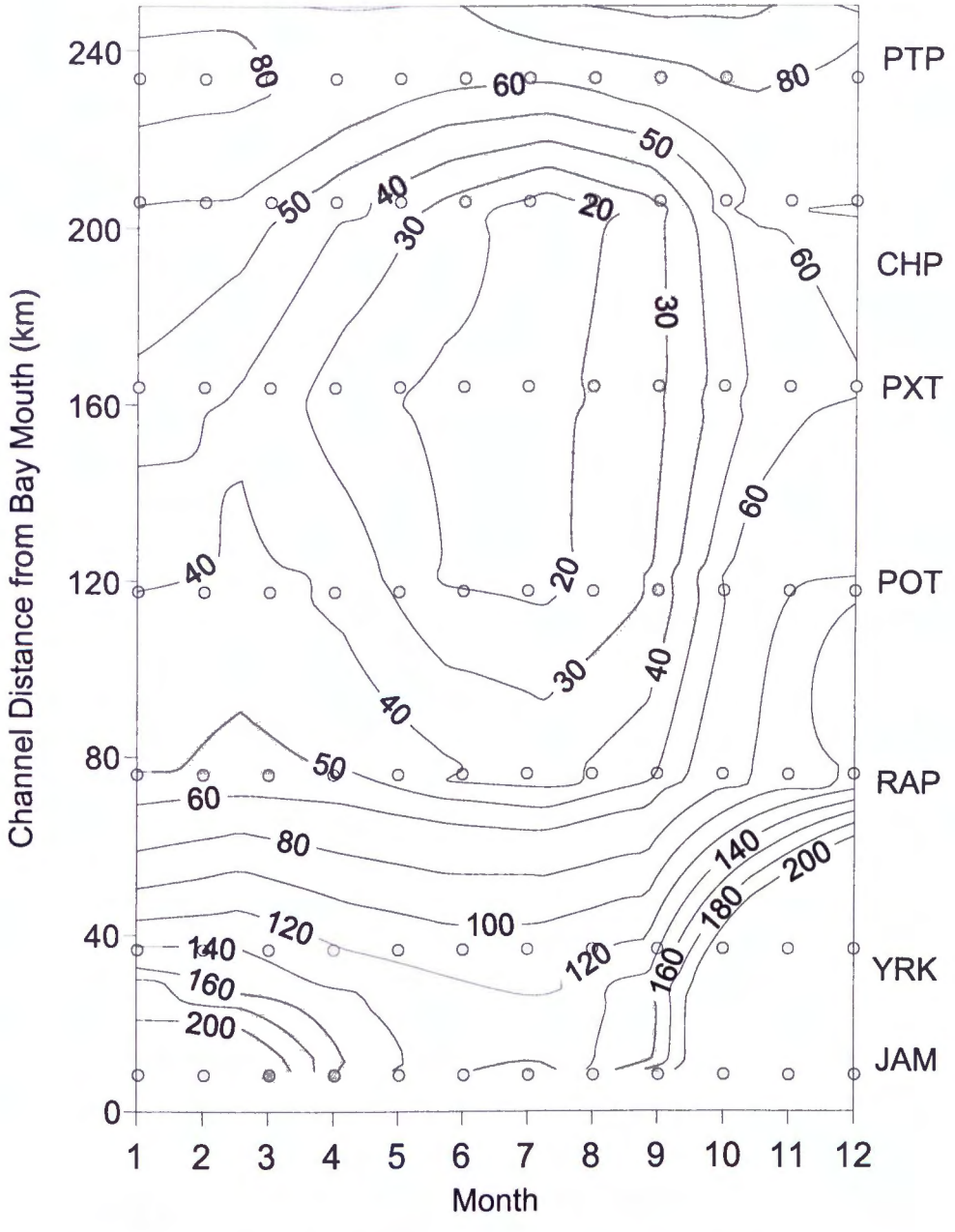


Fig. 2-9. Seasonal and spatial patterns in average non-advective exchange velocity (cm d^{-1}) in Chesapeake Bay as computed by the box model. Shaded circles indicate the time/location combinations obtained from the box model and used to generate the contours. Codes on the right refer to the locations of the major tributary rivers, and are described on Fig. 2-5. This quantity is the non-advective exchange coefficient (E_{vm}) scaled by the pycnocline area of the respective model segment.

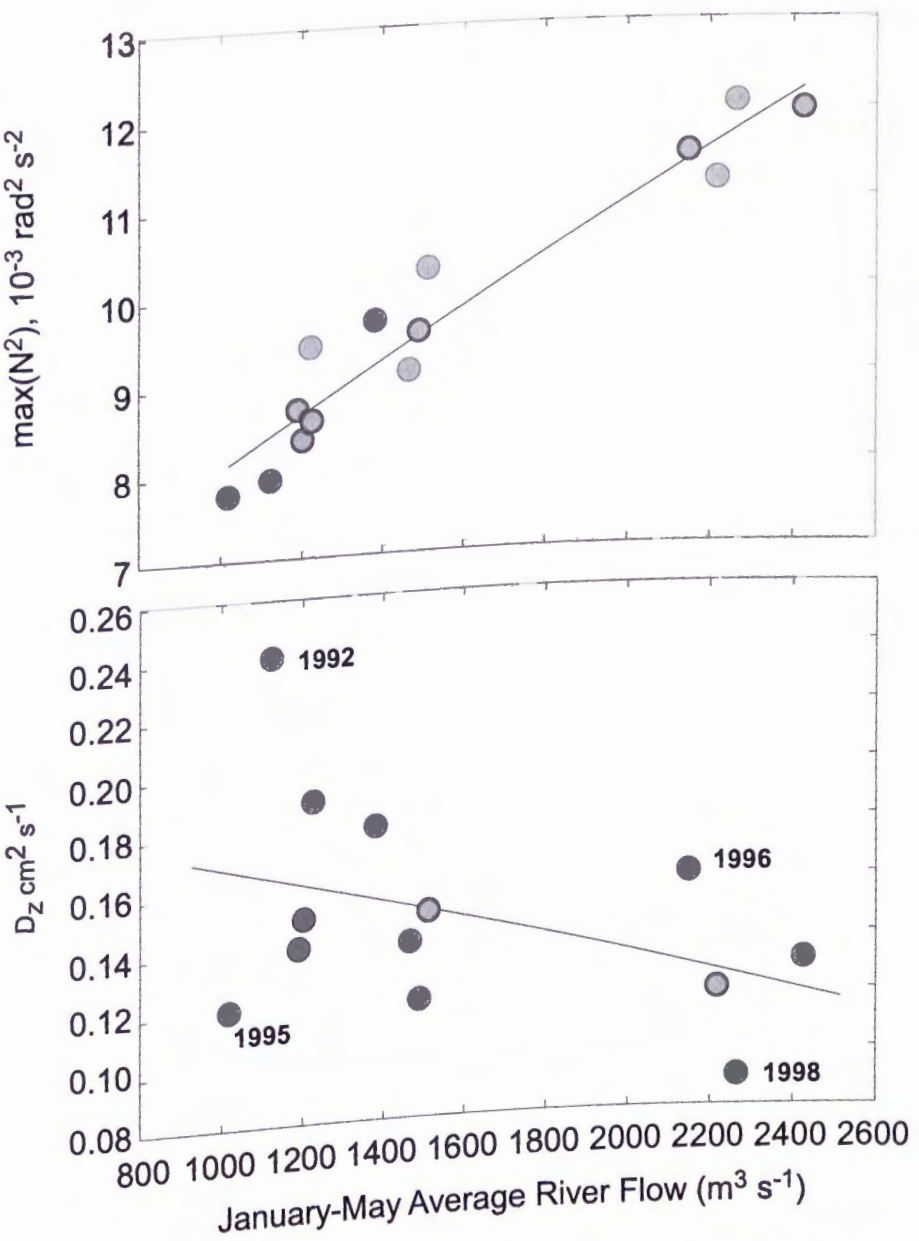


Fig. 2-10. Upper Panel - The relationship between January-May average Susquehanna River flow and April-September average water column stratification index, max(N^2), in the mesohaline Chesapeake Bay. The indicated line is the least-squares regression line (r^2=0.90). Lower Panel - The relationship between April-September median vertical diffusivity (D_z) and January-May average river flow. The indicated line is the interatively-reweighted (robust) least squares regression line (SAS Institute 1990).

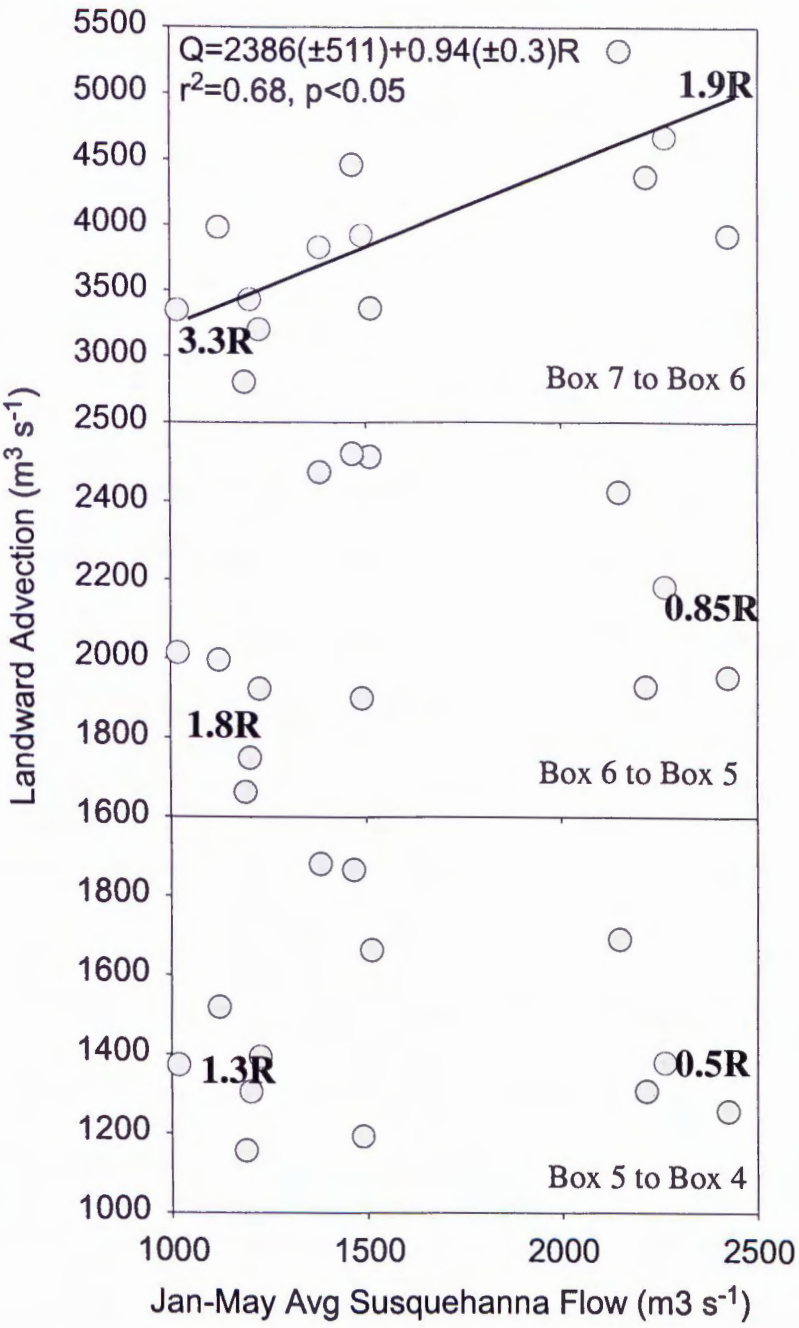


Fig. 2-11. Average up-estuary advection within the mid Bay region related to January-May average Susquehanna River flow (m^3 s^{-1}). Multiples (i.e. 2.5R) refer to the relative magnitude of the landward advective flow compared to the freshwater input. Multiples are <u>not</u> comparable to those in Fig. 4 (they are smaller) since these compare summer advection to spring freshwater inflow.

Chapter 3:

HYPOXIA IN CHESAPEAKE BAY, 1950-2000: PROGRESSIVE DEVELOPMENT AND RIVER FLOW EFFECTS

Abstract

A 50-year record of dissolved oxygen in Chesapeake Bay was analyzed to describe the progressive development of hypoxia and anoxia in Chesapeake Bay pelagic and benthic habitats since 1950. The effect of Susquehanna River flow on hypoxia was examined to separate changes in hypoxia associated with river flow from changes due to other effects that may have varied over time. From 1950-2000, mid-summer hypoxic volume increased substantially and at an accelerating rate. At average river flow, near anoxic volume ($DO<0.2$ mg l^{-1}) increased from zero in 1950 to $3.7x10^9$ m^3 in 2000. Moderate hypoxia increased from $1.7x10^9$ m^3 to $6.5x10^9$ m^3 over the same period, while mild hypoxia ($DO<2.0$ mg l^{-1}) increased from $3.6x10^9$ to $9.7x10^9$ m^3. Hypoxic volume was positively correlated with January-May average Susquehanna River flow throughout the 50-year period, but this correlation did not explain the long term trend. The area of benthic habitat affected by hypoxia was estimated to have increased nearly in proportion to the hypoxic volume.

Analysis of river flow-related effects showed that anoxia occurred earlier in years with higher spring river flow and warmer early-spring water temperatures. This severely narrowed the window of time during which temperature and dissolved oxygen (DO) were simultaneously adequate for significant macrobenthic activity. Vertical diffusive DO inputs to mid Bay bottom water increased over 1950-1999, but horizontal advective DO inputs decreased due to increased depletion of DO in the

lower Bay in recent years. The result was a net decrease in physical DO transport to the lower water column of the mid Bay during summer, exacerbating possible increases in metabolic rates over the same period. The unstable configuration of positive feedbacks contributes to the difficulty of predicting hypoxic volumes, even when external forcing varies substantially. The implications for management are clear. Nutrient loading rate reductions should lead to improvements in hypoxia, but patience and persistence will be needed in the face of inevitable natural variability.

Introduction

Depletion of dissolved oxygen (DO) from deep waters is a common feature in estuaries and other coastal systems where seasonally or permanent stratification if the water column restricts re-aeration of bottom waters by the atmosphere (e.g. Chesapeake Bay-Officer et al. (1984); Long Island Sound - Welsh et al. 1994; Black Sea - Zaitsev 1992; Baltic Sea - de Jonge et al. 1994; Gulf of Mexico- Rabalais et al. 1999). Hypoxia here refers to the existence of DO concentrations sufficiently low to harm biota directly or adversely affect normal ecological interactions. The exact DO concentration that defines hypoxia is nearly arbitrary since a continuous spectrum of effects has been observed as DO declines from a level not far below saturation. Chronic, non-lethal effects on ecological interactions have been observed when DO was only moderately depressed (~ 4.0 mg l^{-1} or about 75% saturation at Chesapeake Bay summer temperatures, Breitburg et al. 1997). Ritter and Montagna (1999) identified 3 mg l^{-1} as a critical threshold for macrobenthos in Corpus Christi Bay, TX. In contrast, some hypoxia-tolerant species survive DO as low as 1.0 mg l^{-1} (Diaz and

Rosenburg 1995). However, even hypoxia-tolerant benthic communities are adversely affected when DO is less than 1 mg l^{-1}, with reduction to 0.6 mg l^{-1} being particularly harmful (Diaz and Rosenburg 1995).

In Chesapeake Bay, hypoxia or anoxia presently affects much to all of the below-pycnocline waters between 37° 44'N and 39° 04'N (Fig. 1) for most or all of the summer. Events in which a combination of wind- and tide-driven tilting of the pycnocline brings hypoxic below-pycnocline waters into shallower areas, or even to the surface, are common in the mesohaline Bay (Malone et al. 1986; Sanford et al. 1990; Breitburg 1990). Consequently, hypoxia may also adversely affect many shallower habitats in the mesohaline Bay at some time each summer. Many of the major tributaries of Chesapeake Bay are also affected (Hagy and Boynton 2000). Management efforts directed toward reducing hypoxia by reducing nutrient loading (N and P) to the estuary are being implemented on the basis of a scientific consensus that nutrient enrichment has led to the present status of hypoxia in Chesapeake Bay (EPA 2000). However, it is not clear how much improvement in hypoxia should be expected from achievable reductions in nitrogen and phosphorus loading rates. Regrettably, a present lack of estimates of nutrient loading to Chesapeake Bay prior to 1978 precludes approaching this question by regressing hypoxia on nutrient loading rate despite the fact that data sufficient to characterize mid-summer hypoxia in Chesapeake Bay are available for many years back to 1950. As an alternative, if one is willing to assume that nutrient loading rates increased during this period, the trend over time suggests the possible consequences of increased nutrient loading, provided that other possible causes can be ruled out. Two studies have evaluated the available

data describing hypoxia in Chesapeake Bay between 1950 and the early 1980's (Flemer et al. 1983; Seliger and Boggs 1988). Unfortunately, these studies did not agree that hypoxia had increased, indicating the need further analysis to resolve this issue.

The substantial interannual variability in hypoxia has greatly complicated assessment of long-term change and is probably a major reason for the discordant conclusions that have been reached. Seliger and Boggs (1988) found that interannual differences in hypoxic volume were related to mean springtime freshwater discharge into the estuary during spring. In their study, accounting for these river flow effects not only explained the interannual differences, but also the apparent long-term increase in hypoxia (Seliger and Boggs 1988). In contrast, Flemer et al. (1983) found no relationship between freshwater inflow and concluded that hypoxia increased dramatically during 1950-1980, probably in response to increased nutrient loading rates. The difference may have resulted from each study utilizing slightly different subsets of the available data or from their slightly different definitions of hypoxia (<0.7 mg l^{-1} vs. 1.0 mg l^{-1}).

The nature of river flow effects on hypoxia in Chesapeake Bay was also a major focus of this study. Previous research suggests that summer hypoxic volume in Chesapeake Bay is more extensive in years with high river flow (Seliger and Boggs 1988, Hagy and Boynton 2000). The effect of average river flow on hypoxia is one among many effects of river flow on the ecosystem. These effects have generally been related to two highly correlated factors, water column stratification and nutrient loading (Boicourt 1992, USGS RIMP, Boynton and Kemp 2000, Chapter 2). The

extent of the correlation between river flow and nutrient loading rates to the Bay since 1978, when direct measurements of nutrient inputs began, is so great that these two effects are statistically confounded. Consequently, a purely correlative approach using only data for 1978-1999 provides no insight into the relative roles of physical factors (not controllable) and nutrient loading-related factors (more controllable) in determining the extent of hypoxia. However, accounting for river flow effects while evaluating trends in hypoxia for the longer record, 1950-1999, provides a means of separating river flow effects from other factors that may have varied during that time, such as nutrient loading rates. The observed 2-3 fold increase in annual average nitrate (NO_3) concentrations in the tidal fresh Chesapeake Bay between 1965 (~0.3 mg N l^{-1}) and 1980 (~1.0 mg N l^{-1}; Flemer et al. 1983) provides at least some direct indication that loading rates increased substantially during that period.

Another factor that could have affected the development of hypoxia over time is the interaction between physical transport regimes and changing DO distributions within the Bay. Kemp et al. (1992) suggested that decreased oxygen concentrations in the lower water column may have increased the physical flux of DO to the bottom layer by intensifying DO gradients. Conversely, an increase in DO due to decreased DO demand by biota would reverse this effect, dampening further increases in DO below the pycnocline. At the same time, Kuo and Neilsen (1987) and Kuo et al. (1991) illustrated the role of horizontal DO fluxes in determining the development of hypoxia.

This chapter describes the results of a detailed analysis of the DO record for Chesapeake Bay since 1950. The extensive measurements of DO collected by the

Chesapeake Bay Institute (1950-1980) and the Chesapeake Bay Monitoring Program (1984-1999) were combined to estimate the long-term change in hypoxia and the effect of river flow as a modulator of that trend, resolving and identifying the causes of discordance in previous studies and expanding on the results using data for recent years. Hypoxia was defined using three different thresholds, 0.2, 1.0 and 2.0 mg l^{-1}, with the results obtained for each being contrasted. For recent years, the extent of hypoxia was also evaluated using a time-space integrating approach. Mechansisms affecting the development and maintenance of hypoxia in the mid Bay were explored by examining the effect of river flow on the rate of spring-time oxygen depletion (e.g. Officer et al. 1984) and using box model based estimates of physical transport rates (Chapter 2).

Methods

Sources of Data and Analytical Methods

This study was based on previously collected water quality and river discharge data. The available data and sources are described in Table 3-1. The Chesapeake Bay Institute (CBI) dissolved oxygen data (1950-1980) were collected by pumping water from depth and measuring DO using a modified Winkler titration (Carpenter 1965a), which has an estimated accuracy of 0.1% (Carpenter 1965b). The Chesapeake Bay Water Quality Monitoring Program (1985-2000) measured water temperature, salinity and dissolved oxygen using an instrument lowered through the water column. Water temperature, salinity and dissolved oxygen were measured using a thermocouple, conductivity cell, and polarographic oxygen probe, respectively. The exact equipment

varied by laboratory and over time but was not specified by the monitoring program's data dictionary (EPA 1993). The precision of the oxygen measurements most likely depended somewhat upon the instrument used; however, precision probably depended to a greater extent on daily calibration and use. Winkler titration was used daily for a subset of measurements to ensure accuracy to within ±0.5 mg l^{-1} (EPA 1993). Experience with similar instruments suggests that accuracy was probably better than ±0.5 mg l^{-1}.

Calculation of Hypoxic Volumes for 1950-1980

Summertime hypoxic volumes were calculated for each year during 1950-1980 for which data was available and for each of three definitions of hypoxia, <0.2 mg l^{-1}, <1.0 mg l^{-1} and <2.0 mg l^{-1}. The middle level corresponds to the definition utilized by Seliger and Boggs (1988). The first level was calculated as an estimate of anoxic or near anoxic water volume. Typically there was one cruise per summer in the CBI data, usually during July. A July cruise was always used where available. In 1958, 1960 and 1972, data from August was used. In 1978, data from September was used (Table 2). If more than one cruise was available, the highest volume was not selected arbitrarily because this would introduce an artifact whereas higher hypoxic volume would tend to be observed when more data was availabile. To calculate hypoxic volume, the available mid-channel oxygen data were interpolated to a 2-D grid with grid cell dimensions of 1 m vertical by 1 nautical mile horizontal. The grid corresponds to tabulated cross-sectional volumes for Chesapeake Bay (Cronin and

Pritchard 1975), which were summed for cells with DO less than the specified maximum to compute hypoxic volume.

The interpolation procedure involved a two step process intended to account for the vastly greater influence of depth on DO distributions as compared to horizontal gradients. First, linear interpolation was used to extrapolate the vertical DO profile at each station to a 1 m interval. Subsequently, linear interpolation was used to extrapolate horizontally at constant depth. The interpolation procedure prevents any extrapolation across unequal depths except within a single vertical profile, a process which due to extreme anisotropy almost always produced unreasonable results, even using data with high spatial resolution. In contrast, this algorithm always produced good results when sampling was thorough, as was always the case with the Chesapeake Bay Monitoring Program data (1984-2000). Sometimes good results were obtained with more sparse data; however some particular data gaps led to interpolation problems. These were identified using contour plots generated for each year prior 1985. To correct these problems, adjustments were made to the interpolated profiles in the following specific situations:

(1) When DO was not measured at the lower extent of the pycnocline, but was measured within the mixed layer, the concentration within the lower mixed layer was assumed to extend upward to the lower extent of the pycnocline.

(2) When DO was not measured within the bottom mixed layer, the DO profile within the bottom mixed layer was interpolated from adjacent up-Bay and down-Bay stations, rather than interpolating vertically through the pycnocline.

(3) Unless data were present to indicate otherwise, the DO contours near the northern extent of the channel trench were assumed to extend unmodified at constant depth to the up-estuary extent of the trench.

These modifications resulted in estimated DO distributions that were structurally consistent with DO distributions observed when sampling was thorough (i.e. 1985-1999). In addition, the estimated distributions were plausible given the known water column structure and approximate physical transport regime.

Calculation of Hypoxic Volumes for 1984-1999

The interpolation algorithm that was used to interpolate 1950-1980 DO profiles was also used for 1984-1999, except that adjustments for incomplete data were never needed because the sampling regime of the monitoring program was thorough and consistent. In addition, because two July cruises and corresponding hypoxic volume estimates were available for each year, the average of the two values was used to determine an estimate of July hypoxic volume for each year.

For 1985-1999 there was a sufficient number of sampling dates each year to characterize the seasonal time-series of hypoxic volume within each year. This increased temporal resolution allowed a time-space integrated measure of hypoxia to be computed by calculating trapezoidal areas underlying a linear-spline fitted time-series of hypoxic volume (Fig 3-2).

Oxygen Input Budgets

Oxygen input budgets were developed for the lower water column in three segments of the mesohaline Chesapeake Bay (Fig. 3-1; Fig 3-3). These budgets were used to compute and compare vertical non-advective, net horizontal advective, and total DO inputs to the lower water column in July during 1950-1999. July rates were computed because most of the early data was for mid summer. In addition, oxygen concentrations typically approached steady-state in July. Therefore, DO inputs to the lower layer in summer approximate DO consumption rates.

For each segment, m, vertical non-advective DO input was calculated using $E_{vm}(c'_m - c_m)$, where E_{vm} is the non-advective vertical exchange coefficient and c'_m and c_m are the bottom and surface layer mean DO concentrations, respectively. Advective DO transport was calculated as the product of advective transport and the DO concentration in the originating model segment (Fig. 3-3). Since the water balance equation $Q'_{m+1} = Q'_m + Q_{vm}$ holds for each segment, the net advective DO input (input minus outputs) can be computed as $Q'_{m+1}(c'_{m+1} - c'_m)$. Total DO input for each segment is the sum of the vertical non-advective DO input and the net advective DO input. All inputs were expressed per unit of pycnocline area (i.e. m^{-2}). River flow dependent estimates of E_{vm} and Q'_m were computed using regression models (Chapter 2).

Statistical Methods

The long-term change in hypoxic volume as well as the effect of river flow was evaluated using multiple regression. The characteristics of the data required special consideration. First, the variability in hypoxic volumes increased with the

mean. The was addressed via log-transformation. Secondly, the long-term change in hypoxic volume was not constant over time. This was addressed by addition of an exponent to the time-term of the model, effectively a shape-parameter. Finally, because hypoxic volume was zero in some years, recoding was needed to permit log-transformation. The resulting model was

$$V' = \beta_0 + \beta_1 (T - 1949)^a + \beta_{2i} Q \qquad (5)$$

where $V' = \ln(V + 1)$ and V is the hypoxic volume. Asymmetric confidence bands for the predicted means were generated by computing confidence limits on the log-scale, then back transforming.

Results

Hypoxia in Chesapeake Bay, 1950-2000

A plot of the hypoxic volumes shows that summer hypoxic volumes increased substantially during 1950-2000 (Fig. 3-4). Regression analysis was used to quantify the rate of increase of hypoxia through time while simultaneously investigating and controlling for suspected effects of variations in average spring river flow on hypoxia (Seliger and Boggs 1988, Boicourt 1992). The optimal period of time over which to average river flow was evaluated by examining several periods. For example, the April-May average river flow used by Seliger and Boggs (1988) was considered, as was the January-March average flow. The January-May average Susquehanna River flow was included in the final model to remove the effect of river flow from the trend estimate because it explained more of the flow dependence than did either of the other two averages. Incorporating several averages in the model by estimating several

model coefficients was also inferior to the longer averaging period. Log-transformation resulted in approximately homoscedastic and normally distributed residuals. Residuals were also not autocorrelated.

According to these regression models, mid-summer hypoxic volume increased significantly and dramatically during 1950-2000, while the level of hypoxia in any given year was also significantly dependent on spring river flow (Table 3-3, Fig. 3-4, Fig. 3-5). The river flow effect was most pronounced for severe hypoxia and least pronounced for moderate hypoxia. At average river flow levels (1,500 $m^3 s^{-1}$), the estimated volume of near-anoxic water increased from zero in 1950 to $3.7x10^9$ m^3 in 2000 (Fig 4). The estimated volume of severely hypoxic water increased 4-fold from $1.7x10^9$ m^3 to $6.5x10^9$ m^3. The estimated volume of moderately hypoxic water increased 2.7-fold from $3.6x10^9$ m^3 to $9.7x10^9$ m^3. Correlation between estimates of the exponent, a, and the slope β_1 inflated the confidence intervals for these model parameters. Therefore, the significance of the trend overall was evaluated by computing confidence intervals for model predictions (means±sd) at several levels of river flow (Fig. 3-5). In addition, 95% confidence limits were computed. As an example, the 95% confidence interval for moderate hypoxia in 2000 does not overlap with the corresponding intervals for all years up to 1980. Similarly, the 95% confidence interval for near anoxia in 2000 does not overlap with the corresponding interval for years up to 1985. The graph of the predicted hypoxic volumes (Fig. 3-5) also illustrates the increasing rate of expansion of hypoxia volumes. Due to the log-transformation and non-linear functional form, this is difficult to describe. The rate of increase for near-anoxia was greater than for moderate hypoxia in the early portion of

the record, but by the end of the record the opposite was true. For example, the annual increase in near-anoxia in 1960 was 2.8 times more than that for moderate hypoxia. In contrast, the annual increase in moderate hypoxia in 1990 was 2.1 times that for near-anoxia.

The spatial pattern of increase in hypoxic volumes was examined by contrasting DO profiles in Chesapeake Bay for years with approximately average spring flow (Fig 3-6). As part of this study, a complete set of similar profiles was produced for all years between 1950 and 1980 and for selected years during 1985-1999. In July 1959, the 1 mg l^{-1} DO contour intersected the channel bottom at 140 km from the Atlantic Ocean, between Point Lookout, MD and Patuxent River (Fig. 3-1, Fig. 3-6). There were no DO observations less than 0.2 mg l^{-1}. The July 1970 DO profile was particularly different from the 1959 profile in that near anoxic or anoxic water was present. In 1980, the 1 mg l^{-1} contour moved down-estuary to ~100 km from the Atlantic Ocean (Smith Point, VA), while the 2 mg l^{-1} contour had changed little from 1959. The 0.2 mg l^{-1} contour was greatly expanded such that in most places the 0.2 mg l^{-1} contour was very near to the 1.0 mg l^{-1} contour. In 1991, both the 1.0 and 0.2 mg l^{-1} contours extended to a shallower depth in the mesohaline region as compared to 1980. Particularly of note was the extension of the 1.0 mg l^{-1} and 2.0 mg l^{-1} contours to include areas further to the south, ~60 km from the Atlantic Ocean near the mouth of the Rappahannock River (Fig 3-1, Fig. 3-6). The most recent years in the record, 1998 and 1999, included a particularly dramatic expansion of the hypoxic zone to the south. In 1998, the 0.2 mg l^{-1} contour extended to between 60 and 240 km from the Atlantic Ocean, or from the Bay Bridge to as far south as the Rappahannock River,

and included all the waters up to ~10 m depth. In 1999, a year with low spring Susquehanna River flow, near-anoxic water in the mesohaline was greatly reduced, but a region with DO<2.0 mg l^{-1} extended to within 30 km of the Atlantic Ocean, separated from the mesohaline Bay by a region of normoxic (i.e. DO>2.0 mg l^{-1}) water.

Over 1950-1999 the ratio between the calculated hypoxic volume and hypoxic benthic area, essentially the mean depth of the hypoxic volume, varied between 5 m and 7 m, with no significant trend over time. It can be inferred that the trend in hypoxic benthic area, to the extent that it can be addressed with this data, was the same as the trend in hypoxic volume. The estimate of hypoxic benthic area may be a minimum estimate because the benthic environment can become hypoxic due to strong local DO demand, even as the overlying water remains normoxic.

Spatial and Temporal Dimensions of Hypoxia

The water quality data available for 1985-1999 were sufficient to quantify both the spatial and temporal extent of hypoxia in Chesapeake Bay for that period by integrating hypoxic volume through the year (Fig. 3-2, Fig. 3-7). These time-space integrals were calculated using the same three DO thresholds previously discussed, DO<0.2 mg l^{-1}, DO<1.0 mg l^{-1} and DO<2.0 mg l^{-1}, and were then related to river flow and time. Unlike July hypoxic volume for 1950-1999, this shorter (15 year) time series was related to spring average river flow but there was no significant increase or decrease over time. As a result, the time component was dropped from the final model (Table 3-4). At average flow (1500 m^3 s^{-1}), the expected amount of hypoxia (DO<1.0

mg l^{-1}) was 43.5×10^{10} m^3-days, while this increased to 56.8×10^{10} m^3-days with flow equal to 2200 m^3 s^{-1}. Time-space integrals of hypoxic volume have been criticized as management tools because, as a somewhat abstract concept, they are not particularly engaging for environmental managers or the public. However, the temporal dimension of hypoxia that they incorporate is important. In particular, increases in the temporal dimension of hypoxia tend to occur via earlier onset of hypoxia in late spring, just when new recruits in the benthic community is beginning to respond to increased water temperatures.

Taft et al. (1980) calculated the rate of decline of bottom water DO at a mesohaline station from winter levels to the minimum concentration during summer for 1964-1971 and 1977. The decline was typically nearly linear and proceeded at rates between 0.04 to 0.15 mg l^{-1} d^{-1}, with an average of 0.106 mg l^{-1} d^{-1} (Table 5). In this study, the series was expanded to include 1985-1999 using bottom water DO data from station CB4.3C, also in the central mesohaline Bay (Fig. 1). The rate of DO decline was estimated by fitting a linear regression to the 3-5 observations describing the spring decline in DO. The date of onset of anoxia was determined with greater precision than the bi-weekly sampling program would otherwise permit by extrapolating this line to zero DO. Typically, these regressions had $r^2>0.95$. Regression slopes averaged -0.119 mg l^{-1} d^{-1}, which is a slightly more rapid decline than was observed for 1964-1977 (Table 3-5). Assuming the typical late winter DO concentration of 9.0 mg l^{-1}, this 0.013 mg l^{-1} d^{-1} increase in the rate of DO depletion leads to onset of anoxia ~9 days earlier during 1985-1999 than during the late 1960's. Compared to the variation within the recent and older data, however, this difference

may be regarded as insignificant. The rate of DO depletion was not significantly correlated with spring average river flow during either period, or in both periods combined.

In contrast to the above results, the date of onset of bottom water anoxia was significantly related to spring average Susquehanna river flow ($p<0.01$; Fig 3-8). During 1985-1999 this date varied between May 2 and July 5 (Table 3-5). January to May average river flow was the best predictor of the date of first anoxia. January-March or April-May average flow did not predict or were substantially inferior predictors, respectively. Assuming that it was correctly determined that DO did not decline faster at high river flow, but did reach hypoxic levels earlier, one or both of two possibilities are suggested: the DO decline either began earlier or started at a lower initial DO, or both. It was hypothesized that earlier declines and/or lower initial DO might be related to warmer water temperatures in early spring. To examine this, March bottom water DO and March bottom water temperature were added to river flow as explanatory variables in a multiple regression predicting the date of onset of hypoxia.

Water temperature ($p<0.05$) along with spring river flow ($p<0.01$) explained ~55% of the variance via the multiple regression

$$D = 241 - 0.028Q - 7.26T \qquad (6)$$

where D is the calendar date on which anoxia first occurred, Q is the January-May average river flow ($m^3\ s^{-1}$) and T is the March bottom water temperature at CB4.3C

(Fig 3-8). March bottom water DO was negatively correlated with bottom water temperature, indicating that the effect of temperature was to lower the initial DO level. Linear decline of DO did not tend to begin as early as March, perhaps due to the strength of storms at that time of year. According to eq. 6, an increase in average spring river flow of 1000 $m^3 s^{-1}$ results in anoxia occurring 28 days earlier. Similarly, the observed range in March bottom water temperature (3.1 - 6.8 °C) was associated with a 27 day change in the date of onset of anoxia. Because of the rapid increase in water temperature during spring, the date of onset of anoxia dramatically affected the range of water temperatures available to the benthos prior to the onset of anoxia. As an example, eq. 6 predicts that bottom water reaches anoxia on 6/15 when Q=1200 $m^3 s^{-1}$ and T=5.5°C. Bottom water temperature on 6/15 is ~18°C and has exceeded 15°C, sufficient for increased activity by the benthos, for about 22 days (Fig. 3-8). In contrast, with Q=2200 $m^3 s^{-1}$ and T=5.5°C, anoxia occurs on 5/18, by which time bottom water temperature is only ~14°C, living no window at all for growth of benthic opportunists. The effect of water temperature shifts on the water temperature at anoxia was relatively smaller, especially considering that March temperature anomalies tended to persist throughout spring.

Oxygen Input Budgets

Oxygen inputs budgets were used to examine the relative importance of the two sources of DO to the lower water column, horizontal advection and vertical diffusion. Of particular interest was how these sources may have changed over time as DO distributions in the Bay changed. The computations showed that in mid

summer, for the mid Bay as a whole, the input of DO due to horizontal advection of water from the lower Bay (less DO advected out of the lower water column) was 2-3 fold greater than vertical diffusive inputs (Fig. 3-9). Vertical diffusive inputs increased slightly over 1950-1999. In recent years, the effect of river flow on vertical diffusivity was particularly evident in vertical diffusive DO inputs, reflecting both large interannual variations in freshwater inflow and substantial differences between DO above and below the pycnocline. Net advective DO inputs decreased over 1950-1999. Although landward advection increased with spring freshwater input rate, net advective DO inputs reflected the gradient in DO concentration at least as much as the difference in advection. The lowest advective input rate occurred in 1999. In this year, freshwater inflow was at a record low in Maryland, but was not as low in Virginia. Hypoxia extended well outside the mesohaline region of the Bay. By depleting the DO concentration in the inflowing water, the advective input was decreased greatly.

Discussion

Patterns and Trends in Hypoxia, 1950-2000

The results of this study show that the volume of water affected by hypoxia in mid-summer in Chesapeake Bay increased dramatically over 1950-2000 and that this long-term trend, although modulated by average springtime river flow, was not caused by an increase in river flow. Moreover, the increase appears to have accelerated, especially in the case of milder hypoxia ($DO<2.0$ mg l^{-1}) as compared to near-anoxia ($DO<0.2$ mg l^{-1}). Whereas the principal change during 1950-1980 was that anoxia,

which was previously not a regular feature of Chesapeake Bay, became an annual certainty, the principal change during 1980-2000 was that milder hypoxia expanded dramatically to the south as compared to the region previously affected. The results of earlier studies (i.e. Flemer et al. 1983; Seliger and Boggs 1988) may have depended upon particular issues of interpolation methods, inclusion or exclusion of data from certain years, and the means by which river flow effects were included in the analysis. In contrast, the basic conclusion of this study that hypoxia has increased since 1950, independently from river flow, is insensitive to the choice of any reasonable interpolation method and is robust to inclusion or exclusion of observations from any particularly year.

The trend in hypoxia during 1985-2000 was less obvious only because the analyses based only on data for this period indicated no significant time trend. In contrast, within the context of the longer time series it appears that the upward trend in hypoxia was accelerating, rather than stabilizing, in recent years. The large interannual variability, which could not be overwhelmingly related to river flow, may have weakened the power to resolve time trends from the shorter time series. If the volume affected has in fact increased since 1985, it appears that much of this increase may be in the form of milder hypoxia at the southern extent of the mesohaline region, or even within the polyhaline region of the Bay (Fig. 3-4, Fig. 3-6). Perhaps not coincidentally, this pattern of expansion to the south corresponds directly to the pattern of increase in phytoplankton biomass in the southern Bay, observed for 1950-1994 by Harding and Perry (1997). Both patterns may be related to a long-term increase in nutrient inputs, while the increased phytoplankton production documented

by Harding and Perry (1997) may be the major contributor to increased oxygen depletion in the lower Bay.

There are few systematic records of hypoxia for other estuaries in the world with comparable detail and duration. One example is the Northwest Shelf (NWS) area of the Black Sea in which nitrogen and phosphorus loading increased 56% and 400% respectively between the 1960's and 1980's (Zaitsev 1992). Seasonal hypoxia in bottom waters on the NWS was first recorded in the late 1960's and increased ~5-fold by the 1980's, affecting waters between 7-8 and 35-40 m. Zaitsev (1992) also noted that in some recent years, meteorological conditions led to hypoxia persisting for only a few days. In contrast, hypoxia persisted in some places for most or all of the summer in Chesapeake Bay. Other shallow water areas are also becoming subject to increased hypoxia. For example, Rabalais et al. (1999) has shown that the hypoxic zone beneath the Mississippi River plume in the Gulf of Mexico has increased in recent years. Shallower areas of the Baltic Sea region have also begun to experience hypoxia (Baden et al. 1990 cited by Diaz and Rosenburg 1995).

A huge area of the central Black Sea, which exceeds to 2000 m depth, is permanently and probably naturally anoxic. Permanent anoxia is also present in a large and growing area of the Baltic Sea at >65 m depth (de Jonge et al. 1994) and certain areas of the coastal ocean (e.g. Arabian Sea, Peruvian Shelf; Diaz and Rosenburg 1995). Such persistent hypoxia and anoxia is not uncommon worldwide and appears to be increasing due to anthropogenic effects (Diaz and Rosenburg 1995). However, hypoxia and anoxia in shallow waters may be of particular importance because of the profoundly negative consequences on these otherwise productive

habitats which are tightly coupled to heavily exploited and valuable demersal and pelagic fisheries. For example, Zaitsev (1992) concluded that the effect of hypoxia in the NWS of the Black Sea was to eliminate 100-200 tons wet weight of benthic macrofauna and demersal fishes per km^2 (20-40 g AFDW m^{-2}, assuming 0.2 g AFDW/g WW). Sturgeon and turbot catches in the NWS region decreased to 22% and 10% of earlier levels, respectively (Zaitsev 1992).

Significance of Increased Hypoxia

There are no studies that have shown that declines in commercial fisheries, as mentioned above for the Black Sea, have occurred in Chesapeake Bay as a direct result of increased hypoxia and anoxia. However, there are several other ways that the significance of the increase in Chesapeake Bay hypoxia since 1950 could be evaluated. The fraction of total water volume and benthic habitat that is affected is one indicator of significance of the observed increase in Chesapeake Bay hypoxia. In 1950, severe hypoxia (DO<1.0 mg l^{-1}) affected about 20% of the volume and sediment area below 10 m depth in the mesohaline Bay. Compared to the overall volume of the mesohaline region or to the entire Bay, the hypoxia-affected fraction was small, approximately 6% and 2.5%, respectively. For a year with average river flow in the late 1990's, however, hypoxia affected a volume and area equal to the entire mesohaline region below 10 m and equal to 46% of the total area and 26% of the total volume in the mesohaline Bay. Compared to the entire mainstem Chesapeake Bay, the areas affected by moderate hypoxia constituted a significant fraction of both the sediment area (18%) and total water volume (12%).

In Chesapeake Bay, the results of this study suggest that benthic and pelagic habitats at all depths may have been productive as late as the 1950's, even if the deeper benthic habitats were limited to hypoxia-tolerant species and subject to periodic hypoxia induced mortality in high flow years (e.g. 1952). However, the increase in near-anoxia in Chesapeake Bay since 1950 probably degraded deeper habitats by 1980. The presence of near-anoxic water near the pycnocline since 1980 (Fig. 3-6) could also have degraded shallower habitats by increasing the effect of aperiodic events that bring below-pycnocline waters onto shallower flanks of the Bay (Malone et al. 1986, Breitburg 1990, Sanford et al. 1990). While benthic communities can potentially survive moderate hypoxia until normoxic conditions return by using a variety of adaptive strategies (Diaz et al. 1992), mortality tends to be more rapid under more severe hypoxia and in the presence of H_2S (Diaz and Rosenburg 1995). Thus, while aperiodic events bringing below-pycnocline waters into shallower habitats have probably always occurred, the detrimental effects of these events may now be much greater due to anoxia.

The increase in anoxia has probably affected the biogeochemistry of the Bay, perhaps accounting in part for the accelerating increase in hypoxic volume. Based on the estimated effects of anoxia on N and P efflux from sediments, and the estimated increase in the sediment area affected by anoxia, the effect of increased anoxia on nutrient dynamics in Chesapeake Bay is probably significant. The P efflux from anoxic mesohaline sediments in mesohaline Chesapeake Bay is 50-150 $\mu mol\ m^{-2}\ h^{-1}$, while P efflux from oxic sediments is apparently negligible (Cowan and Boynton 1996). For the estimated anoxic sediment area in the 1990's, ~ $5.7(10^8)\ m^2$, this

amounts to an additional 2.1-6.3(10^4) kg P d^{-1}, ~ 3-10 times recent annual average P loading rates from Susquehanna River to Chesapeake Bay. Similarly, anoxia prevents coupled nitrification-denitrification, which occurs at significant rates in warm, organic rich, but oxic sediments (Seitzinger 1988). Summertime NH_4^+ efflux from the mesohaline Bay sediments in recent years were substantially greater than elsewhere in the Bay (Cowan and Boynton 1996), perhaps reflecting this limitation of coupled nitrification-denitrification by anoxia. Assuming a reasonable potential for summertime denitrification is 50-100 μmol m^{-2} h^{-1} (Seitzinger 1988), the additional NH_4^+ efflux associated with anoxia amounts to 9.6-19.2(10^3) kg N d^{-1}, or ~10% of the annual average and 11-23% of summer average Susquehanna River total N loading rates for 1984-1996. The N efflux may be especially important due to the close spatial proximity to the N-limited phytoplankton community in the surface layer during summer (Fisher et al. 1992).

Long-Term and River Flow Dependent Changes in Oxygen Transport

It has long been recognized that DO patterns reflect a combination of several biological and physical processes. Kuo et al. (1991) used a Lagrangian model to examine DO distributions in the Rappahannock River. One of their major conclusions was that residual advective velocity was an important factor determining the maximum extent of DO depletion, principally because it determined the residence time of a parcel of water in the lower water column. Kemp et al. (1992) used an entirely different approach, inferring physical transport rates from the balance of measured biological rates. They concluded that both transport processes were

important, but that vertical diffusion was 4-fold more important in two of three summer months. In contrast, this study found that horizontal advective inputs were usually the larger flux, although not by a large margin (Fig 3-9). Amazingly, the residual current velocity Kemp et al. (1992) inferred from biological rates was similar to the rate estimated for this study using a box model, about 5 cm s^{-1} (Chapter 2). Therefore, it is not surprising that their estimated horizontal DO transport rates were not substantially different from the present estimates. However, their estimate of vertical diffusivity, about 0.2 cm^2 s^{-1}, was at the high end of the flow-dependent range of rates estimated for this study (0.09-0.24 cm^2 s^{-1}, Chapter 2). Due to lower estimates of D_z the vertical DO flux was estimated to be smaller, lending relatively larger importance to the horizontal advection of DO. The results of this study also reveal, however, that these processes vary either inversely or independently, but they are not positiively correlated. Therefore, their relative importance varies. Location within the Bay was also very important. At the north end of the mesohaline region of the Bay, vertical diffusion was the only source of DO when the advecting source water was anoxic or nearly anoxic.

Of greater interest here was how the relative importance and total magnitude of these DO fluxes changed during 1950-1999. Here, physical transport rates were a noisy, but essentially stationary background, i.e. neither vertical diffusivity nor the residual current velocity changed directionally over this period of time. Directional changes in the physical transport of DO (Fig. 3-9) were therefore due to changes in the spatial distribution of DO within the Bay. The increase in hypoxia over time increased vertical diffusion of DO predictably (Fig. 3-9). However, the average surface layer

DO concentrations decreased somewhat, despite high DO in the top several meters due to high rates of phytoplankton production (not shown). This was likely due to increased DO demand at the pycnocline, due to both downward DO diffusion, and, under the worse anoxic conditions, scouring of DO within the pycnocline by hydrogen sulfide (Kemp et al. 1992). As a result, vertical diffusion of DO increased only slightly during 1950-1999, and with great variability. In contrast, horizontal advective inputs into the mid Bay decreased more substantially (Fig. 3-9), reflecting the previously described southerly expansion of hypoxia (Fig. 3-6). The net effect of changes in the spatial distribution of DO during 1950-1999 has been to exacerbate the depletion of DO in the mid Bay by decreasing the DO flux due to advection. At the scale of the mid Bay, this observation counters the observation of Kemp et al. (1992) that the magnitude of DO response to changing DO inputs would be buffered by coupled biological-physical interactions, leading to initially rapid, but proportionately decreasing improvements in water quality. Rather, these results suggest that the biologically-mediated physical transport effects act together with the positive feedbacks due entirely to biological processes (e.g. sediment NH_4^+, PO_4^{3-} and H_2S efflux). The combined positive feedbacks likely contribute to the increasing rate of expansion of the near anoxic zone that has been described (Fig. 3-4). At the larger scale of the whole Bay, the DO flux to the bottom layer must decrease as average DO levels increase. However, the inputs to the mid Bay, the only place where severe anoxia and associated effects have occurred, are the most relevant. The implications for management are favorable. Since all the feedback processes appear to be positive, water quality changes associated with decreased nutrient loading should bring about

significant beneficial effects, reversing the unfavorable trend followed to date. The dynamically unstable configuration of feedbacks (i.e. all feedbacks are positive) suggests why the unexplained variability in hypoxic volumes is so large. Prediction is possible only because of the very large range in ecosystem forcing in recent years (river flow and flow-dependent nutrient loading) and over the long-term (river flow and nutrient loading both dependent on and independent of flow).

Prospects for Restoration

While this study does not give estimates of nutrient loading rate targets needed to reach hypoxia-related restoration goals, the detailed characterization of the temporal pattern in hypoxia will be useful as estimates of historical loading rates become available. An effort to obtain these estimates is underway. The results strongly suggest that some decrease in hypoxia should be expected from any decrease in nutrient loading and that any improvement in water quality will promote additional improvement. That said, interannual variability can be expected to remain large. Therefore, the restoration effort would need to proceed with persistence, rejecting suggestions that current levels of hypoxia are a natural feature of Chesapeake Bay ecology or that hypoxia do not have significant detremental effects on living resources (Chapter 5, Chapter 6).

In upcoming years, restoration efforts will face mounting challenges regarding management of hypoxia. Not only do increasing human pressures on the landscape make it difficult to limit nutrient loading rates, climate change may also affect hypoxia in Chesapeake Bay. Najjar (1999) concluded that annual discharge from the

Susquehanna River could be expected to increase 24% in response to an expected doubling of atmospheric CO_2 and associated global warming. This study showed that both increased river flow and warmer winter water temperatures hasten the formation of anoxia in Chesapeake Bay during late spring and promote the maintenance of hypoxia during summer through both biological and biologically-mediated physical transport effects.

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Table 3-1. Data types, spatial resolution, temporal resolution and sources of data.

Data Type (Period of Record)	Spatial Resolution	Temporal Resolution	Source
Chesapeake Bay Institute DO Data (1950-1980)	~10 stations on Bay axis, 2-4 m vertical resolution with gaps.	1-4 surveys per year, 1-2 per summer	Collected Chesapeake Bay Institute Data Reports, and Special Report. See Table 2.
Chesapeake Bay Monitoring Program DO , Salinity, Temperature Data (1984-1999)	~20 stations on Bay axis, 1 m continuous vertical resolution	~20 suveys per year, bi-weekly during summer	Chesapeake Bay Program web page
River Flow Inputs, Conowingo Dam or Harrisburg, PA[1] (1900-1999)	One Location.	Daily	United States Geological Survey, National Water Information System Web Site

[1] Monthly mean Susquehanna River flow at Conowingo, MD prior to 1968 was estimated from the flow at Harrisburg, PA using a regression model based on the overlappping records since 1968. The Harrisburg flow includes >90% of the flow at Conowingo. This model relating these flows had r^2>0.99.

Table 3-2. Data sources, cruise dates, and calculated hypoxic volumes for Chesapeake Bay from 1950-1999.

Year	Data Source	Dates	Hypoxic Volume, 10^9 m^3 DO<0.2 mg l^{-1}	DO<1.0 mg l^{-1}	DO<2.0 mg l^{-1}	Comment
1950	1	7/14-7/19	0.00	0.98	2.17	
1952	2	7/15-8/6	1.93	3.47	5.78	
1957	3	7/23-7/26	0.51	1.84	2.86	2
1958	4	8/6-8/22	0.41	4.76	7.37	
1959	5	7/6-7/17	0.00	2.61	4.85	
1960	6	8/22-9/9	0.24	3.70	4.20	3
1961	7	7/19-7/31	0.02	4.64	6.35	
1962	8	7/24-8/5	0.00	1.41	3.90	
1963	9	7/30-8/15	0.03	2.67	3.50	5
1965	10	7/1/-7/6	0.00	0.08	2.34	2
1968	11	7/8-7/10	0.75	3.46	4.78	4
1969	12	7/7-7/10	0.74	1.67	2.44	
1970	12	7/9-7/12	0.37	1.36	2.96	
1972	13	8/27-8/31	3.70	5.12	7.64	3
1973	13	6/25-6/29	0.83	2.76	4.93	
1978	14	9/18-9/20	1.84	2.87	4.69	
1979	14	7/9-7/12	1.28	1.79	2.88	
1980	14	7/23-8/2	2.20	3.52	5.03	
1984	15	July Avg.	2.84	4.46	5.49	1
1985	15	July Avg.	0.54	2.47	4.42	1
1986	15	July Avg.	4.23	7.52	11.00	1
1987	15	July Avg.	1.57	5.19	9.30	1
1988	15	July Avg.	2.03	3.61	5.02	1
1989	15	July Avg.	4.21	7.25	11.16	1
1990	15	July Avg.	2.02	3.45	5.86	1
1991	15	July Avg.	2.42	7.35	9.26	1
1992	15	July Avg.	2.52	4.31	6.52	1
1993	15	July Avg.	5.87	9.08	11.95	1
1994	15	July Avg.	3.30	5.70	7.68	1
1995	15	July Avg.	3.36	5.83	9.86	1
1996	15	July Avg.	2.84	4.54	5.84	1
1997	15	July Avg.	4.37	5.71	8.15	1
1998	15	July Avg.	6.25	9.61	12.07	1
1999	15	July Avg.	1.20	5.20	9.33	1
2000	15	July Avg.	3.05	5.25	7.40	1

Table 3-2:

Data Sources: (1) Ches. Bay Institute Data Report #4 (1950); (2) Chesapeake Bay Institute Data Report #18 (1954); (3) Chesapeake Bay Institute Data Report #33 (1962); (4) Chesapeake Bay Institute Data Report #38 (1962); (5) Chesapeake Bay Institute Data Report #41 (1962); (6) Chesapeake Bay Institute Data Report #44 (1962); (7) Chesapeake Bay Institute Data Report #47 (1962); (8) Chesapeake Bay Institute Data Report #48 (1962); (9) Chesapeake Bay Institute Data Report #50 (1963); (10) Whaley et al. (1966); (11) Chesapeake Bay Program Database; (12) Taylor and Cronin (1974); (13) Chesapeake Bay Program Database; (14) Cronin et al. (1982); (15) Chesapeake Bay Water Quality Monitoring Program, Annapolis, MD.

Comments: (1) Average of two July cruises; (2) No data south of Potomac River, but available data fully delineates the 1 mg l^{-1} and lower contours; (3) Cruise dates later than likely period of maximum hypoxic volume; (4) DO concentration in lower pycnocline and upper portion of lower layer poorly described. Pycnocline depth considered when interpolating DO profile; (5) No data south of Potomac River. Data do not fully delineate DO contours greater than 0.2 mg l^{-1}. Therefore, hypoxic volumes for 1.0 mg l^{-1} and 2.0 mg l^{-1} are lower bounds.

Table 3-3. Estimated parameters of the non-linear multiple regression, $\ln(V+1) = \beta_0 + \beta_1 (T-1949)^a + \beta_2 Q + \varepsilon$, relating hypoxic volume (10^9 m^3) to time (year) and January-May average Susquehanna River flow (m^3 s^{-1}). Significance levels for β_1 and a are not shown. Due to the fact that the estimates of these parameters are strongly and negatively correlated (r<-0.98), their confidence intervals are meaninginless except in a bivariate context. The significance of the trend over time can be evaluated via confidence bands for the predicted values (Fig. 3-5).

DO Threshold (model r^2)	Intercept, β_0 $P(H_0: \beta_0=0)$	Time Trend, β_1 $P(H_0: \beta_1=0)$	Exponent a	River Flow-Dependence, β_2 $P(H_0: \beta_2=0)$
DO<0.2 mg l^{-1} (r^2=0.69)	-0.67	$1.76(10)^{-2}$	1.15	$4.05(10)^{-4}$ (p<0.05)
DO<0.7 mg l^{-1} (r^2=0.67)	0.58	$2.11(10)^{-3}$	1.57	$2.75(10)^{-4}$ (p≈0.05)
DO<2.0 mg l^{-1} (r^2=0.62)	1.30	$2.33(10)^{-4}$	2.08	$1.47(10)^{-4}$ (p≈0.05)

Table 3-4. Regressions relating hypoxic-volume-days (units: 10^{10} m^3-days) for Chesapeake Bay for 1985-1999 to January-May average Susquehanna River flow (units: m^3 s^{-1}). The three regressions reflect hypoxic volume calculated using the three different DO thresholds, DO<0.2, 0.7 or 1.0 mg l^{-1}.

DO Threshold	Intercept (±S.E.)	Slope (±S.E.)	
DO<0.2 mg l^{-1}	-6.57 (±4.51)	0.017 (±0.003), p<0.01	r^2=0.76, n=15
DO<1.0 mg l^{-1}	14.95 (±7.27)	0.019 (±0.004), p<0.01	r^2=0.59, n=15
DO<2.0 mg l^{-1}	47.5 (±9.14)	0.015 (±0.005), p=0.01	r^2=0.38, n=15

Table 3-5. Estimated rates of spring DO decline in bottom waters at station 845G (Fig. 4) for 1964-1977 (Taft et al. 1980) and at station CB4.3C for 1985-1998 (this study). Rates for 1964-1977 were transformed via 1.0 ml l^{-1} d^{-1} = 1.4 mg l^{-1} d^{-1}. Taft et al. (1980) did not estimate the date of first onset of anoxia.

Station	Year	Rate of DO Decline (mg l^{-1} d^{-1})	Onset of Anoxia (Date)
845G	1964	0.14	
	1965	0.11	
	1966	0.08	
	1969	0.15	
	1970	0.08	
	1971	0.04	
	1977	0.13	
CB4.3C	1985	0.103	6/20
	1986	0.096	6/22
	1987	0.146	5/28
	1988	0.182	5/26
	1989	0.093	7/5
	1990	0.119	5/20
	1991	0.089	6/6
	1992	0.095	7/3
	1993	0.184	5/21
	1994	0.100	6/3
	1995	0.075	7/3
	1996	0.107	6/10
	1997	0.085	6/28
	1998	0.196	5/2
	1999	0.114	6/14

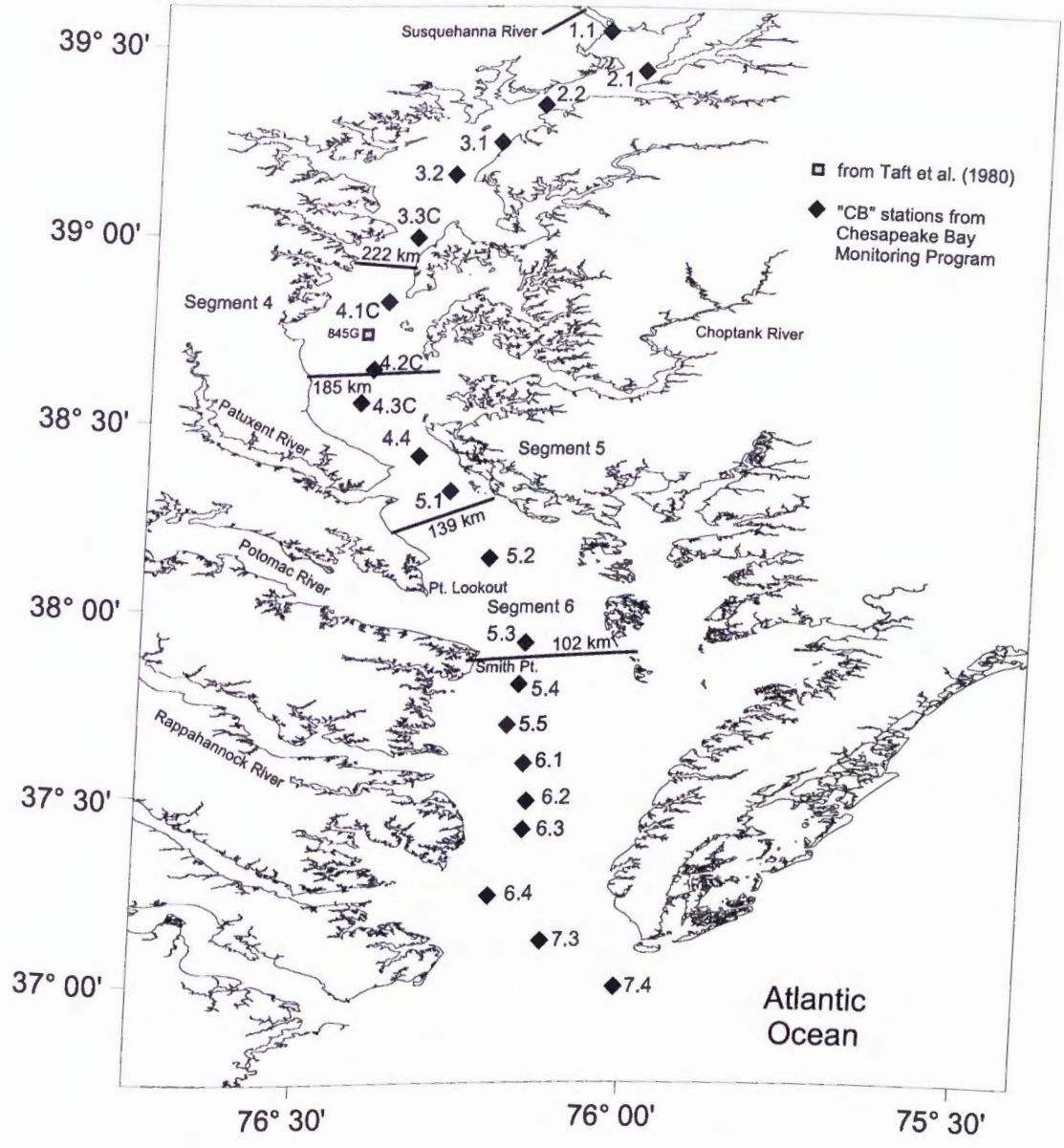


Fig. 3-1. A map of Chesapeake Bay showing the locations and identifications of Chesapeake Bay Monitoring Program Water Quality Monitoring stations used for this analysis. Note that the aspect ratio of the map has been distorted to provide more horizontal space to label stations. The boundaries of the mesohaline region, between 102 and 222 km from the Atlantic Ocean, are indicated. The additional boundaries at 139 and 185 km define the box model segments used for the DO input budgets.

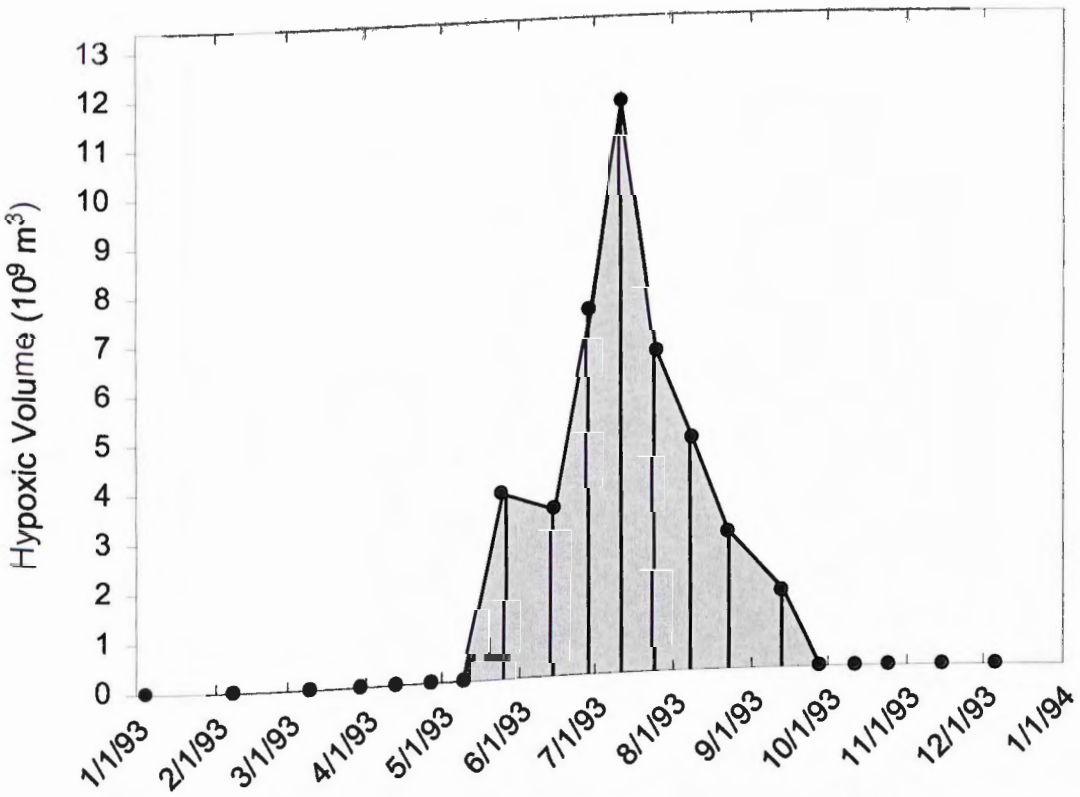


Fig 3-2. The time-series of hypoxic volume (DO<1.0 mg l^{-1}) in Chesapeake Bay in 1993. The shaded area is the integrated hypoxic-volume-days for 1993, computed by summing the areas of the indicated trapezoids.

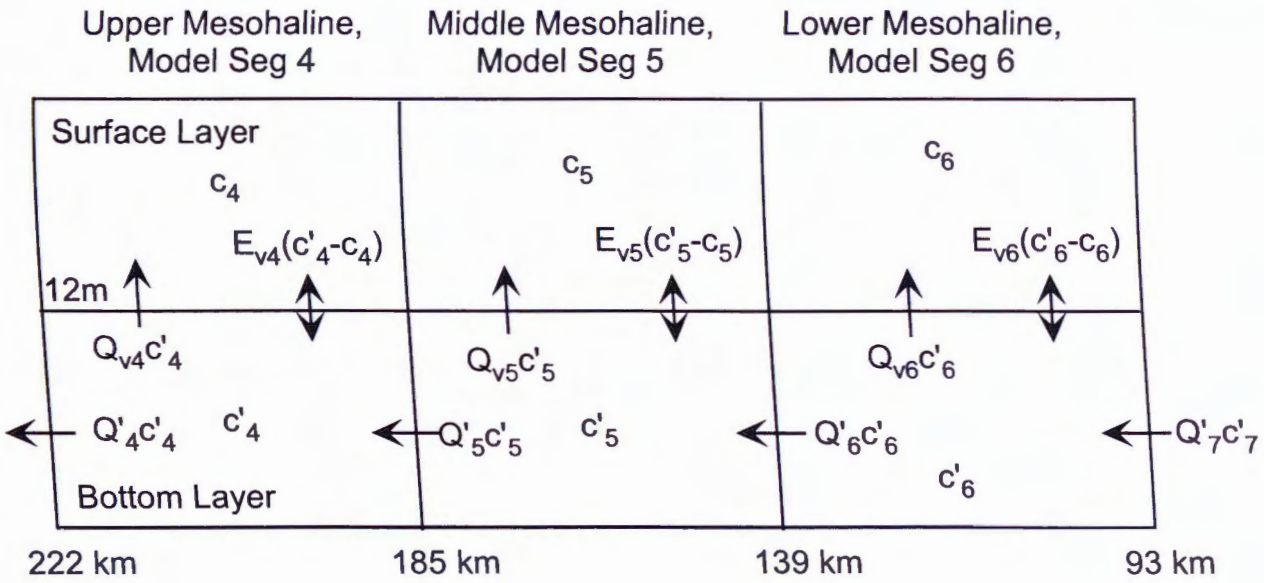


Fig 3-3. A schematic diagram of the physical transport of dissolved oxygen into and out of three segments within the mesohaline Chesapeake Bay. The location of the segment boundaries is indicated in kilometers from the mouth of Chesapeake Bay. The pycnocline is located at 12 m depth. Vertical non-advective exchange is designated E_{vm}, where m is the segment number. Landward flowing advection is designated Q_m, while vertical advection (upwelling) is designated Q_{vm}. All the vertical transport estimates were computed using the box model in Chapter 2. Dissolved oxygen concentrations are designated c_m (surface layer) or c'_m (bottom layer).

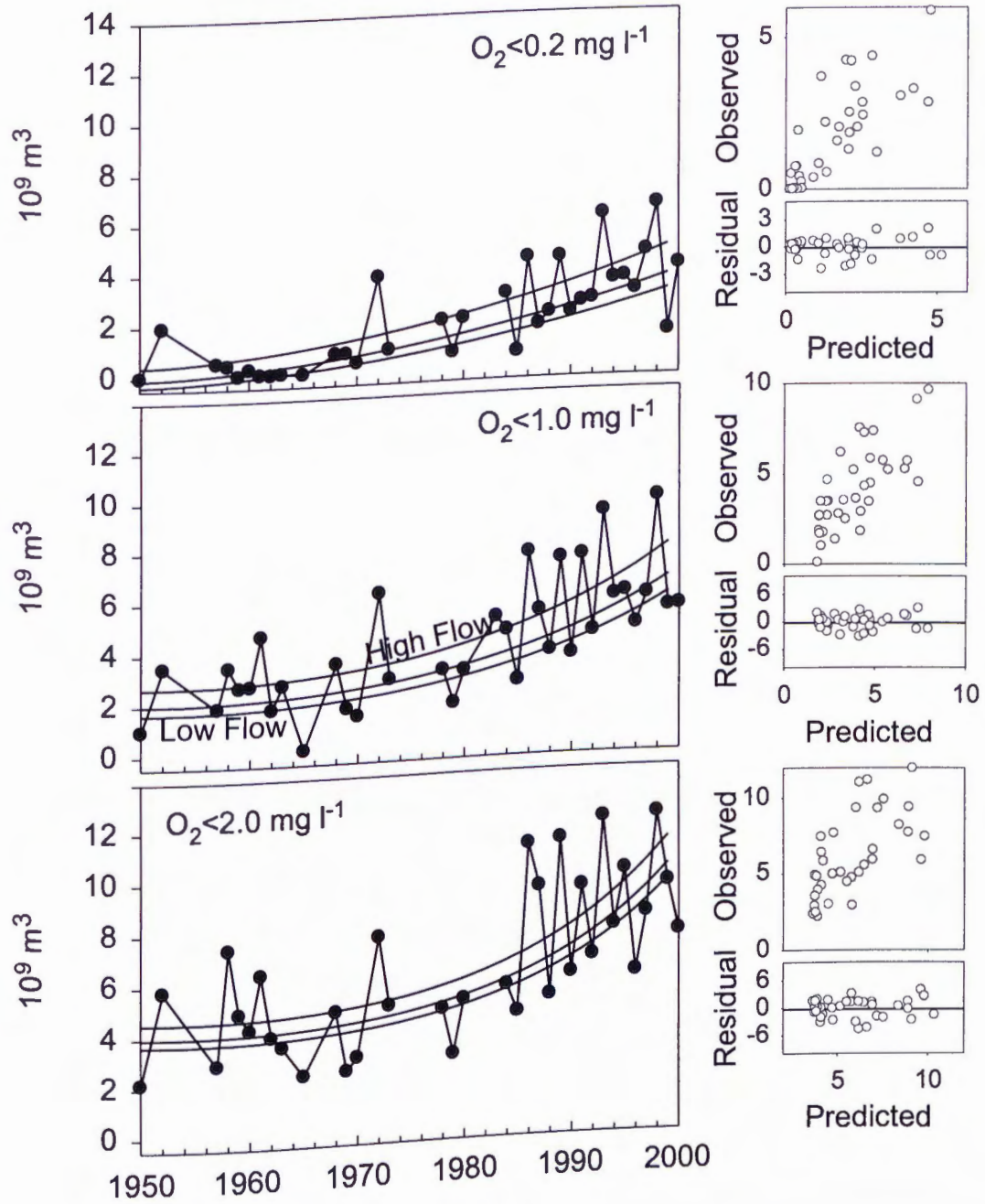


Fig 3-4. Calculated summertime hypoxic volumes for Chesapeake Bay during 1950-2000 as reported in Table 3-2. Nonlinear regression lines show predictions of multiple regression on time and January-May average Susquehanna river flow (Table 3-3). The three lines in each family of curves indicate predictions at 1100 m^3 s^{-1} (low flow), 1500 m^3 s^{-1} (average flow, unlabelled line) or 2200 m^3 s^{-1} (high flow). The figures to the right provide a sense of the goodness of fit.

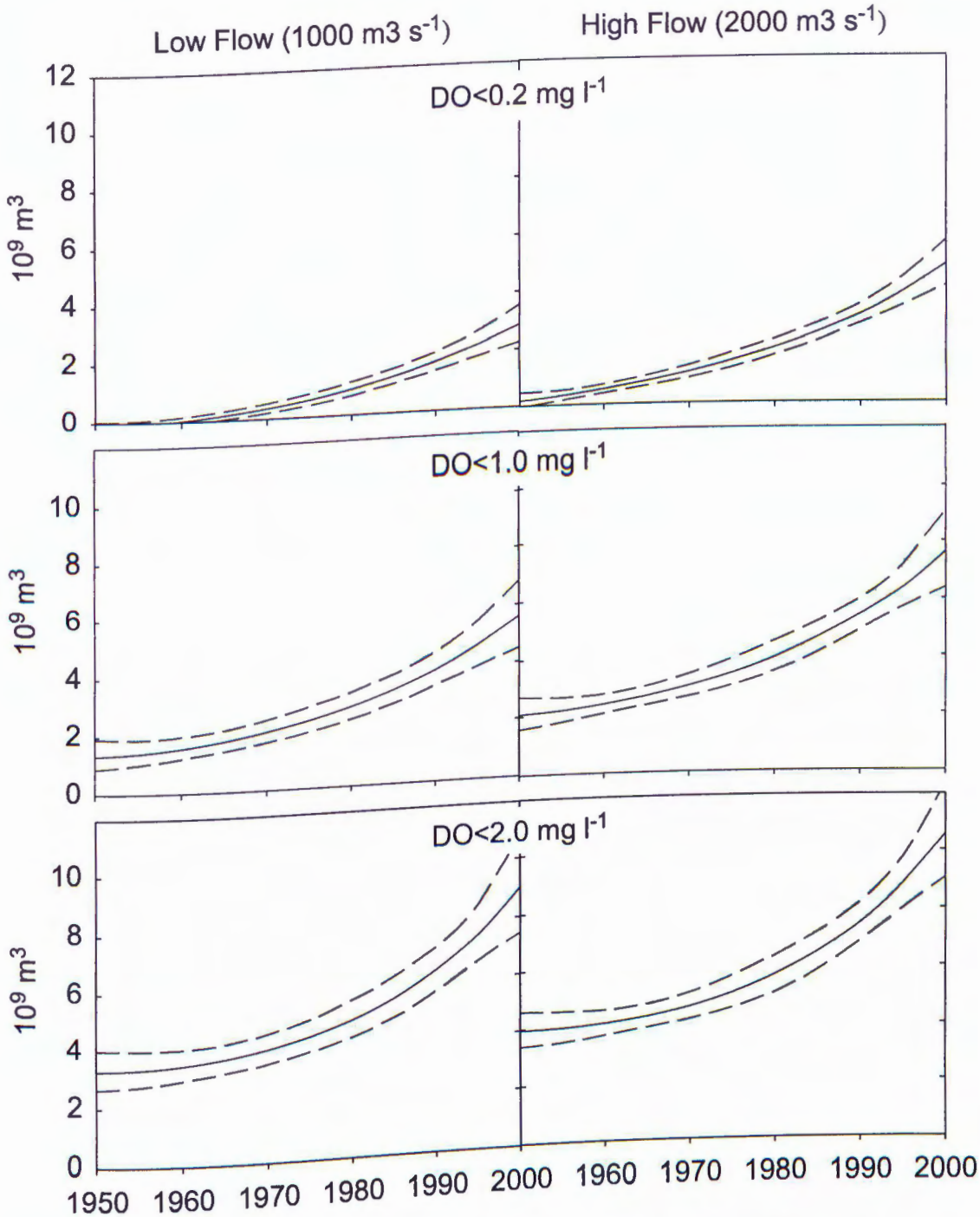
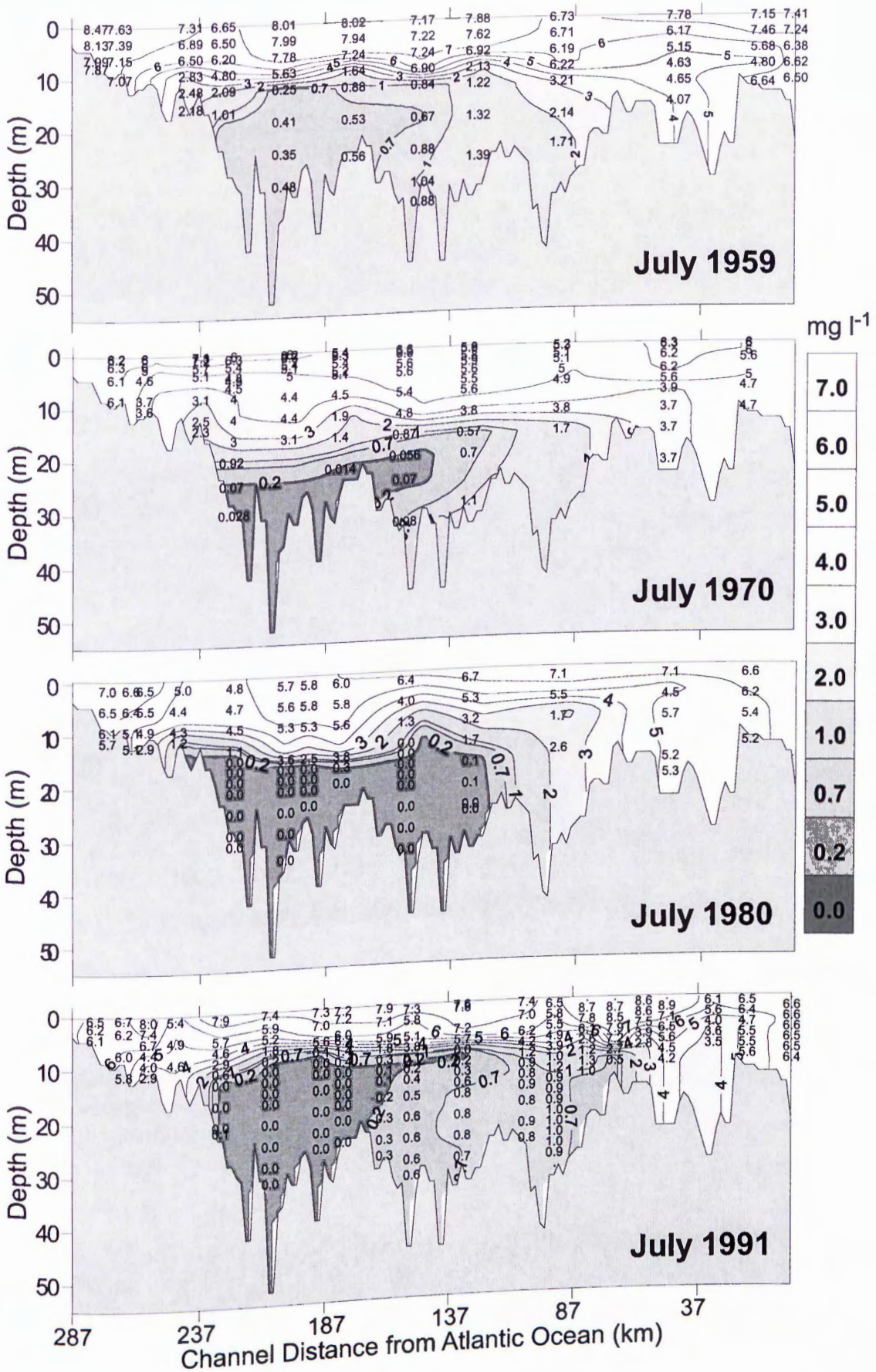


Fig. 3-5. Predictions and asymmetric confidence bands (± standard error of mean) for July hypoxic volume (at each of three definitions) as a function of time and January-May average Susquehanna River flow based on the non-linear regressions fitted to data in Fig. 3-4. Two levels of river flow are indicated corresponding to low flow and high flow conditions.

Fig 3-6. Summer dissolved oxygen profiles in Chesapeake Bay during four years with near average January-May Susquehanna river flow (approx 1,600 $m^3 s^{-1}$). Individual values indicate the locations of observations used in the contouring. Data for 1959 are from the Chesapeake Bay Institute Data Report #41 (1962). Data for 1970 are from Taylor and Cronin (1974). Data for 1980 are from Cronin et al. (1982). Data for 1991 were obtained from the Chesapeake Bay Water Quality Monitoring Program.


July 1959
July 1970
July 1980
July 1991
Depth (m)
0
10
20
30
40
50
mg l-1
7.0
6.0
5.0
4.0
3.0
2.0
1.0
0.7
0.2
0.0
287
237
187
137
87
37
Channel Distance from Atlantic Ocean (km)

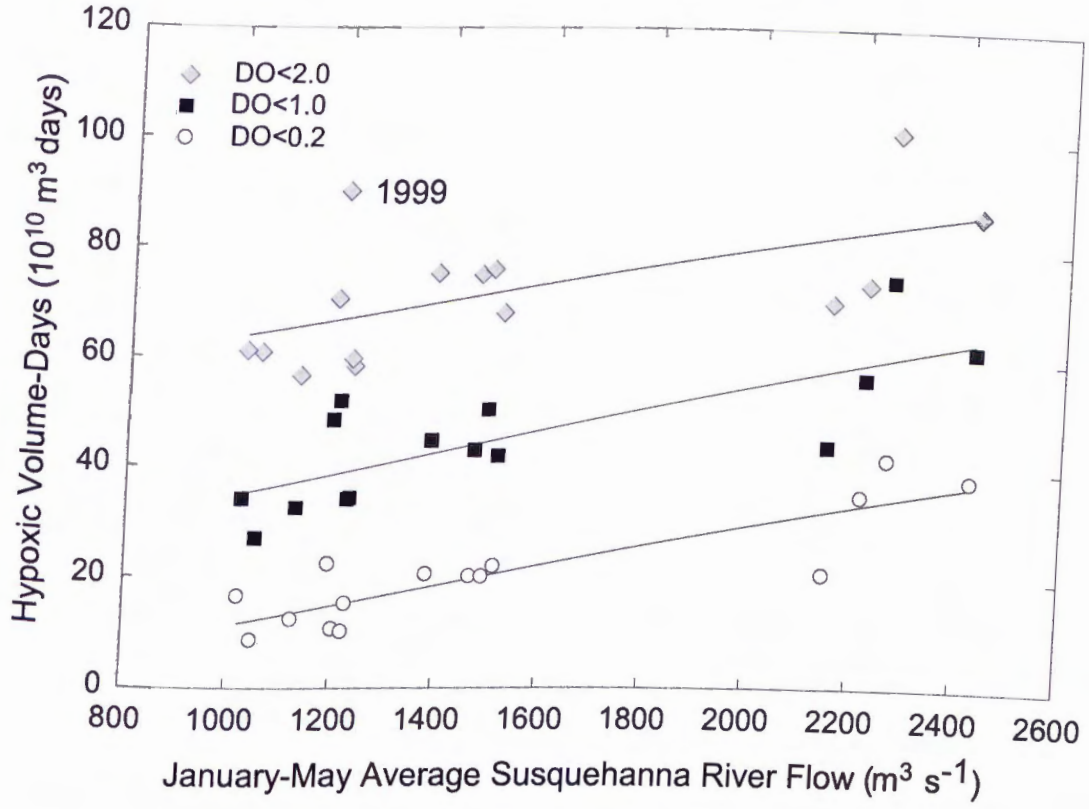


Fig. 3-7. The relationship between January-May average Susquehanna River flow and time-integrated hypoxia (annual hypoxic-volume-days), where hypoxia is defined as either dissolved oxygen less than 0.2, 1.0 or 2.0 mg l^{-1}. The period encompassed is 1985-1999 the period covered by the Chesapeake Bay Water Quality Monitoring Program, from which the data were computed.

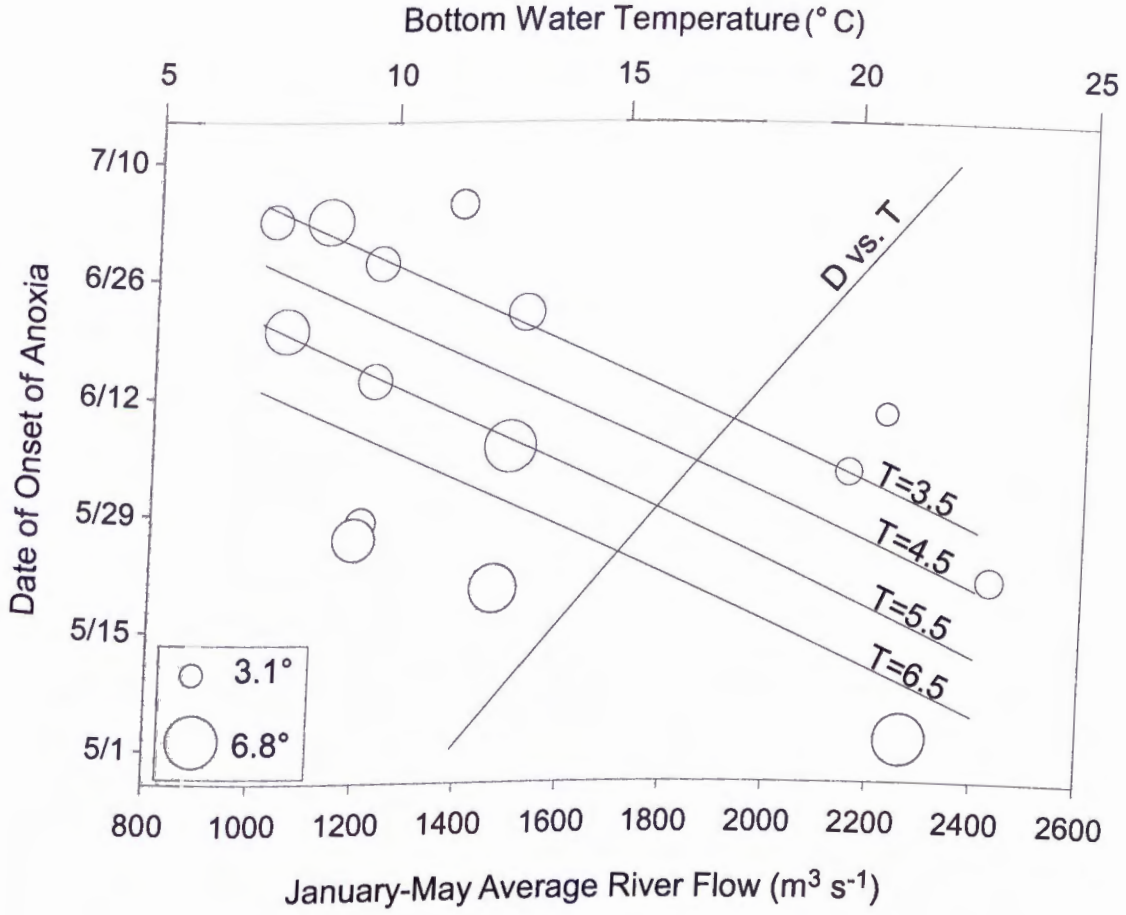


Fig. 3-8. The relationship between January-May average Susquehanna River flow, March bottom water temperature, and the date of onset of anoxia in bottom water at station CB4.3C (Fig. 3-2), located in the mesohaline Chesapeake Bay, as determined via multiple regression. Bubble size indicates the March bottom water temperature at station CB4.3C. Right sloping lines indicate the family of date (D) vs. flow (Q) relationships associated with different March bottom water temperatures (T) as expresed by eq. 6. The upward sloping line (D vs. T) indicates the seasonal increase (corresponding to dates on y-axis) in bottom water temperature (top axis) at CB4.3C (r^2=0.96). The water temperature at the time of onset of hypoxia can be determined by chosing flow and temperature and determining the date of onset of hypoxia from the family of lines, then referring to the date vs. temperature line. All the water quality data was obtained from the Chesapeake Bay Water Quality Monitoring Program. River flow averages were computed from daily discharge values reported by the United States Geological Survey.

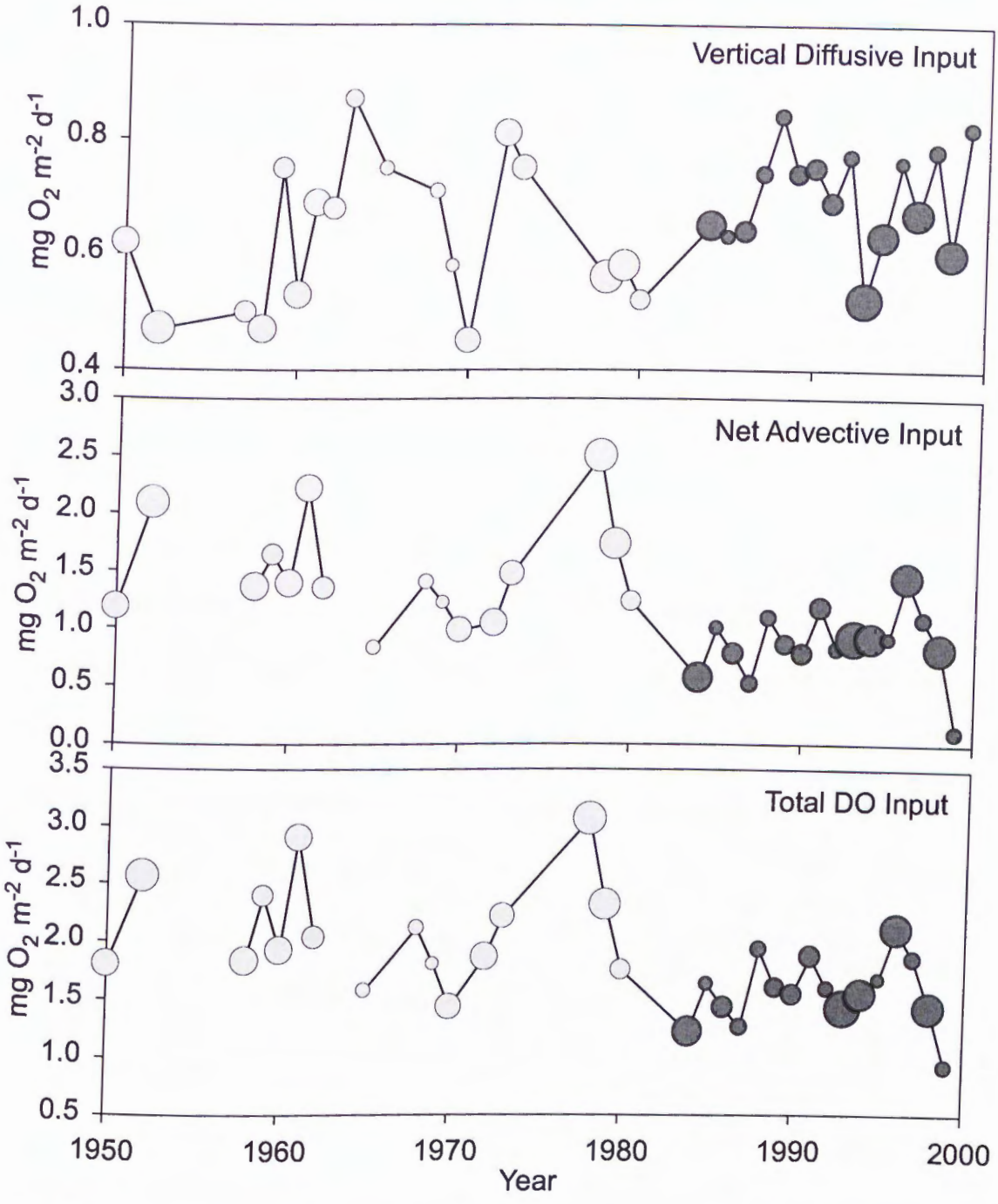


Fig. 3-9. Average vertical diffusive, net horizontal advective, and total dissolved oxygen (DO) inputs to the mid Bay region of the Chesapeake Bay during 1950-1999. Physical transport rates and their dependence on spring average river flow was computed using a box model (Chapter 2). Advective and diffusive DO transport rates were computed as the product of historical average DO concentrations (see Table 3-2 for data sources) and corresponding transport rates (see. Fig. 3-3). The size of the plot symbol indicates the magnitude of January to May average Susquehanna River discharge, whereas large symbols indicate high flow. Dark symbols correspond to the period covered by the more detailed Cheapeake Bay Water Quality Monitoring Program data.

Chapter 4:

PHYTOPLANKTON DEPOSITION TO CHESAPEAKE BAY SEDIMENTS DURING WINTER-SPRING

Abstract

The often rapid deposition of phytoplankton to sediments at the conclusion of the spring phytoplankton bloom is an important component of benthic-pelagic coupling in temperate and high latitude estuaries and other aquatic systems. However, quantifying the flux is difficult, particularly in large and spatially heterogeneous environments. Surficial sediment chlorophyll-*a* (chl-*a*), which can be measured quickly at many locations, has been used effectively by previous studies as a biomarker indicating deposition of phytoplankton to estuarine sediments. In this study, surficial sediment chl-*a* was mapped in late spring at 20-50 locations throughout Chesapeake Bay during 8 years (1993-2000). A model was developed to estimate chl-*a* and carbon deposition using these measurements, while correcting for chl-*a* degradation during the time between deposition and sampling.

Bay-wide, the springtime accumulation of chl-*a* on sediments by late spring averaged 171 mg m^{-2}, from which the chl-*a* and carbon sinking fluxes, respectively, were estimated to be 353 mg m^{-2} and 26.5 g C m^{-2}. These deposition estimates were ~50% of estimates based on a sediment trap study in the mid-Bay. During 1993-2000, the highest average chl-*a* flux was in the mid-Bay (248 mg m^{-2}), while the lowest was in the lower-Bay (191 mg m^{-2}). Winter-spring average river flow was positively correlated with increased phytoplankton biomass in the lower Bay water column, increased chl-*a* deposition to sediments and down-Bay translation of chl-*a* deposition.

In the 8 years of observation, estimates in several years diverged strongly from the overall pattern. A comparison of the C flux associated with the deposition of the spring bloom with annual benthic carbon budgets indicated that the spring bloom did not contribute a disproportionately large fraction of annual C inputs to sediments. Regional patterns in chl-*a* deposition did not correspond with the strong regional patterns that have been found for net plankton metabolism during spring.

Introduction

The spring increase in phytoplankton production and biomass is a well-known feature of the phytoplankton dynamics of Chesapeake Bay and other temperate and high latitude aquatic ecosystems. In Chesapeake Bay, the spring increase in phytoplankton biomass typically begins in March. Subsequently biomass begins to decline some time in April and the bloom concludes by the end of May (Fig. 4-1). Decline of spring phytoplankton blooms in Chesapeake Bay has been attributed to phosphorus and dissolved silica limitation (Conley and Malone 1992, Malone et al. 1996). Nutrient limitation promotes a physiological response leading to increased sedimentation of diatoms (Conley and Malone 1992), which are a major component of the winter-spring phytoplankton assemblage in Chesapeake Bay (Marshall and Nesius 1996). Excluding picoplankton, diatoms in winter-spring accounted for ~80% of phytoplankton cells in the lower Bay, 67% of cells in the mid-Bay (above pycnocline), and 56% of cells in the upper Bay (Chesapeake Bay Monitoring Program, unpublished data). Diatoms accounted for similar proportions of phytoplankton carbon (R. Lacouture, personal communication, Table 4-1). Physiological responses to bloom

senescence, such as formation of large aggregates, also enhance sedimentation and are an important aspect of the life cycle of diatoms (Smetacek 1985). Consequently, sinking is a quantitatively important fate of diatom blooms. In a mesocosm experiment simulating a spring bloom in Narragansett Bay, Keller and Riebesell (1989) estimated that sedimentation accounted for 14-65% of gross production.

Rapid sedimentation of intact phytoplankton to sediments is an important pulsed input of organic matter to benthic communities in many marine systems (e.g. St. Lawrence River, Townsend and Cammen 1988; Chesapeake Bay, Malone 1992). The importance arises not only from the quantity of the input, but from the high nutritional quality of the input, which has been shown to stimulate rapid increases in macrobenthic production (Graf et al. 1982, Marsh and Tenore 1990), microbial processes, and nutrient regeneration (Jensen et al. 1990). Townsend and Cammen (1988) suggested that the large spring flux of organic matter to sediments could play a role in recruitment success of juvenile demersal fishes. Spring bloom phytoplankton deposition has been identified as a key annual event in Chesapeake Bay, linking ecosystem processes in the winter-spring period to subsequent summer conditions, including hypoxia and summer phytoplankton blooms (Malone 1992, Chapter 6).

Because of the potential importance of spring bloom deposition to ecosystem processes, quantifying the flux is of particular interest. Unfortunately, this is technically challenging, a fact reflected in the paucity of flux estimates. Sediment traps have been used to quantify vertical fluxes of particles in various aquatic systems (e.g., Smetacek et. al. 1978), including in Chesapeake Bay (Boynton et al. 1993). Although effective and useful, there are significant complications associated with the

design and use of sediment traps (Blomqvist and Håkanson 1981, Knauer et al. 1984, Butman 1986, Butman et al. 1986, Asper 1987). Among other problems, the effort and expense required to deploy and maintain sediment traps severely limits the number of traps that can be deployed. In spatially heterogeneous environments such as estuaries, this means that the small number of sediment traps likely to be employed may not adequately characterize the vertical particle flux. For example, if phytoplankton production is localized outside the vicinity of the trap, the measurement will underestimate the flux. Alternatively, an overestimate could result from phytoplankton being localized in the area surrounding the sediment trap. Therefore, an approach that can estimate the flux at many locations is preferable.

Previous studies have demonstrated that chlorophyll-*a* (chl-*a*) and other phytoplankton pigments are effective indicators of fresh phytoplankton inputs to sediments (Sun et al. 1991, Josefson and Conley 1997). Where sediments are not euphotic, production of chl-*a* on sediments will be small compared to deposition of phytoplankton. This study used sediment chl-*a* measured in late spring as an indicator of deposition to sediments of phytoplankton originating from the spring bloom. Since spring bloom sedimentation appears to occur rapidly and in relatively cold water, degradation rates are likely to be small relative to sedimentation rates. This suggests that chl-*a* accumulation in late spring, with an appropriate correction for degradation, could be used to estimate recent deposition of phytoplankton to sediments. To obtain adequate spatial resolution, sediment chl-*a* was mapped on a regular grid throughout the estuary. Recognizing the significant interannual variability, particularly in association with freshwater input rates (Boynton and Kemp 2000), sediment chl-*a* was

mapped annually for 8 consecutive years. Interpretation was supported by comparison with contemporaneous estimates of phytoplankton biomass in the water column, sedimentation estimates from a sediment trap study, estimated phytoplankton sinking rates, and by comparison with net plankton community production estimates.

Study Site

Chesapeake Bay is a large, partially stratified estuary that extends 300 km from the mouth of the Susquehanna River in Maryland to the Atlantic Ocean between Cape Henry and Cape Charles, VA. The oligohaline upper Bay has a mean depth of 4.5 m with a deeper (~10 m) channel near the eastern margin. The mesohaline mid-Bay has a deep central channel, 20-50 m, flanked by shallower shoal areas to the east and west, giving it a deeper mean depth of 10.3 m. The polyhaline lower Bay is broader with a wide central channel region averaging ~15 m depth as well as broad shoal areas on the flanks of the channel. The mean depth is 9.2 m.

The physical transport regime throughout most of the estuary is best characterized by 2-layer gravitational circulation in which net up-estuary advection occurs below the pycnocline and net down-estuary advection occurs in the surface layer (Pritchard 1952). In the upper Bay, the circulation is initially down-estuary at all depths and at some point down-estuary makes a transition to the two-layer circulation.

Sediment-types vary throughout the estuary. North of Patuxent River and in the western half of the Bay south of Patuxent River (Fig. 4-2), sediments are >80% silt-clay except in shallow waters. In these shallow waters, and in deeper areas of the

eastern half of the south Bay, more porous sandy sediments (>80% sand) predominate (Kerhin et al. 1983, Chesapeake Bay Benthic Monitoring Program, unpublished data).

Methods

Field Methods

Sediment cores were obtained throughout the Bay during mid to late April in each year during 1993-2000 (Table 4-2, Fig. 4-3). Sampling cruises were conducted aboard the R/V Cape Henlopen and were part of a multi-disciplinary research project (Chesapeake Bay Land Margin Ecosystem Research Program).

Cores with an undisturbed sediment-water interface were obtained using a 0.25 m^2 Smith-Macintyre coring device at 20-50 locations usually located along horizontal transects spaced ~20 km apart. In 1993-1995, when the highest numbers of stations were sampled, additional stations were occupied between transects. Cores were obtained in waters from the deepest portions of the Bay to as shallow as 8 m. Shallower depths were not sampled due to draft limitations of the research vessel.

Once onboard, a sub-core was obtained using a modified 60 cc plastic syringe. This provided a sample of precise cross-sectional area and 1 cm depth, which was frozen immediately in a plastic centrifuge tube. In 1993, the top 2 mm from 2 sub-cores was combined in a single centrifuge tube, rather than 1 cm from a single sub-core. In 1994-1995, two samples were obtained at each station. One sample included the top 1 cm from a single sub-core, while the other included the top 2 mm from 2 sub-cores, as in 1993. This provided a means for comparing the two types of samples.

The reasons for these changes in field methods were unrelated to this study, but provided a limited means to examine the vertical distribution of chl-*a* in Chesapeake Bay sediments.

Pigment Analysis

Frozen sediment samples were briefly thawed at room temperature, then 40 ml of 90% acetone was added. Samples were extracted for 12 hours in a dark refrigerator, shaking 2-3 times during the course of the extraction, then centrifuged at ~1760 rpm for 5 minutes before decanting into a cuvette. Total chl-*a*, active chl-*a* and phaopigment concentrations in the acetone extracts were determined fluorometrically using the acidification method described in Strickland and Parsons (1972) and Parsons et al. (1984). Only the total chl-*a* and phaopigment data were examined in this study. The laboratory utilized a Turner Designs Model TD700 fluorometer calibrated against a spectrophotometer using pure chlorophyll-*a* from spinach (Sigma Chemical Company, C 5753), or liquid standards from Turner Designs, #10-850.

The extraction method that was used was later found to be different from that used by some published studies (e.g. Sun et al. 1991). Specifically, sediments were not sonicated prior to extraction, and only a single extraction was used. Therefore, a method comparison study was undertaken to determine whether the results would have differed significantly by use of sonication and/or an additional extraction. In this experiment, surficial sediments were obtained from box cores collected on Patuxent River, then processed in the field as described above. In the laboratory, the samples were thawed, then homogenized. Fifteen equal size aliquots from the continuously

stirred mud-slurry were extracted as described above after one of three sonication treatments. The treatments were: (1) no sonication (control); (2) microsonication for 3 minutes; and (3) sonication in a sonicator bath. The extracted pigments were decanted and analyzed as above. A second extraction of each sample was also analyzed as above, with the sum of the first and second extractions being recorded as the value for double-extraction. No sonication was performed prior to the second extractions. Although this design resulted in 30 values describing each of 6 treatment combinations, there were only 15 independent observations. Therefore, statistical significance was evaluated using repeated measures ANOVA. A comparison of single vs. double extraction (without any sonication) was also done on 7 non-homogenized samples from different locations in Patuxent River.

Interpolation Methods

Sediment chlorophyll-a data were interpolated to a regular grid for the purpose of contouring and computing regional means using the kriging procedure of Surfer software (Golden Software, Inc., Golden, CO). A quadrant search algorithm was selected such that a maximum of four observations were selected from each of 4 quadrants divided by north-south and east-west oriented axes.

Water Column Chlorophyll-a

Water column chlorophyll-a data were obtained from the Chesapeake Bay Water Quality Monitoring Program. Chlorophyll-a concentration was determined spectrophotometrically from acetone extractions of ground filters (EPA 1993).

Seasonal and regional integrated chlorophyll-a distributions as well as regional mean integrated chlorophyll-a concentrations were computed from interpolated distributions based on data from a series of approximately 20 stations located down the axis of the estuary (Fig. 4-1). Integrated chlorophyll-a was computed from vertical profiles of chlorophyll-a weighted by cross-sectional volumes per meter depth (Cronin and Pritchard 1975). Integrated chlorophyll-a was extrapolated in time and horizontal space using linear interpolation with quandrant searching on north-south and time axes.

Results and Discussion

Pigment Analysis Method Comparison. The results of a method comparison experiment showed that sonication and multiple extraction of sediment samples (e.g., Sun et al. 1991) could be expected to give sediment chl-a measurements 15.6% higher that those obtained using the method used in this study (Table 4-3). The difference was found to be a nearly constant proportion of chl-*a* as measured using a single extraction and without sonication, allowing a correction to be applied. Compared to the control (no sonication, single extraction), 3% more chl-*a* was extracted after use of a sonicator bath and 4.6% more chl-*a* was extracted after microsonication ($p<0.01$, Table 4-3). The second extraction removed 9.9-11.3% additional chl-*a* ($p<0.01$), depending on the sonication treatment ($p<0.01$). A larger amount was extracted on the second extraction if microsonication was used prior to the first extraction. Sediment chl-*a* measured in 7 non-homogenized sediment samples from Patuxent River using a single extraction and no sonication varied between 77 and 148 mg chl-a m^{-2}. A

second extraction obtained 11.0±0.5% (mean±std error) additional chl-*a*, a proportion comparable to that obtained for the corresponding treatments using homogenized samples (Table 4-3). This indicated that a proportional (15.6%) correction could be applied to the 1993-2000 Chesapeake Bay samples, which were previously processed with a single extraction and without sonication, with a high degree of confidence. Although this correction is not large compared to other possible sources of uncertainty, it was applied in the interest of beginning the analysis with the most accurate measurements that could be obtained.

Computing Sediment Total Chlorophyll-a Inventories. Due to vertical mixing of sediments on short time scales (days to weeks), the total inventory (i.e., vertically integrated concentration) of recently deposited chl-*a* may not have been accurately represented by the inventory within the top 0-10 mm of sediments. This leads to an underestimate of chl-*a* deposition, and, to the extent that sediment mixing could differ regionally, could affect comparisons among regions. The simultaneous collection of 0-2 mm and 0-10 mm sediment samples during 1994-1995 provided an opportunity to examine this issue and compute the sediment chl-*a* inventory. Bay-wide, the ratio of the 0-10 mm to 0-2 mm chl-a inventories was estimated to be 2.75. As the ratio is substantially less than 5, this indicates a decline in chl-*a* concentration with depth in the sediments. Because of poor compliance with the assumptions of ANOVA, a non-parametric ANOVA was used to test for differences in the mean ratio in the three regions. The ratio was found to differ significantly among regions of the Bay (Kruskal-Wallis Test; $p<0.05$). The respective median ratios for the upper-, mid- and lower-Bay regions were 2.7, 2.3, and 3.1. Using more detailed vertical profiling of

sediment chl-*a* in the top 10 cm of Long Island Sound sediments, Sun et al. (1994) observed an exponential decrease in chl-*a* with depth below the sediment-water interface. This model has been assumed to apply to Chesapeake Bay as well. Accordingly, the chl-*a* inventory (C_{int}) integrated to a depth h, is

$$C_{\text{int}} = C_{\max} \int_{z=0}^{z=h} e^{-kz} = C_{\max} \frac{1}{k}\left(1 - e^{-kh}\right) \tag{1}$$

where C_{max} is the maximum (surface) concentration and k is the rate of decrease with depth. Using this expression, the ratio, R, between the 0-10 mm concentration and the 0-2 mm concentration is $R = \frac{1 - e^{-10k}}{1 - e^{-2k}}$, which gives k=0.19, 0.25, and 0.14 for the upper-, mid- and lower-Bay. Using these estimates of k, the top 10 mm was estimated to include (in same order) 85%, 92% and 76% of the total chl-*a* inventory ($\approx$ 0-10 cm integrated chl-*a*). These factors were used to compute the chl-*a* inventory from the measured concentrations.

The regional differences in vertical chl-*a* distribution (i.e., in k) may reflect differences in sediment properties and/or mixing processes. The mid-Bay is characterized by fine, silty sediments (Fig. 4-2), deep and seasonally anoxic water, and lower physical energy (i.e. waves and currents) than other areas of the Bay. This would be expected to minimize physical and biological mixing of sediments. In contrast, the lower Bay is shallower and has an increased prevalence of sandy sediments. During winter-spring, the penetration depth of ^{7}Be (half-life= 53 d) in the lower Bay was 3-5 cm, with physical mixing due to tidal current and wave action being dominant (Dellapenna et al. 1998). This may explain the deeper mixing of

deposited chl-*a* in the lower Bay, although no comparable data are available for the mid Bay or upper Bay. An April minimum in sediment mixing in the lower Bay, prior to a summer increase associated with bioturbation (Dellapenna et al. 1998), suggests that macrobenthic activity was suppressed by low water temperature (5-15 °C) up until the time that surficial sediment samples were collected. This is important to the overall approach of this study because losses of chl-*a* due to macrobenthic activity could be more variable and therefore difficult to quantify.

Phaopigments. Phaopigments are a product of the early breakdown of chl-*a*. As such, they are also an indicator of deposition of phytoplankton to sediments. Macrobenthic biomass has been found to be positively associated with phaopigments (Josefson and Conley 1997); however, this may be due to the presence of phaopigments in feces of plankton and macrobenthos and the slow degradation rate of phaopigments as compared to chl-*a* (Furlong and Carpenter 1988). With this in mind, a high ratio of chl-*a* to chl-*a*+phaopigments suggests that substantial deposition of chl-*a* occurred recently. For the 84 measurements Bay-wide in 1996-2000 in which sediment phaopigment concentration was measured, chl-*a* accounted for an average of 47% (range=38-58%) of chl-*a*+phaopigments. This is regarded as a high ratio (Josefson and Conley 1997), suggesting that a significant amount of phytoplankton was deposited to Chesapeake Bay sediments each spring.

Distributions of Sediment Total Chlorophyll-*a*. The computed sediment total chl-*a* inventory averaged 175 mg m^{-2} over 272 observations Bay-wide during 1993-2000. The median value was 164 mg m^{-2} (interquartile range= 88-234 mg m^{-2}).

Regional and overall mean chl-*a* was calculated for each year from interpolated distributions to account for the non-random distribution of observations. Computed in this way, the long-term overall mean was 171 mg m^{-2}, very close to the unweighted average of all observations. However, regional means, particularly the upper Bay mean, were slightly more sensitive to the averaging procedure. Therefore, the interpolated fields were used to compute means rather than the raw data. The highest average chl-*a* inventory, 195 mg m^{-2}, was found in the mid-Bay. Lower chl-*a* was found in the lower Bay (148 mg m^{-2}) and the upper Bay (172 mg m^{-2}, Table 4-4). Interannually, the highest Bay-wide mean chl-*a* inventory was 244 mg m^{-2} in 1999, while the lowest was 117 mg m^{-2} in 1995, a >2-fold range (Table 4-4). The distribution of raw observations illustrates the patterns and magnitude of spatial and interannual variability in sediment chl-*a* (Fig. 4-3).

Both the regional distribution of chl-*a* within the Bay and the Bay-wide average sediment chl-*a* concentration were related to the magnitude of winter-spring (Jan-Apr) total discharge of freshwater into Chesapeake Bay, which over the past 15-years was highly correlated (r^2=0.91) with the Jan-Apr discharge from the Susquehanna River, the largest tributary of the Bay (Fig. 4-4, Chapter 2). Bay-wide, the average sediment chl-*a* increased with spring river flow, a pattern also observed for the lower Bay and less obviously for the mid-Bay. This positive association likely reflects a nutrient enrichment mechanism operating at a seasonal/whole-estuary scale. Since nutrient loading is positively and strongly correlated with river flow (Boynton and Kemp 2000), increased river flow can be expected to increase phytoplankton biomass and production when nutrient limitation is important. Since nutrient

limitation, principally by phosphorus and silicate (for diatoms), is well known near the end of spring in the mid- and lower-Bay (Conley and Malone 1992; Fisher et al. 1992; Fisher et al. 1999), it is not surprising that a strong positive correlation between river flow and spring average water column chl-*a* was observed for the lower Bay (Fig. 4-5). This increased phytoplankton biomass apparently contributed to increased chl-*a* export to sediments (Fig. 4-6). Physical transport processes associated with high flow may enhance nutrient enrichment in the lower Bay by decreasing water residence times in the upper Bay (Hagy et al. 2000), thereby increasing down-Bay nutrient transport. Whether by a river flow-dependent mechanism (this study) or in association with a flow-independent long-term nutrient loading rate increase (Harding and Perry 1997), the effects of increased nutrient loading on primary production appear most dramatic in the lower Bay.

In contrast to the mid and lower Bay, sediment chl-*a* in the upper Bay tended to decrease with increasing river flow (Fig. 4-4). One possible explanation is that high river flow decreased water residence time and increased turbidity. This would be expected to translate phytoplankton biomass and primary production down-estuary, precluding deposition to sediments in the upper Bay region. If this were a sufficient explanation for decreased sediment chl-a in high flow years, then one would expect to make two observations: (1) water column chl-*a* and river flow would be strongly and negatively correlated and (2) water column chl-a would be positively correlated with sediment chl-*a*. The first expectation did not hold. Although a broad negative association was present between water column chl-*a* and river flow, the correlation was not strong. In fact, the negative correlation between river flow and sediment chl-*a*

(Fig. 4-4) was stronger. The second expectation also did not hold. Instead, in 6 of 8 years, sediment chl-*a* was lower when water column chl-*a* in the upper Bay was higher (Fig. 4-6). A speculative explanation for this general observation is that high phytoplankton deposition to sediments may cause low phytoplankton biomass in the water column due to low primary production and negative net plankton production (Smith and Kemp 1995). Conversely, in the presence of low rates of primary production, high phytoplankton biomass can generally only occur in the absence of high deposition rates. Of course, as originally hypothesized, simultaneously low phytoplankton deposition to sediments and low phytoplankton biomass in the water column could result from very high flushing rates. This "wash-out" could have occurred during the record floods of spring 1993, explaining the low sediment chl-a that year (Fig. 4-6, upper panel). On the other hand, sediment chl-*a* in the upper Bay in 1999 was consistent with expectation based on low river flow in that year (Fig. 4-4), but water column chl-*a* remained high. This made 1999 an outlier in the water column vs. sediment chl-*a* relationship (Fig. 4-6). The explanation for this departure from the general pattern observed in other years is not known.

The species composition of the winter-spring phytoplankton assemblage in 1993-2000 was examined in an effort to explain more of the variability that was observed in sediment chl-a those years (Chesapeake Bay Phytoplankton Monitoring Program, unpublished data). It was hypothesized that higher sedimentation in some years was due in part to a greater relative abundance of diatoms, whose tendency toward sinking has been noted (Smetacek 1985). Some suggestive results were obtained. In the lower Bay, diatom counts largely paralleled average chl-*a* due to the

dominance of diatoms in the winter-spring phytoplankton community. However, diatom counts did not predict sediment chl-*a* as well as water column chl-a did, probably due to larger random variability in diatom counts due to less frequent sampling. Sediment chl-*a* in the upper Bay appeared to increase with average diatom counts, apparently contradicting the results based on chl-a. However, there were two substantial outliers and a weak relationship among the remaining observations, suggesting that the appearance of any relationship was due to chance. Thus, the analysis of phytoplankton species data neither contradicted nor supported the hypothesis, in significant part because the temporal resolution of these labor-intensive data collections was too low to adequately characterize the highly variable phytoplankton community during the winter-spring period.

As the above discussion illustrates, a variety of ecosystem processes can affect relationships among river flow, water column chl-*a* and sediment chl-*a*. These clearly have the potential to cause dramatic departures from relationships expressed by empirical models. However, the predictable ecosystem responses that were observed among many observations indicates that, on a region-specific basis, certain mechanisms appear to maintain first-order importance and drive large (2-3 fold) responses. In some cases, outliers illustrate that an implicit assumption of the model was not met. For example, the conceptual basis for Figs. 4-6 implicitly assumes a Jan-Apr time domain for forcing and response. The 1997 outlier, in which water column chl-*a* in the mid- and lower-Bay was much higher than expected, may reflect the unseasonably high flow that occurred during fall 1996. This river flow substantially increased January nutrient concentrations (N, P, Si) in surface waters at a station in the

lower Bay from their long-term (1984-1999) averages. Total N increased from 27 to 41 μM, total P from 0.88 to 1.16 μM and dissolved Si from 5.5 to 11.6 μM (Chesapeake Bay Monitoring Program, unpublished data). These high January nutrient concentrations reduced the importance of a normal spring freshet for supplying the 1997 spring phytoplankton community with nutrients.

Another possible source of uncertainty in the observed relationships (Fig 4, Fig. 4-6) is the variable timing of the ecosystem response, specifically the dates of maximum phytoplankton biomass accumulation and bloom collapse relative to the dates of the sediment chl-a surveys (Fig. 4-7). For example, peak water column chl-*a* in 1996 occurred on 5/14/96 in both the mid- and lower Bay, one week after sediment sampling was concluded. This may explain why Bay-wide average sediment chl-*a* in 1996 was lower than expected from the level of spring river flow. In contrast, peak water column biomass in the mid and lower Bay in 1997 occurred on 4/3, ~2 weeks prior to sediment sampling (Fig. 4-7). This probably contributed to the high sediment chl-*a* observed in that year. Peak phytoplankton biomass also occurred very close to the sediment sampling dates in 1998 and 2000. In 1999, the highest sediment chl-*a* deposition was observed despite the lack of any large accumulation in the water column before or after sampling. Importantly, 1996, 1998 and 2000 were not substantial outliers in the analysis (Fig. 4-4, Fig. 4-6) as was 1997 in Fig. 4-5. This suggests that deposition of chl-*a* to sediments occurred at least in part in a relatively steady-state process whereas some fraction of production was continuously deposited to sediments. Deposition could not be explained simply by a pattern of biomass accumulation in the water column followed by mass deposition to sediments.

Estimates of Chlorophyll-a Deposition. A simple diagenetic model was used to estimate the deposition of phytoplankton to sediments during spring in each year using the observed accumulation of sediment chl-*a*. A few simplifying assumptions were needed due to data limitations. It was assumed that the input to sediments occurred at a constant rate, I (mg m^{-2} d^{-1}) over a period of t days, during which time deposited chl-*a* decayed at a first-order decay rate, k (d^{-1}). The net accumulation rate of chl-*a* on the sediment surface can be described by $dC/dt = I - kC$. Solving under the boundary condition that when $t=0$, $C=C_0$ yields

$$C_t = \frac{I}{k} + \left(C_0 - \frac{I}{k} \right) e^{-kt} \qquad (2)$$

Solving for I gives

$$I = \frac{k\left(C_t - C_0 e^{-kt}\right)}{1 - e^{-kt}} \qquad (3)$$

Although not immediately obvious, it can be shown using L' Hôpital's rule that $\lim_{k \to 0} I = \frac{C_t - C_0}{t}$. Thus, if the degradation rate is very small, and minimal chl-*a* was present prior to the period of interest ($C_0 \approx 0$), total deposition equals the observed accumulation (C_t) and is insensitive to t. In contrast, the deposition rate depends inversely on t. As the degradation rate (k) increases relative to the deposition rate (I), a steady state model as suggested by Sun et al. (1991) may be more appropriate. In Chesapeake Bay, the time period, t, during which most spring bloom phytoplankton deposition occurs probably varies from year to year (Fig. 4-7), but it was assumed that

most deposition occurred between mid to late February and the time of the sediment surveys, a period of ~60 days. Based on Fig. 4-7, a range of 30-75 days was considered possible. A few measurements of sediment chl-*a* in Chesapeake Bay in early January-February were available for a number of years during the 1980's (Garber et al. 1989). These values varied between 37-83 mg m^{-2} and averaged 58 mg m^{-2}, providing a base case and range of variability for C_0. Estimates for the first-order chl-*a* decay rate (k) were obtained by considering the work of Sun et al. (1993a) and other studies by Sun and colleagues (Sun et al. 1991, Sun et al. 1993b, Sun et al. 1994). These studies provide a good assessment of chl-*a* degradation under a variety of conditions. The rates most applicable for this study appear to be those obtained for un-frozen, oxic sediments (Sun et al. 1993a), although it is possible that sediments at 1 cm depth were completely anoxic in some places. Oxic degradation of chl-*a* is highly temperature-dependent, with the first-order decay constant for free chl-a (k_d) increasing 4-fold between 5 °C and 25°C (Sun et al. 1993a). The first-order rate for release of chl-*a* from a particle-bound state to a free state (k_r), which was required for most chl-*a* degradation, also increases more than 6-fold over the same temperature range (Sun et al. 1993). Over 5-25 °C, k_r was 30-50 times greater than k_d; therefore, only the smaller rate is relevant here. During the period from mid-March through May 1, bottom water temperature increased from 4 to 15 °C in the upper and lower Bay and from 4 to 13 °C in the mid-Bay. The average in all regions during March-May was ~7-9 °C. In this temperature range, k_d was 0.028 d^{-1}. Thus, 0.028 d^{-1} was used as a base case estimate for k in eq. (1) and eq. (2), with values between 0.02 and 0.04 considered as a reasonable range of variability.

Estimates of chl-*a* deposition (±standard deviation) were computed for each region and year using Monte-Carlo simulations (Table 4-5, Table 4-6). In these simulations, the parameters C_0, t and k were chosen randomly from triangular distributions specified using the estimated min, max and mode, which is equal to the base case estimate for each parameter (Table 4-5). For each value of C_t (i.e. each region, year), many (10^4) estimates of the average daily deposition rate (I) and total deposition (It) were computed using eq. 3. Means and standard deviations were then computed (Table 4-6). The 1993-2000 average chl-*a* deposition rate was estimated to range from 5.08 mg m^{-2} d^{-1} in the lower Bay to 6.81 mg m^{-2} d^{-1} in the mid-Bay. Average cumulative winter-spring chl-*a* deposition varied from 277 mg m^{-2} in the lower Bay to 371 mg m^{-2} in the mid-Bay. Estimated coefficients of variation for chl-*a* deposition rate and cumulative deposition estimates averaged 12% and 16%, respectively. Chl-*a* deposition rate and cumulative deposition were not directly proportional to the late-spring chl-a inventory (C_t) because C_0 was not equal to zero (see eq. 3). However, because C_t was typically much greater than C_0, the ratios I/C_t and It/C_t were much less variable than C_t. For example, I/C_t ranged from 0.032 to 0.036 d^{-1}. The ratio It/C_t ranged from 1.76 to 1.95. In other words, the cumulative winter-spring deposition of chl-*a* was slightly less than two times the observed sediment chl-*a* inventory near the end of April. Therefore, regional and interannual patterns of chl-*a* deposition rates were comparable to corresponding patterns in late spring chl-*a* inventories (Table 4-4, Fig. 4-4, Fig. 4-6).

Boynton et al. (1993) estimated chl-*a* deposition in the mid-Bay during 1985-1992 using consecutive short-term (~1 week) deployments of sediment traps at one

station. In most years, chl-*a* deposition measured just below the pycnocline was ~5-10 mg m^{-2} d^{-1} in late February, then increased to 10-20 mg m^{-2} d^{-1} in April. From the earliest trap deployments in early February until early May, integrated chl-*a* deposition as measured by the traps was 600 to 1200 mg m^{-2} with an average of 789 mg m^{-2}. The comparable mid-Bay estimate from this study is 371 mg m^{-2}, or about 50% of the sediment trap estimate. This study estimated the average chl-*a* deposition rate in the mid-Bay to be 6.81 mg m^{-2} d^{-1}, 71% of the 9.6 mg m^{-2} d^{-1} estimated using the sediment traps. Because of the limitations of sediment traps (Blomqvist and Håkanson 1981, Knauer et al. 1984, Asper 1987) one cannot assume that sediment traps provided a more accurate estimate. It is possible that the sediment traps retained particles more effectively than the sediment surface, leading to an overestimate of the flux to sediments. This "resuspension" effect clearly affected the deeper sediment traps for which the flux measurements were often several times larger than the mid-cup fluxes (Boynton et al. 1993).

Another check on the chl-*a* deposition estimates can be made by using the estimated chl-*a* deposition rate and estimates of water column chl-*a* concentrations to estimate an effective sinking velocity for phytoplankton cells. This velocity can then be compared with measurements from the published literature. This approach requires that one assume a uniform vertical chl-*a* distribution in the water column, which may be appropriate in late winter and early spring in Chesapeake Bay. The effective sinking rate (v_z) can be estimated from the integrated water column chl-*a*

concentration (C_{int}), the mean depth ($\bar{z}$) and the rate of chl-a deposition to sediments (F) using

$$v_z = \frac{F}{C_{wc}}, \text{ where } C_{wc} = \frac{C_{\text{int}}}{\bar{z}}$$

Given C_{int}= 50-100 mg m^{-2} (Fig. 4-2), $\bar{z} \approx 8$ m, and F=6.0 mg m^{-2} d^{-1}, this gives v_z=0.5-1.0 m d^{-1}. Mean upwelling velocities in the range of 0.5 m d^{-1} would affect cells sinking through the water column (Hagy 2001). Thus, the actual sinking rate may be 1.0-1.5 m d^{-1}, approximately the same as the 1.1-1.5 m d^{-1} estimated for larger cells (8-53 μm) within a whole phytoplankton assemblage in an experimental enclosure (Bienfang 1981). This estimate exceeds the minimum sinking rates estimated for *Skeletonema costatum*, the most abundant species in lower Chesapeake Bay in winter-spring (Table 4-1), but approximates the maximal sinking rates for the same species (Smayda 1970). Thus, the observed deposition probably represents sinking of senescent and/or nutrient limited cells, consistent with observations of Smetacek (1985).

The analysis of average sinking rate noted above is intended to show only that the estimated chl-*a* deposition is consistent with reported sinking rates and observed chl-*a* concentrations in the water column. It is not known, however, if the deposition actually occurred at this average sinking velocity. Formation of large "flocs" can lead to settling rates of 10-100 m d^{-1} (Smetacek 1978), sufficient to deposit an entire senescent phytoplankton bloom to Chesapeake Bay sediments within one day.

Carbon Flux to Sediments. Given an estimate of C:chl-*a*, the estimated spring chl-*a* flux to sediments described above can be used to estimate the carbon flux associated with spring bloom phytoplankton deposition. The long-term January-April average C:chl-*a* in mid-Bay and lower-Bay bottom water is ~100 (Chesapeake Bay Monitoring Program Data). In the upper-Bay, average C:chl-*a* during winter-spring was >250. These values are higher than those typical of phytoplankton, indicating a large non-phytoplankton (i.e. detritus) component within the POC. When chl-*a* increased quickly and substantially (e.g. Fig. 4-7), C:chl-*a* decreased to an asymptotic value of ~50, with typical values between 50-100 when chl-*a*>20 $\mu g\ l^{-1}$. Following a bloom, C:chl-*a* was found to increase quickly as chl-*a* decreased. This suggests that the phytoplankton community had C:chl-*a* ≈50-100 and that particles lost at the termination of the bloom, possibly due to sinking, also had a C:chl-*a* in the range of 50-100. This was supported by sediment trap data (Boynton et al. 1993), which showed that the ratio of carbon to chl-*a* sinking flux in March-April was ~75 when the chl-*a* flux was >8 mg $m^{-2}\ d^{-1}$.

Using C:chl-*a*=75 and an average total chl-*a* deposition of 277-371 mg m^{-2} (Table 4-6) the carbon flux to sediments associated with spring bloom phytoplankton deposition is estimated to have been 21-28 gC m^{-2}. Similarly converted to C, the chl-*a* deposition rate was equivalent to 0.51 gC $m^{-2}\ d^{-1}$, 71% of the C flux computed from chl-*a* fluxes to sediment traps (also assuming C:Chl-a=75), but only 36% of the directly measured PC fluxes to the same sediment traps (Fig 8, Boynton et al. 1993). The larger disparity observed between directly measured PC fluxes and estimates from

this study reflects periods in which the sediment traps received particles with C:chl-*a* higher than 75, potentially due to resuspension effects on the sediment traps.

These carbon flux estimates for the spring bloom in Chesapeake Bay are substantially higher than reported carbon fluxes associated with spring phytoplankton blooms in some other systems. For example, a 34-day bloom in the Baltic Sea deposited 6.2 g C m^{-2} to sediments (Smetacek et al. 1978, cited in Keller and Riebesell 1989). A 25-day bloom in the Kiel Bight deposited 11.5 g C m^{-2} (Peinert et al. 1982, cited in Keller and Riebesell 1989). The estimated C flux rate for Chesapeake Bay is similar to that of the Kiel Bight bloom, but persisted for a longer period of time, leading to a larger cumulative C flux (Table 4-6). This seems reasonable given the eutrophic condition of Chesapeake Bay.

The estimated carbon flux associated with the spring bloom (21-28 gC m^{-2}) sediments accounts for 10-14% of annual benthic respiration (163 g C m^{-2} y^{-1}) plus carbon burial (39 g C m^{-2} y^{-1}, Kemp et al. 1997), slightly less than proportional to the fraction of the year encompassed (60/365 days = 16%). That the spring bloom deposition did not support a larger fraction of annual metabolic C demand was surprising considering the clear seasonality of phytoplankton biomass (Fig. 4-1) and net plankton metabolism (Kemp et al. 1997), and the importance generally ascribed to this annual ecosystem event. Assuming that the spring bloom deposition was not larger than estimated, but that it was important to the macrobenthic community as has been suggested, one may conclude that the importance arises from food quality rather than quantity (e.g. Marsh and Tenore 1990).

Another surprising result is that the spring phytoplankton deposition differed only slightly by Bay region and that the regional variation did not parallel regional differences in net plankton metabolism (NPM, Smith and Kemp 1995), which increased strongly down-estuary. For the mid-Bay, the estimated carbon flux (0.51 g C m^{-2} d^{-1}) is slightly greater than NPM (=0.41 gC m^{-2} d^{-1}) estimated by Smith and Kemp (1995; converted from O_2 flux using g C=0.375 g O_2). In contrast, the estimated winter-spring carbon deposition to sediments in the lower Bay (0.38 gC m^{-2} d^{-1}) was only 24% of the much higher estimate of NPM for the lower Bay (1.6 g C m^{-2} d^{-1}, Smith and Kemp 1995). The fate of the apparent surplus production in the lower Bay is unknown, but may include export to the mid-Bay via the landward advection in the lower water column, or possibly export to the coastal ocean. The presence of significant chl-*a* fluxes to sediments in the upper Bay, despite negative NPM may indicate that allochthonous C inputs supported plankton respiration and reduced NPM, while autochthonous phytoplankton production supported vertical C fluxes to sediments.

Conclusions

Surficial sediment chlorophyll-a can be used effectively as a biomarker for spring bloom phytoplankton deposition to sediments. These deposition estimates obtained are the only known Bay-wide estimates for Chesapeake Bay. Deposition was 2-4 times greater than estimated spring bloom deposition from some other estuarine and coastal systems, illustrating the intense primary production associated with spring phytoplankton blooms in Chesapeake Bay. Deposition increased with river flow and

was translated down-Bay in high flow years, suggesting the importance of both nutrient enrichment and physical transport processes in determining phytoplankton deposition to sediments during spring. The estimated deposition, although large, did not account for a larger than proportional fraction of annual benthic metabolic requirements. A lack of regional correspondence between net plankton production and deposition to sediments leaves important questions about this important benthic-pelagic coupling mechanism.

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Table 4-1. The most abundant phytoplankton taxa (excluding picoplankton) in three regions of Chesapeake Bay during spring and the average fraction of total phytoplankton carbon contributed by diatoms. Phytoplankton species counts from unpblished Chesapeake Bay water quality monitoring program data (available from USEPA Chesapeake Bay Program web site). Unpublished carbon composition data provided by R. Lacouture (personal communication).

Region	Most Abundant Phytoplankton Taxa (excluding picoplankton) during Jan-Apr. (% of cells)	% of Total Phytoplankton Counts	% of Total Phytoplankton Carbon
Upper Bay	unclassified centric diatoms[1] (23%), *Katodinium rotundatum*[2](12%), *Skeletonema costatum*[1](12%), *Crytomonas* spp.[3](12%), *Cyclotella* spp.[1](8%), *Skeletonema potamos*[1](7%).	56%	59%
Mid Bay	unclassified centric diatoms[1](17%), *Katodinium rotundatum*[2](15%), *Crytomonas* spp.[3](15%), *Cyclotella* spp.[1](12%), *Cerataulina pelagica*[1](9%), *Skeletonema costatum*[1](9%), *Chaetoceros* spp.[1](5%)	67% (above pycnocline)	69% (above pycnocline)
Lower Bay	*Skeletonema costatum*[1](20%), unclassified centric diatoms[1](18%), *Cerataulina pelagica*[1](9%), *Crytomonas* spp.[3](9%), unclassified pennate diatoms[4](9%), *Nitzschia pungens*[4](8%), *Rhizosolenia fragilissima*[4](4%), *Rhizosolenia delicatula*[4](3%).	83% (above pycnocline), 84% (below pycnocline)	n/a

[1]centric diatoms, [2]dinoflagellates, [3]crytomonads, [4]pennate diatoms,

Table 4-2. Cruise dates for sediment chlorophyll-a surveys and the number of sediment cores collected in each region of the Bay.

Year	Cruise Dates		Number of Cores		
	Begin	End	Upper Bay	Mid Bay	Lower Bay
1993	5/8/93	5/12/93	8	25	23
1994	Mid May		9	21	33
1995	4/28/95	5/3/95	7	25	31
1996	4/27/96	5/7/96	8	13	10
1997	4/20/97	4/24/97	7	17	7
1998	4/11/98	4/15/98	6	13	15
1999	4/19/99	4/23/99	6	11	14
2000	4/29/00	5/2/00	6	8	6

Table 4-3. Results of a method comparison experiment used to evaluate the effect of three sonication treatments and single vs. double extraction on the amount (mean±se, % change from control) of chl-*a* (μg/g) extracted from 15 aliquots of homogenized Chesapeake Bay sediments. Each sonication treatment was replicated 5 times. All effects (sonication,extraction and interaction effect) were statistically significant (Repeated-measures ANOVA, $p<0.01$).

	Single Extraction, μg/g	Double Extraction, μg/g
No Sonication	9.35 (0.02, 0%)*	10.32 (0.02, +10.4%)*
Microsonication	9.78 (0.05, +4.6%)	10.84 (0.06, +15.9%)
Sonicator Bath	9.63 (0.03, +3.0%)	10.56 (0.04, +12.9%)

* these treatments were also compared using 7 non-homogenized samples. The mean difference in those samples was 11.0±0.5%

Table 4-4. Regional/annual mean sediment total chlorophyll-*a* inventories. These were computed from 0-1 cm chl-*a* inventories by adjusting for mixing to below 1 cm on short time scales (i.e. days-weeks). Calculation of the overall mean accounts for differences in the area of the respective regions and is therefore not the mean of the regional means.

Year	Upper Bay	Mid Bay	Lower Bay	Overall	Jan-Apr Flow ($m^3 s^{-1}$)
1993	84	182	161	155	2989
1994	147	217	187	191	2624
1995	139	130	98	117	1206
1996	107	132	146	134	2383
1997	223	243	231	235	1403
1998	195	169	122	153	2471
1999	315	323	150	244	1392
2000	162	162	92	137	1739
Average	172	195	148	171	2026

Table 4-5. Minimum, maximum and modal values used to specify triangular distributions for parameters in eq. 3. Parameter values were randomly drawn from these distributions and used in Monte Carlo simulations to estimate the mean and standard deviation of chl-*a* deposition in each region and year.

Parameter	Min	Mode	Max
Initial chl-a concentration, C_0, mg m^{-2}	30	58	80
First-order decay coefficient, k, d^{-1}	0.02	0.028	0.04
Period of Bloom deposition, t, days.	30	60	75

Table 4-6. Estimated average (±standard deviation) chl-*a* deposition rates (mg m^{-2} d^{-1}) and total winter-spring chl-a deposition (mg m^{-2}) for winter-spring in the upper, mid and lower Chesapeake Bay during 1993-2000.

(a) Average deposition rate during winter-spring (mg m^{-2} d^{-1})

Year	Upper Bay	Mid Bay	Lower Bay
1993	2.69±0.34	6.34±0.73	5.56±0.64
1994	5.04±0.58	7.64±0.88	6.52±0.74
1995	4.74±0.55	4.40±0.52	3.21±0.39
1996	3.55±0.43	4.48±0.52	4.99±0.59
1997	7.86±0.90	8.61±0.98	8.16±0.94
1998	6.81±0.79	5.85±0.67	4.10±0.49
1999	11.29±1.28	11.57±1.33	5.14±0.59
2000	5.59±0.65	5.59±0.64	2.99±0.37
Average	5.95	6.81	5.08

(b) Winter-spring chl-*a* deposition (mg m^{-2})

Year	Upper	Bay	Mid
1993	148±28	345±54	304±49
1994	275±45	415±63	355±55
1995	258±42	241±41	175±32
1996	193±34	244±41	272±44
1997	429±65	470±70	444±67
1998	371±57	319±51	224±38
1999	613±90	631±92	280±45
2000	305±49	305±48	163±30
Average	324	371	277

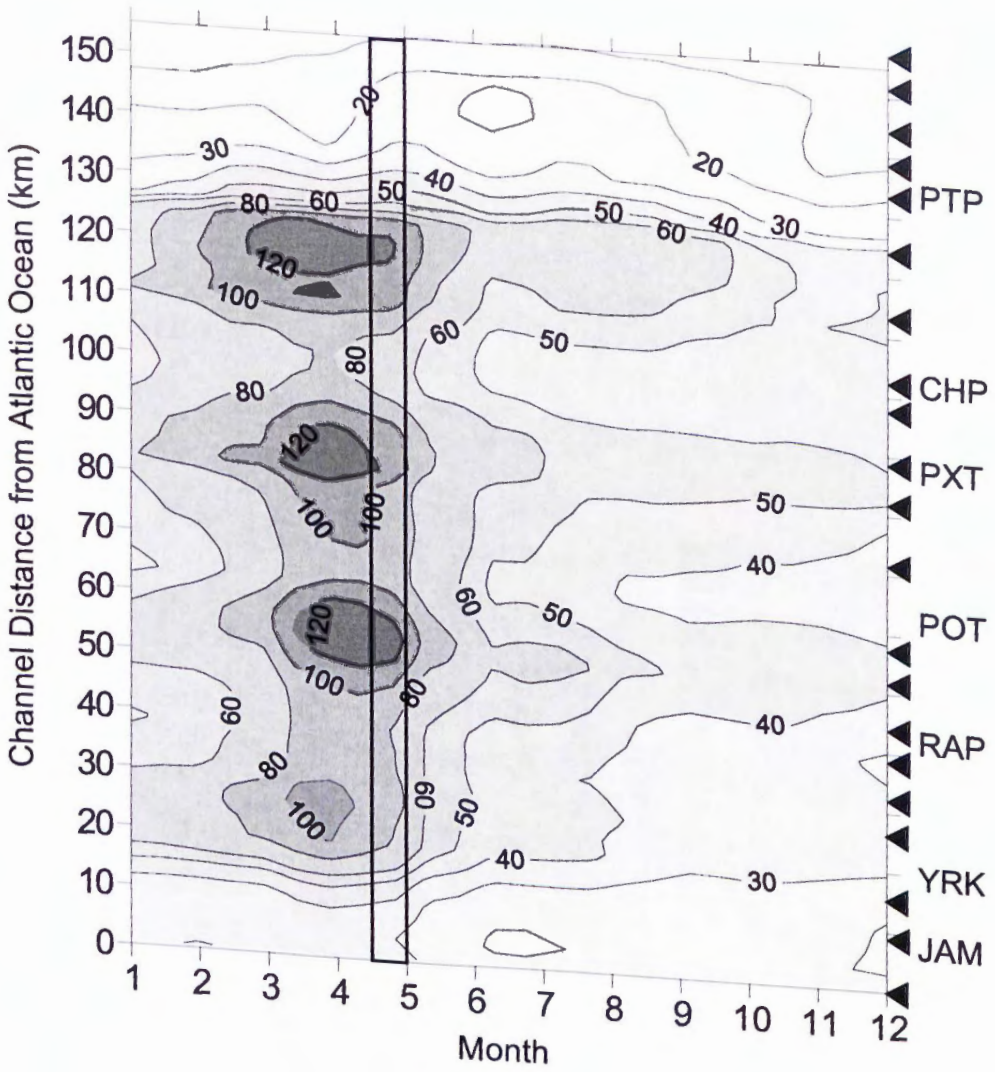


Fig 4-1. Average seasonal distribution of water column integrated chlorophyll-a (mg m^{-2}) in Chesapeake Bay (1984-1999). Arrows on the right (◀) indicate the locations along the central axis of the Bay of the Chesapeake Bay Water Quality Monitoring Program stations used to generate the plot. Three letter codes refer to the major tributary rivers and are as follows: JAM=James River, YRK=York River, RAP=Rappahannock River, POT=Potomac River, PXT=Patuxent River, CHP= Choptank River, PTP=Patapsco River. The rectangle indicates the time period during which surficial sediment sampling was usually conducted. Exact dates are in Table 1.

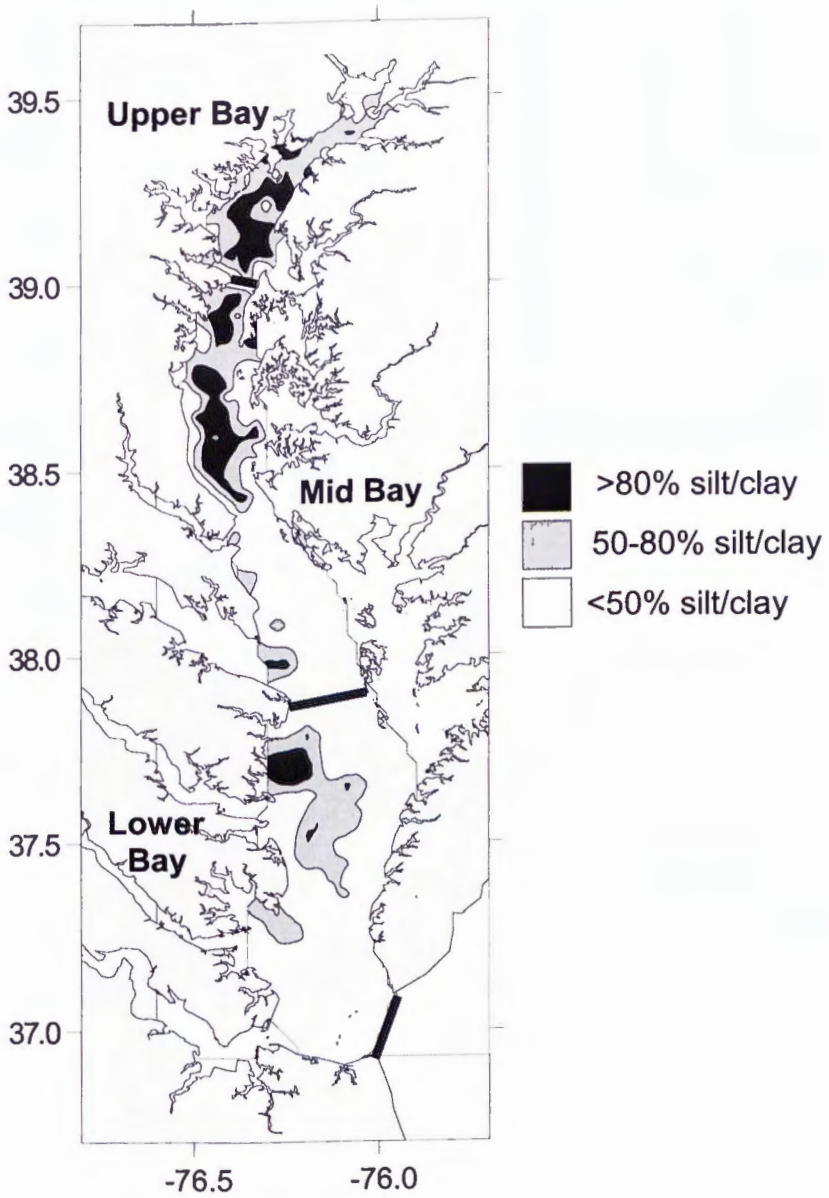
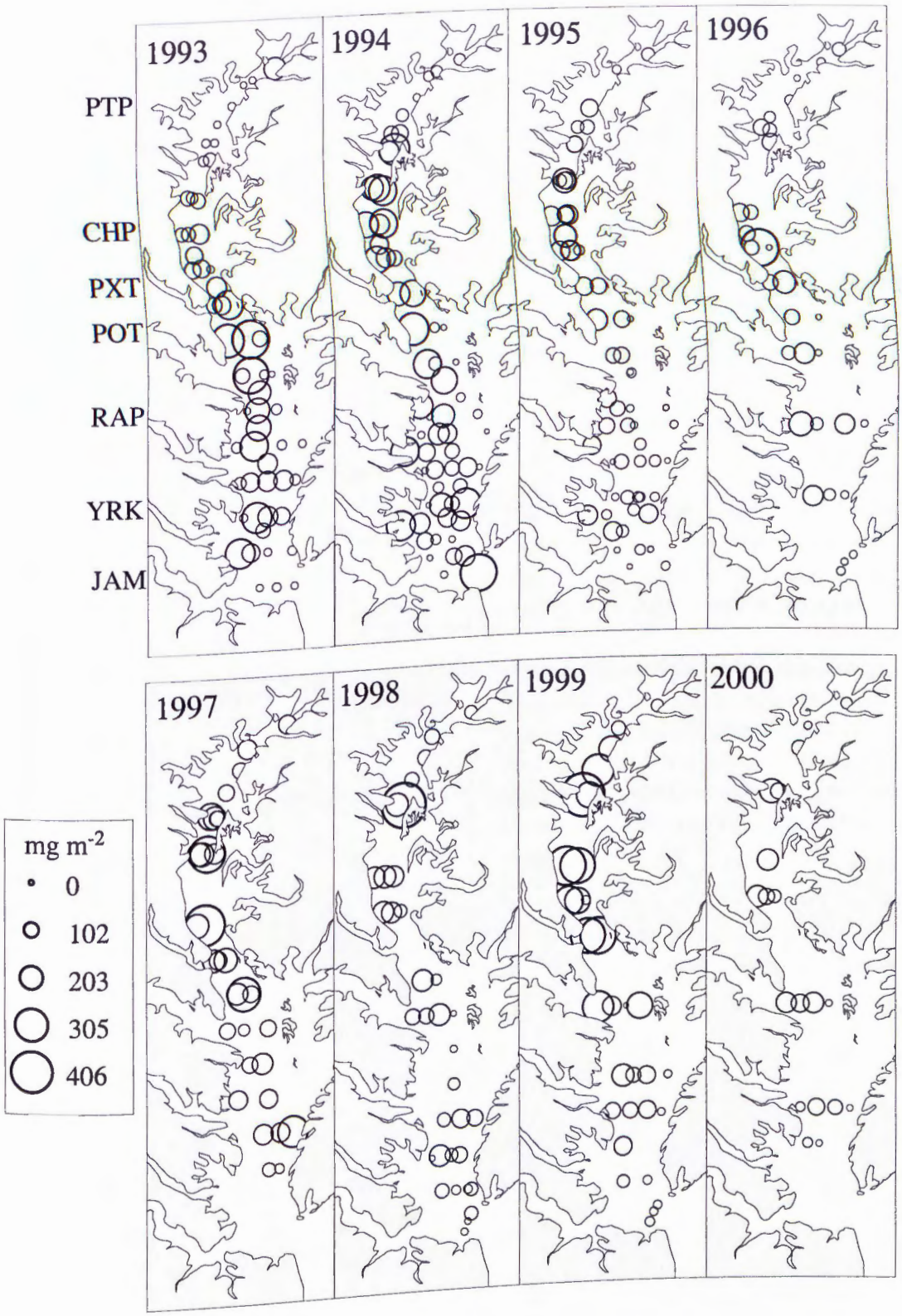


Fig. 4-2. A map of Chesapeake Bay indicating regional boundaries and the distribution of sediment types as computed from the Chesapeake Bay Monitoring Program Benthic Data (data available from US EPA Chesapeake Bay Program Web Site). Distribution of sediment types is comparable to Kerhin et al. (1983).

Fig. 4-3. The distribution of total chlorophyll-a in the top 1 cm of Chesapeake Bay sediments during late spring in 1993-2000. The center of each circle indicates the location at which the core was collected, while the size of the circle indicated total chlorophyll-*a* values. The values for 1993 are estimated from total chlorophyll-*a* in the top 2 mm. The three letter codes adjacent to the 1993 map identify the major tributaries referenced in Fig. 4-1.


1993
1994
1995
1996
PTP
CHP
PXT
POT
RAP
YRK
JAM
1997
1998
1999
2000
mg m-2
0
102
203
305
406

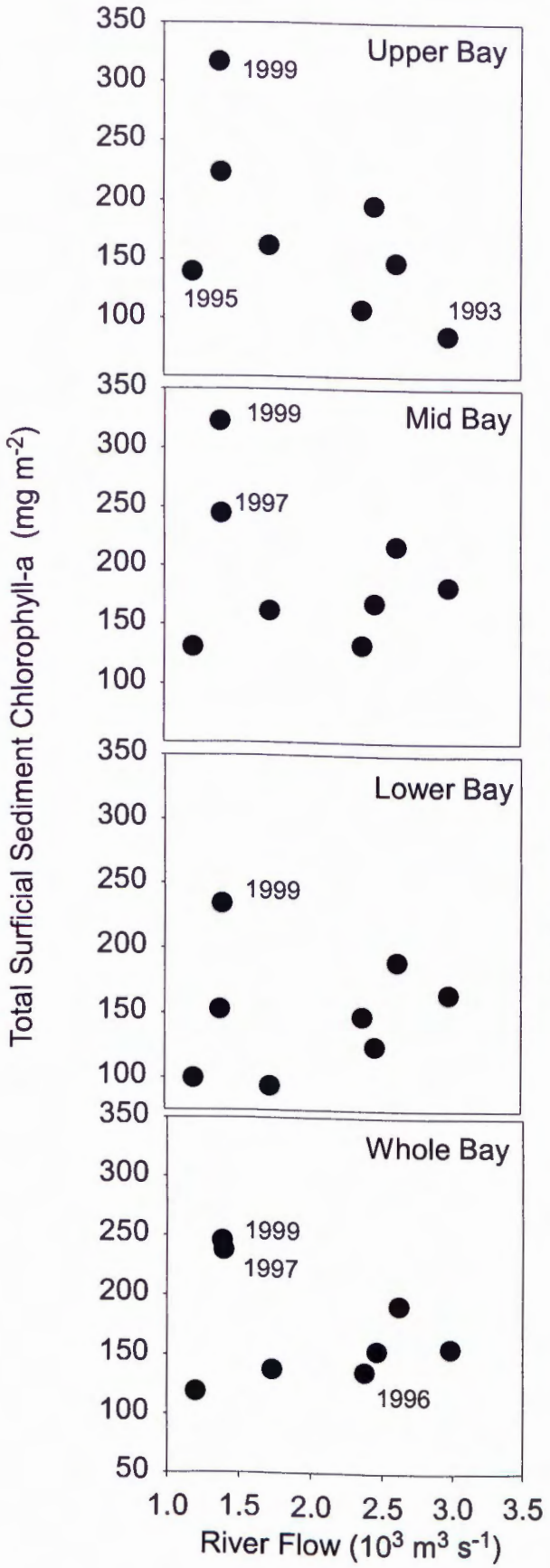


Fig 4-4. Regional and overall mean sediment total chlorophyll-a inventories in late spring related to winter-spring (Jan-Apr) average Susquehanna River flow. Sediment inventories were computed from 0-1 cm cores. The whole Bay mean reflects differences in the size of the respective regions. Note the y-axis scales, which vary to emphasize within-region pattern rather than among region differences.

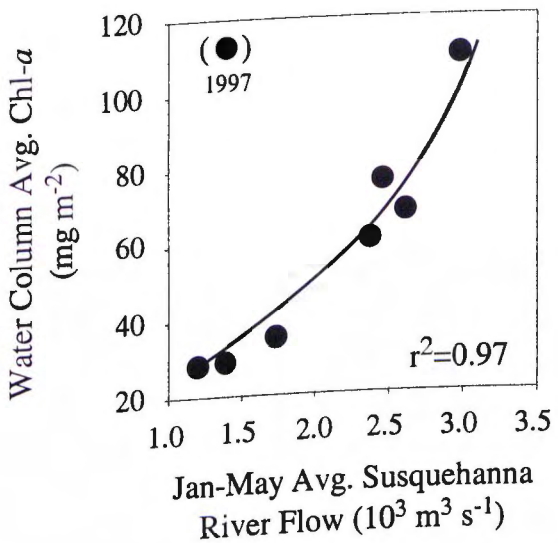


Fig 4-5. January-April average water column integrated chl-*a* in the lower Chesapeake Bay during 1993-2000 related to Jan-Apr average Susquehanna River flow. A second-order polynomial explains 97% of the variation, excluding the 1997 observation.

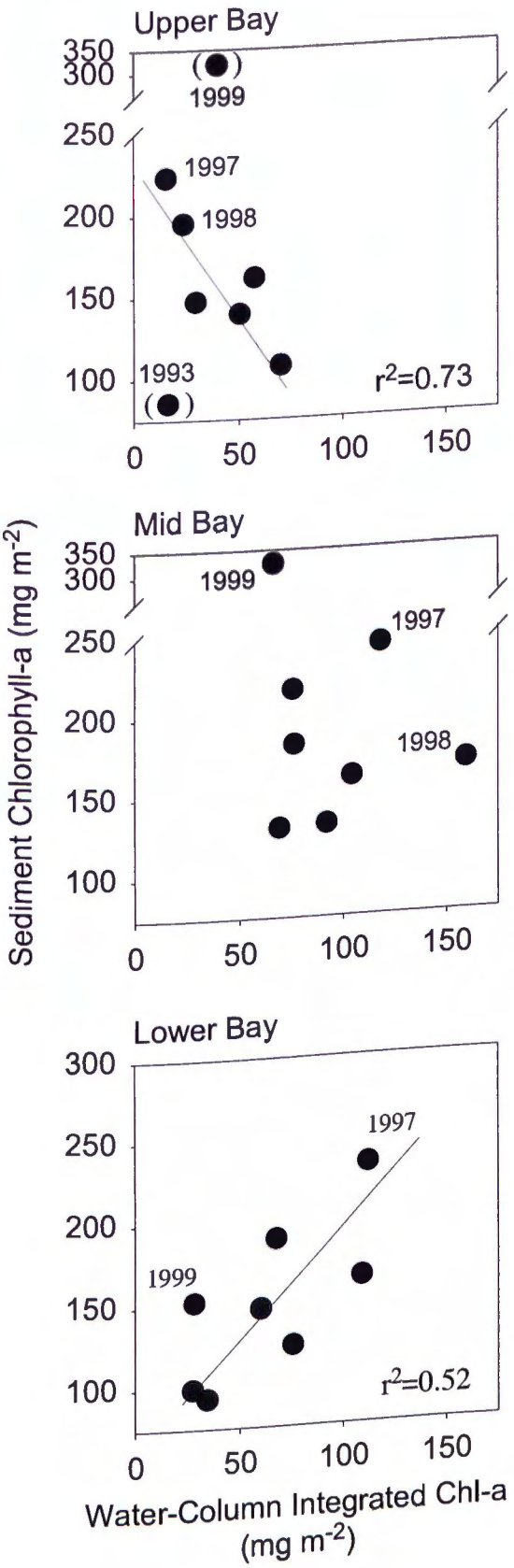


Fig 4-6. The relationship between January-April average water column integrated chlorophyll-a and sediment chlorophyll-a in each of three regions of Chesapeake Bay. There is a significant correlation in the lower Bay; the indicated line is the model II regression line. For the upper Bay, the trend line indicates the model II regression line excluding the 1993 and 1999 observations.

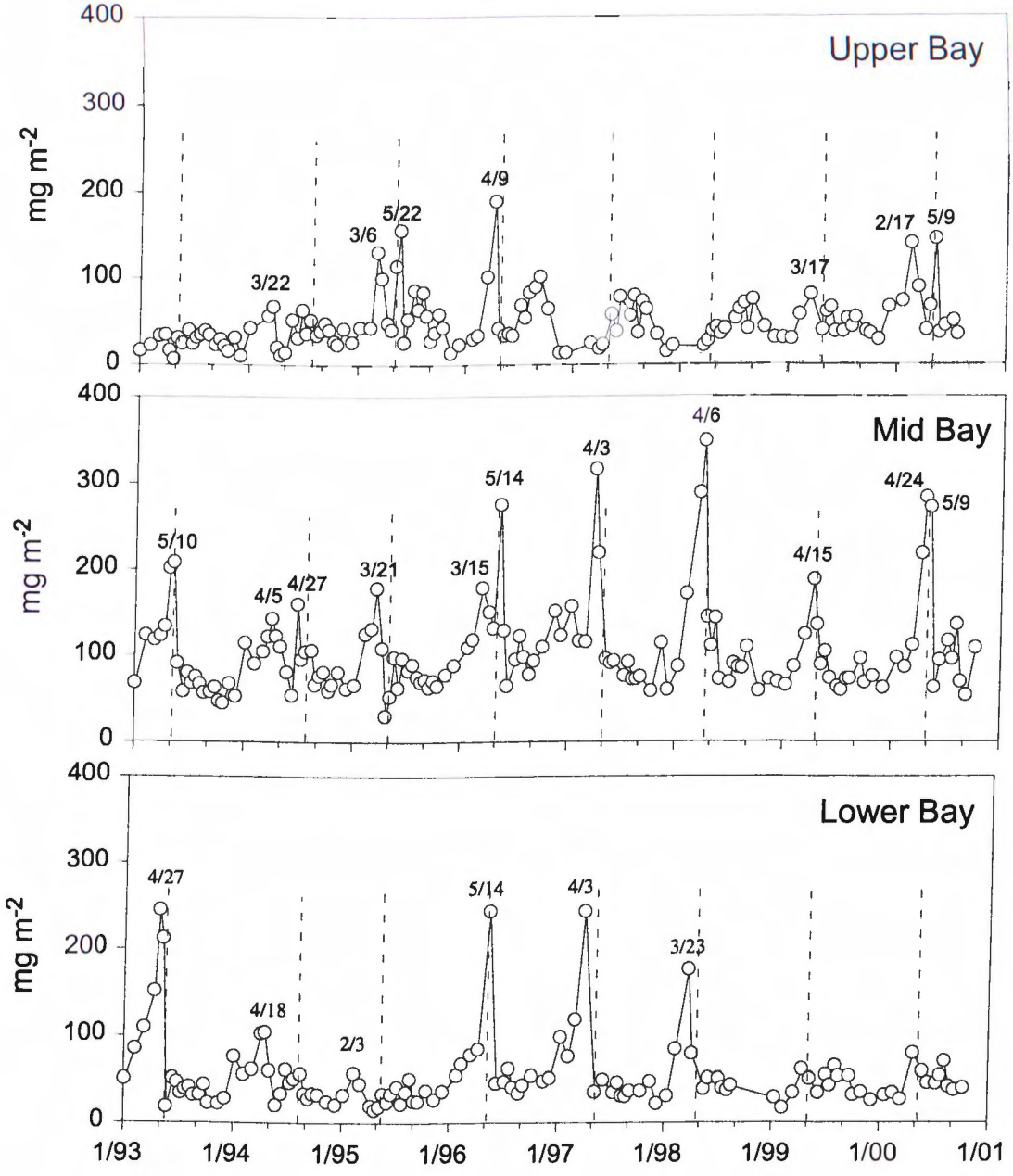


Fig. 4-7. Water column integrated chlorophyll-a concentrations in Chesapeake Bay averaged by region. Vertical dotted lines indicate the dates of sediment chlorophyll-*a* mapping studies. Dates indicate the date of the adjacent water column chl-*a* observation, which can be compared to the sediment chl-a mapping dates indicated in Table 2.

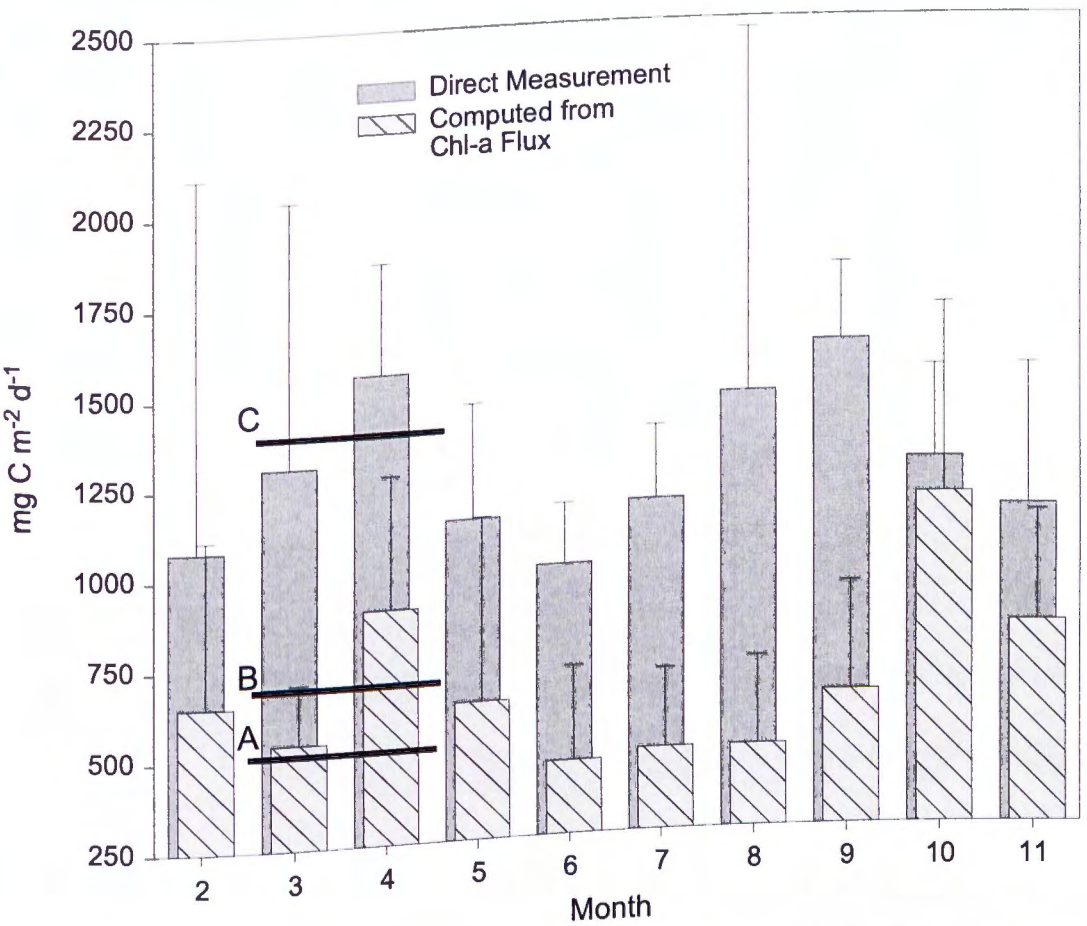


Fig. 4-8. Monthly means and standard errors of particulate carbon (PC) sinking fluxes measured using sediment traps just below the pycnocline in the mid Chesapeake Bay during 1984-1992. Sediment trap data from Boynton et al. (1993) and related unpublished data. Stippled bars indicate vertical PC fluxes computed from chl-*a* fluxes. Reference lines indicate: A=spring average PC deposition (510 mgC m^{-2} d^{-1}, this study); B=March-April average PC deposition computed from chl-*a* flux to sediment traps (720 mgC m^{-2} d^{-1}); C=March-April average deposition computed directly from PC flux to sediment traps (C:chl-*a*=75 in all cases)

Chapter 5:

PATTERNS OF MACROBENTHIC BIOMASS AND COMMUNITY BIOENERGETICS IN CHESAPEAKE BAY DURING SUMMER IN RELATION TO HABITAT QUALITY AND ORGANIC CARBON SUPPLY

Abstract

Macrobenthic biomass and bioenergetic rates in the mainstem of Chesapeake Bay were related to bottom water quality and sediment characteristics and estimates of carbon supply. The source of data for this analysis was a 15-year monitoring record describing biomass, abundance and species composition for 1664 sampling events. Independent variables, collected concurrently with the macrobenthic data, included water temperature, salinity, dissolved oxygen (DO), sediment % silt-clay, % nitrogen and % carbon. Although univariate and multiple linear regression models were poor predictors of biomass (r^2<0.35), a tree-structured regression model predicted biomass with r^2=0.59. In the tree-structured model, DO was the most important independent variable, followed by salinity and % silt-clay. Other variables were less important. Daily macrobenthic production was estimated via a temperature-dependent allometric relationship. Body size was greater in the upper Bay and lower Bay compared to the mid Bay region, leading to higher estimates of production/biomass (P/B) ratios for the mid Bay, especially for the deep water benthos. However, regional mean summertime P/B ratios varied only ~2-fold, while regional mean biomass varied ~100-fold. Thus, summertime macrobenthic production was determined primarily by the biomass distribution, not P/B.

Bioenergetic rates for the benthos during summer were estimated using a range of values for net growth efficiency and assimilation efficiency. Daily carbon requirements were compared to net plankton production and the ration potentially available via suspension feeding, two indicators of organic carbon availability. Actual and potential suspension feeding was estimated using a simple particle mixing model and clearance rates estimated via an allometric relationship. Organic carbon available to the benthos greatly exceeded the daily ration in the mid Bay (>10-fold) and was adequate elsewhere. Overall, the results suggest that degraded benthic habitat, food quality, predation, or other factors, but not organic carbon supply, limited biomass and productivity of the mid Bay benthos. The results also suggested that organic carbon limitation of the upper and lower Bay macrobenthos was unlikely, but the carbon surplus was smaller than in the mid Bay.

Introduction

Macrobenthic communities are an important component of many aquatic food webs because they can consume significant amounts of organic matter and also provide an important trophic link between primary producers and detritus and larger consumer organisms (Diaz and Schaffner 1990). Compared to other marine systems, the benthos in coastal and estuarine environments can be particularly important because relatively shallow water depth increases the interaction between the pelagic and benthic communities (Kemp and Boynton 1992). Suspension feeding benthos may be able to access the entire water column in shallower habitats, increasing their production potential and allowing them to exert significant grazing pressure on the

phytoplankton community (e.g. San Francisco Bay, Cloern 1982; Chesapeake Bay, Gerritsen et al. 1994; Thompson 2000; Great Lakes, Budd et al. 2001). The passive organic flux to sediments may also be increased in shallow water because respiratory losses in the water column are reduced. Even in deeper waters, rapid deposition of intact phytoplankton following the conclusion of spring phytoplankton blooms can stimulate benthic production (Graf et al. 1982, Kitazato et al. 2000).

Despite these general observations, estuarine and coastal benthic communities do not always have high biomass, nor are they always highly productive. Even among highly productive estuaries, benthic communities range from extremely productive (Pfitzenmeyer and Drobeck 1963, Phelps 1994) to mostly afaunal (Holland et al. 1977). The universe of possible factors that can adversely affect the benthos is large and may include predation, physical-transport regimes, physical disturbance, food quantity and quality, sediment characteristics, salinity, water temperature, dissolved oxygen, and toxic contamination (reviewed by Diaz and Schaffner 1990, Herman et al. 1999, Diaz and Rosenburg 1995). The large number of factors and the likelihood that effects interact and are non-linear or discontinuous (e.g. thresholds), complicate the task of formulating statistical relationships that predict benthic biomass. Even if one restricts the analysis to readily observed variables such as water quality and sediment characteristics, the number of factors and interactions remains large. The challenge of fitting an adequate statistical model may lead investigators to find only weak effects, even for variables known anecdotally or via experimental evidence to be important (e.g. Holland et al. 1987).

In the face of these challenges, describing patterns of abundance and production of organisms, and developing an ability to predict and explain the patterns quantitatively is fundamentally important for understanding estuarine benthic communities (Constable 1999). Moreover, this type of information can help resolve and predict long-term trends in naturally varying environments. Without highly resolved models, larger changes are needed before detection is possible. With this in mind, an objective of this study was to investigate the habitat characteristics that influence biomass and production of Chesapeake Bay benthic communities using tree-structured data analysis (Breiman et al. 1984), a new statistical procedure that is particularly well-suited to the task of formulating predictive models when there exist many possible explanatory variables, complex interactions, and non-linear and/or discontinuous responses.

Another objective of this study was to examine the hypothesis that food resources (e.g. primary production) do not limit benthic communities in Chesapeake Bay. This hypothesis is suggested by the substantial increase in phytoplankton biomass and primary production that occurred in the Bay over the past 50 years (Harding and Perry 1997), which has not been accompanied by a similar increase in macrobenthic biomass and production. Rather, a decline has been observed in some benthic infaunal communities (Holland et al. 1987). In general, this hypothesis runs counter to studies of the macrobenthos, which often find that biomass and production are enhanced by additions of organic matter, particularly organic matter with appropriate nutritional composition (Graf et al. 1982, Marsh and Tenore 1990, Josefson and Conley 1997, Hansen 1999). Comparative ecological studies show that

increased macrobenthic biomass is assocated with elevated primary production or algal biomass in both lakes and marine systems (Hanson and Peters 1983, Kemp and Boynton 1992, Herman et al. 1999). However, these observations can potentially be reconciled with the hypothesized lack of food limitation via the observation of Pearson and Rosenburg (1978) that organic enrichment often leads to habitat degradation, principally via oxygen stress. This degradation promotes successional changes in the benthic community that include a decline in biomass, ultimately to zero.

The potentially competing effects of organic enrichment on the Chesapeake Bay benthos have been examined by at least two studies. Blumenshine and Kemp (1999) focused on the mid Bay, developing monthly organic carbon budgets for the macrobenthos and relating likely carbon requirements to estimates of the carbon available. Their analysis, most appropriate for a community of deposit feeders, assumed that the organic carbon resource available to the benthos was determined by net plankton metabolism. They also related benthic biomass in the mid Bay to an index of oxygen stress, directly addressing the potential for control of the benthos by habitat quality. In contrast, Gerritsen et al. (1994) focused on the mid- and upper Bay suspension-feeding communities, estimating the carbon that could be obtained via a particle mixing model and estimates of clearance rates. Both studies concluded that, in contrast to general trends observed in comparative studies, organic carbon was rarely limiting to the benthos in the regions of Chesapeake Bay that they examined. This study adds significantly to the contributions of the former studies by expanding the results to include all regions of Chesapeake Bay and by implementing the

computations using the large quantity of data accumulated by the Chesapeake Bay Benthic Monitoring Program.

Study Sites

Chesapeake Bay and its tributaries form a large estuarine complex within the middle Atlantic region, USA (Fig. 5-1). The salinity gradient (0-32 ppt) of the mainstem Bay extends over 300 km. The estuary is commonly construed to consist of three somewhat distinct ecological zones, characterized by differing physical circulation regimes, salinity-dependent differences in biota, and a gradient in community metabolism (e.g. Kemp et al. 1997). Sediments in the Bay range from sand to organic-rich silt/clay; silt-clay content generally decreases southward in the Bay, but all sediment types are present in each region (unpublished data, Chesapeake Bay Benthic Monitoring Program, Chapter 4).

The mid-Bay region is characterized by strong summertime water column stratification at ~10 m depth. Combined with high metabolic rates, this promotes seasonal hypoxia and anoxia that first develops in late spring in deep water near 39°N and expands southward to ~ 37°40', often extending up to or into the pycnocline (see Chapters 2 and 3). Periodic hypoxic events have been noted in shallower waters along the mid-Bay mainstem (Malone et al. 1986, Breitburg 1990). Although less prevalent, hypoxia also occurs in other regions of the Bay and in the major tributaries (Hagy and Boynton 2000).

Methods

Data Sources

The data source for this study was a 15-year record of species-level macrobenthic biomass and abundance for Chesapeake Bay and tributaries collected between 1985 and 1999 by the Chesapeake Bay Benthic Monitoring Program (CBBMP). The database describes the benthic macrofauna (abundance, biomass, and taxonomic composition) collected in more than 6,000 cores collected in all seasons throughout Chesapeake Bay and tributaries (EPA2000a,b,c). Concurrently collected data describes water quality (water temperature, salinity, dissolved oxygen) at the time of collection as well as sediment properties (%sand, %silt-clay, C-H-N) at most sites. The sampling protocol changed over the period of record and includes a mixture of sites with fixed locations and sites that were randomly located within spatial strata. As this study was not designed to investigate temporal trends at fixed sites, both random and fixed sites were considered together in order to achieve the largest possible number of observations.

Survey design, as well as sampling and analytical methods are described in the documentation for the database (EPA 2000a, b, c). Sampling gears varied over time and according to the total depth at the site. In shallow water, a post hole digger or Petite Ponar Grab was used. In deeper waters, a Ponar grab, a WildCo or other box corer, or a Young-modified Van Veen grab was used (e.g. Holland et al. 1987). For most samples, the gears sampled 175 or 250 cm^2 of sediment surface and penetrated ~25 cm into the sediments. Some investigators have reported that gear limitations may have prevented the CBBMP from properly sampling key larger, deep-dwelling

animals, particularly the polychaete *Chaetopterus variopedatus*, a dominant organisms in the lower Bay (Thompson 2000, L. C. Schaffner, pers. comm.). Separate estimates of biomass and production for *C. variopedatus* in the lower Bay were therefore obtained from Thompson (2000). All samples collected by the CBBMP were sieved to 0.5 mm and fixed in buffered formalin. Methods for ash-free dry weight (AFDW) determinations varied over time. In some years, all samples were dried and ashed, while in other years AFDW determinations were made only for certain abundant species using regressions on morphometric measurements. In these cases, the abundant taxa accounted for most of the total biomass.

Tree-Structured Regression Models

Measures of community biomass were related to possible habitat factors (e.g. sediment percent silt-clay, water temperature, salinity, dissolved oxygen, etc.) using CART (Classification and Regression Trees; Breiman et al. 1984, see also Hagy 2000), a tree-structured data analysis algorithm used by CART Software for Windows (Salford Systems, Inc., Steinburg and Colla 1995). Hereafter, I use the term "CART" to refer to both the CART algorithm and it's the implementation by CART software. CART can be used for both regression and classification; however, this study only used CART for regression. Therefore, all subsequent discussion refers to regression-tree models. CART employs a recursive partitioning algorithm that finds a binary question, or splitting rule (e.g. Is salinity ≤ 18.5?), that divides a group of observations (parent node) into two groups of observations (child nodes) such that the variance of the target variable is minimized within the child nodes. The best splitting rule is

determined by examining all possible rules. The algorithm then treats the child nodes as parent nodes, recursively identifying splitting rules until each child nodes contains too few observations to be split further. The resulting tree is called the maximal tree.

While the maximal tree always has the minimal residual error, a smaller tree often has the minimal error when tested against data not used in model construction. For this reason, a cross-validation procedure was used to determine error rates. For this study, CART was configured to use 10-fold cross-validation (the recommended default option; Breiman et al. 1984, Steinberg and Colla 1995). In this procedure, all the data, 10% at a time, are set aside from model development as validation observations. The results are then pooled such that all the data are used both in model formation and in cross-validation.

CART computes the cross-validation error rate for the maximal tree, then considers smaller trees through a process called "pruning." Pruning involves collapsing child nodes back into parent nodes, then recomputing the cross-validation error rate. The nodes that account for the smallest decrease (or an increase) in error rate are pruned first, followed by other nodes. CART initially selects the tree that has the lowest cross-validation error rate, but the investigator may choose among models along a continuum of complexity vs. error rate. Experience indicates that there is often a "break" point where additional reduction in model complexity results in a large increase in the error rate, making the model selection relatively clear.

Because CART selects splitting rules by minimizing within-node variance, regression trees are sensitive to heterscedasticity, which can lead to spurious splits of parent nodes with high mean and variance and undersplitting of low mean and

variance nodes (Steinburg and Colla 1995). To minimize this effect, biomass values were re-coded and transformed using $X' = \log(X + 0.01)$. Back-transformed predicted values give the geometric means, which are less than the arithmetic means. The latter, used to preserve mass for bioenergetic computations, were computed from untransformed observations classified to each node. These were similar to predicted values back-transformed using $\overline{X} = 10^{\overline{x}' + \sigma^2/2} - 0.01$, where σ^2 is the node variance.

Community Biomass and Production

Community biomass was determined by summing the ash-free biomass of all the taxa in each replicate sample. Thus, all reported biomasses are ash-free dry weights unless otherwise indicated. Average community biomass for sites with replication were computed by averaging the replicates.

Daily production was computed for each taxa in each sediment core in the benthic database using the empirical model of Edgar (1990), which was derived from a meta-analysis of production estimates for benthic macrofaunal populations (Edgar 1990). This model relates daily production (P, μg d^{-1}) for a single macrobenthic animal to body size (B, μg AFDW) and water temperature (T, °C) with r^2=0.94. Edgar (1990) formulated different models for different taxonomic groups (e.g. bivalves, crustaceans, polychaetes) but found them to be indistinguishable from the general model. Therefore, this study used the general model:

$$P = 0.0049 B^{0.80} T^{0.89} \qquad (1)$$

The Edgar (1990) model was derived from data describing daily growth of 41 invertebrate species varying in size from 10^{-5} g to 1 g and was reported to be applicable for water temperatures from 5-30 °C. It was assumed for this study that the model is also applicable to temperatures below 5°C (10% of cases) since it predicts minimal production, the expected result for a temperate estuary during winter. To apply the model to the Chesapeake Bay benthos, bottom water temperature was obtained from the concurrently collected water quality data. Where water temperature was less than zero (0.3% of cases), a temperature of zero was assumed. If bottom water temperature was missing (0.6% of cases), a seasonal mean was used. Body size was computed by dividing the total biomass of each taxa by the reported abundance. If either the abundance or biomass was missing (10% of cases), the missing value was computed using the median body size for that taxa, which was computed from the remainder of observations. Because the effect of body size is non-linear (eq. 1), community production was computed as the sum of production for each taxa, rather than as the production for the average size organism in the community. Thus, community production (P, $\mu g\ m^{-2}\ d^{-1}$) was computed as

$$P = \sum_i N_i P_i \qquad (2)$$

where P_i is the production per individual of the i^{th} species and N_i is the abundance of that species (m^{-2}).

Carbon Requirements for the Benthos

Carbon budgets were formulated for Chesapeake Bay benthic communities for the purpose of comparing likely carbon demand to the organic matter supply rate. The scope of this study was limited to summer (June-August). These budgets have the form $C = P + R + U$, where C=consumption, P=production, R=respiration and U=excretion+egestion (feces production). Ash-free dry weights for all organisms were converted to carbon using 500 mgC = 1 g AFDW (Jørgensen 1979). R and U were computed from production via ratios based on published results of both empirical and theoretical studies (Schroeder 1981, Bayne and Newell 1983, Peters 1983, Schwinghamer et al. 1986). Respiration was computed via the net growth efficiency, $NGE = P/(P+R)$. Consumption was computed via the gross growth efficiency (GGE), which is equal to the product of NGE and assimilation efficiency (AE), where $GGE = P/C = NGE \cdot AE$. Both the technical challenges of measuring these ratios and real variability make precise estimates for these ratios for all the taxa unattainable. However, most estimates fall within a range of uncertainty, the extremes of which were considered as alternative cases. NGE was assumed to vary between 30% and 56%, while AE was assumed to vary between 40-60% (Banse 1979, Schroeder 1981, Bayne and Newell 1983). Resulting estimates of GGE are 12-34%, similar to the range utilized by Blumenshine and Kemp (2000). Gerritsen et al. (1994) assumed GGE=10%, most likely yielding a generous estimate of carbon demand.

Carbon Flux to the Benthos

The carbon available to the benthos was computed in two ways. In the first approach, the carbon supply was estimated as net plankton production plus the net subsidy of carbon to each region due to physical transport of organic matter from adjacent regions of the Bay. By mass balance, this approach effectively provided an estimate of the carbon actually delivered to the benthic community. Net plankton production was computed for different regions of the Bay using estimates of gross primary production and plankton community respiration computed from data reported by Kemp et al. (1997), Smith (2001) and Harding et al. (2001) (see also Appendix). NPP was computed using $NPM = GPP - R_p\bar{z}$, where GPP=gross plankton production (g O_2 m^{-2} d^{-1}), plankton respiration (g O_2 m^{-3} d^{-1}) and $\bar{z}$ = mean depth (m). For the mid-Bay, R_p was reduced by 62-100% in deep water (Kemp et al. 1997) and these lower rates were used for depths >10 m. Because metabolic rates based on net O_2 evolution include both production and respiration, these were converted to carbon assuming the photosynthetic quotient (PQ) = respiratory quotient (RQ) =1.0 (Stokes 1996).

Net physical carbon inputs were estimated for the three major regions, but not for sub-regions and depth zones. The Susquehanna River was assumed to be the only significant allochthonous source of total organic carbon (TOC) to the upper Bay region (Kemp et al. 1997). Monthly mean TOC loading from the Susquehanna River at Conowingo Dam was computed from data obtained from the United States Geological Survey River Input Monitoring Program (described by Langland et al.

2001). Net physical particulate organic carbon (POC) transport among the regions and between the lower Bay and the Atlantic Ocean was assumed to be negligible, consistent with the strong particle trapping properties that have been observed for the Bay in general and the upper Bay in particular (Schubel and Carter 1977, Hobbs et al. 1992). Although these studies refer to sediments in general, it was assumed to apply to POC as well. Dissolved organic carbon transport among regions was estimated as the product of monthly surface layer and bottom layer average DOC concentration and corresponding average advective transport rate (Chapter 2, also see Hagy 1996).

A second approach to computing the carbon supplied to the benthos involved using a random walk (Brownian motion) model to examine the volume of water that could be and actually is filtered by the suspension feeding benthos during summer in three regions of Chesapeake Bay (Gerritsen et al. 1994). Gerritsen et al. (1994) developed and applied the model for the upper and mid Bay, while this study extended its application to the lower Bay as well. Gerritsen et al. (1994) derived the model and described it in significant detail. Therefore, only an abbreviated description follows. The estuarine cross section was divided into 4 compartments (Fig. 5-2). These include two littoral zones flanking a pelagic surface mixed layer (SML) on its eastern and western margins. Suspension-feeding was assumed to occur only in the littoral zone. The SML overlies the deep mixed layer ("profundal zone"), which in summer was assumed to be completely isolated from the SML by the pycnocline. The random walk model computed the mean time required for a randomly mixing parcel of water to reach the bottom (t_v, days) as

$$t_v = \frac{Z^2}{3D_v} \tag{3}$$

where Z is the mean depth (m) and D_v is the vertical dispersion coefficient ($m^2\ d^{-1}$). A value 10 $cm^2\ s^{-1}$ was assumed for D_v (Gerritsen et al. 1994). Accordingly, the probability that a parcel of water approaches the bottom in 24 hours is

$$P_v = 1 - \exp(-1/t_v) \tag{4}$$

The mean time for probability that a parcel of water in the SML reaches the boundary with either (east or west) littoral zone (t_h, days) was computed as

$$t_H = \frac{X^2}{12D_H} \tag{5}$$

where X (meters) is the average width of the SML and D_H is the lateral dispersion coefficient. A value of 10 $m^2\ s^{-1}$ was assumed for D_H, much greater than D_v (Gerritsen et al. 1994). Analagous to eq. (4), the probability that a water parcel in the SML crosses into either littoral zone (P_H) was computed as

$$P_H = 1 - \exp(-1/t_H) \tag{6}$$

Since the exchange of water into and out of the littoral zones is continuous, some water crossing into the littoral zone is not "new" water. The fraction of "new" water from the SML approaching the bottom of the littoral zone (P_{HV}) was computed as

$$P_{HV} = P_H\{1 - t_v[1 - \exp(-1/t_v)]\} \tag{7}$$

Using these expressions, the volume of water approaching the littoral zone bottom each day (V_B) was computed as

$$V_B = V_L P_L + V_S (2P_{HV} - P_H P_V) \quad (8)$$

where V_L is the combined volume of the littoral zones and V_S is the volume of the SML. Thus, the fraction of the combined volumes of littoral zones and SML reaching the bottom each day is $V_B/(V_L + V_S)$.

The Gerritsen et al. (1994) mixing model was modified for the lower Bay by assuming that there is not a central pelagic channel in the lower Bay, isolated from the benthos (see also Thompson 2000). Thus, the volume of water approaching the benthos (V_B) in this "one box" formulation (Fig. 5-2, lower panel) was simply VP_v where V is the total volume. Although Gerritsen et al. (1994) partitioned the upper Bay in the same way as the mid Bay (Fig. 5-2, upper panel), their value of X was sufficiently small that eq. (8) effectively reduced to $V_B = VP_v$. Therefore, this study simplified the model for the upper Bay, assuming a "one box" model.

The clearance rates of suspension feeders (m^3 $animal^{-1}$ d^{-1}) was computed using $C = 0.120W^{0.75}$ where W is body size (g DW). Gerritsen et al. (1994) applied a temperature correction to this equation. Because this study was limited to summer, the temperature correction factor was always 1.0 (Gerritsen et al. 1994). A species-specific clearance rate model, $C = (24/1000)(22.17W + 0.048)$, where W=0.025 g AFDW, was used for the abundant suspension feeding polychate *Chaetopterus variopedatus* (Thompson 2000).

The probability that a parcel of water approaching the bottom that will be filtered by a suspension feeder (P_F) was computed as

$$P_F = 1 - \exp(-C/V_B) \quad (9)$$

and the volume actually filtered is $V_F = V_B P_F$. The daily ration (R, mg C m^{-2} d^{-1}) associated with the clearance estimate was computed using

$$R = P(V_F/V_T)(A_T/A_L) \quad (10)$$

where P is net primary production ($H^{14}CO_3^-$ assimilation, mgC m^{-2} d^{-1}), V_F = daily volume filtered, V_T = total segment volume, A_T = total segment surface area, and A_L = the area of the littoral zone. In the case of the upper Bay and lower Bay $A_T = A_L$. This approach assumes complete mixing within the littoral segments and within the pelagic SML. Estimates of summer primary production in each region of the Bay were obtained from Harding et al. (2001).

Results and Discussion

Patterns of Macrobenthic Biomass vs. Habitat Factors

Macrobenthic biomass varied between zero and 717 g m^{-2}, with a median and mean among 1664 observations of 1.4 and 10.6 g m^{-2}, respectively. Plots of macrobenthic biomass vs. depth, water temperature, salinity, dissolved oxygen, and percent silt-clay in sediments illustrated how this overall range of values was distributed with respect to these variables (Fig. 5-3). While these plots showed that none of these variables was a strong predictor of biomass, several obvious features were apparent. For example, the highest biomass was found consistently at sites less than ~5 m in depth and very low or zero biomass was rarely observed at those depths.

There was not, however, a clear overall relationship between biomass and depth. Similarly, while temperature was not a good predictor of biomass, the lowest biomass values were found only at summer water temperatures. Biomass also followed distinctive patterns with respect to salinity. Nearly or completely afaunal sites were found almost exclusively at mesohaline sites. In contrast, polyhaline sites had moderate to high biomass with little variability and biomass was more variable among oligohaline sites. Hypoxic sites contained many, but not all, of the low biomass values and none of the highest biomass values. Finally, sediments at most sites were either muddy (> 75% silt-clay) or sandy (<5% silt-clay) and both the lowest and highest biomass was found at muddy sites (Fig. 5-3).

From the perspective of statistical modeling, these relationships posed several challenges. All of the univariate relationships are weak and most are not monotonic (DO is an exception), either in terms of mean or variance. Some of the patterns can be explained in terms of water quality patterns characteristic of the estuary. For example, hypoxia and anoxia occurs reliably only in deep waters of the mesohaline zone of the Bay during summer. In these areas, sediments tend to be muddy. This is a likely explanation why many of the afaunal observations occurred where depth >10m, water temperature is between 23-27 °C, salinity is between 10-24 ppt, and silt-clay content is >75%. It was of interest, however, to predict biomass for less obvious circumstances.

A multiple linear regression model was used to relate macrobenthic biomass to water quality and sediment characteristics (Table 5-1). The model included DO, salinity, water temperature, %silt-clay in sediments and all two-way interactions among those variables. In addition, the model included season (Dec-Feb, Mar-May,

June-Aug, Sept-Nov) as a categorical variable. The model explained 35% of the variance and included many significant sources of variation. Dissolved oxygen and its interactions with water temperature and % silt-clay content in sediment were most important. Such a model could likely be improved by adding additional terms to account for more of the apparent non-linearity. For example, DO might be recoded as a classification variable indicating "hypoxic" or "normoxic." However, that approach would involve imposing arbitrary thresholds determined by the investigator, even if those threshold were loosely based on graphic observation, and would likely lead to simple confirmation of patterns already known to exist. As an alternative, tree-structured regression (CART) was used to identify optimal rather than arbitrary thresholds and to uncover where possible any less obvious patterns of biomass in relation to the explanatory variables.

The CART model included the same explanatory variables as the multiple regression model, except that sediment % carbon and % nitrogen were also added due to the fact that CART does not exclude observations that have missing values for explanatory variables. Seasonality was modeled via the month of the year rather than a seasonal classification variable because CART does not assume a linear response. Therefore, CART can determine seasonal definitions without *a priori* specification. The CART regression-tree with minimum error on cross-validation had 27 terminal nodes (Fig. 5-4). Variable importance statistics computed by CART indicated that dissolved oxygen was the most important variable, giving it a relative importance score of 100 (Table 5-2). The other variables, in order of decreasing importance were salinity (71), percent silt-clay (63), total depth (58), month (39), water temperature

(38), percent carbon (8) and percent nitrogen (5). Variable importance statistics are computed by CART and are based not only on the appearance of a variable as a primary splitting rule, an obvious indicator of importance, but also as competitors. For example, if a splitting rule based on variable X_2 was nearly as predictive as the primary splitting rule, based on X_1, then X_1 and X_2 would have similar importance scores, even though X_1 was the primary splitting variable. One way this can occur is if X_1 and X_2 are (locally) correlated, although this is not the only way. Considering only primary splitting rules reduced the relative importance of salinity, percent silt-clay, month and water temperature, and decreased the importance of percent carbon and nitrogen to zero (Table 5-2).

Box plots of the distribution of biomass among observations classified into each of the 27 terminal nodes showed that the regression tree was able to predict benthic biomass, but that the 27 nodes resolved some different types of habitats that had similar levels of biomass (Fig. 5-5). Many of the terminal nodes had substantial numbers of observations (25-75), but three nodes (12, 15 and 23) had particularly large number of observations. These types of sites were particularly well studied due to the relatively constant nature of the monitoring program. Predicted values were correlated with observations with r^2=0.59 (Fig. 5-6), indicating that this model achieved the goal of improved prediction compared to multiple regression. As a cautionary note, while certain aspects of this model may be generally applicable, the scope of inference for this model is limited to the mainstem Chesapeake Bay. A more generally applicable model could be constructed using CART, but would require data from other estuaries.

Observations based on the regression tree (Fig. 5-4, Table 5-3) are described below. Dissolved oxygen (DO), the most important predictor of macrobenthic biomass, initially divided the sample (N=1664) into two groups, one with DO $\leq$ 2.34 mg l^{-1} (N=242). Among these low DO observations, the highest biomass was found among observations from May or June (1.5 g m^{-2}; Table 5-3 node T1), when seasonal hypoxia had developed only recently (e.g. Chapter 2). Among observations from July or later, depth was important, whereas observations from above the usual depth of the pycnocline (<10.4 m) had an average biomass of 1.1 g m^{-2} and those from deeper waters had negligable biomass, <0.1 g m^{-2}. The higher biomass among shallower hypoxic sites suggests that the observed hypoxia may have been an intermittent event, either due to advective intrusion of hypoxic water (e.g. Breitburg 1990) or temporary DO depletion. Macrobenthos may survive temporary exposure to hypoxia, but are less likely to survive the persistent hypoxia that occurs at deeper depths (Diaz and Rosenburg 1995). At all depths severe hypoxia was associated with lower macrobenthic biomass than moderate hypoxia at comparable depth, indicating more rapid and extensive mortality when DO was very low (Diaz and Rosenburg 1995).

At most sites for which benthic data were collected, DO was >2.34 mg l^{-1} (N=1422). Although it is evident that deep habitats known to suffer persistent hypoxia or anoxia were sampled less frequently, this also reflects the fact that hypoxic conditions are a relatively restricted phenomenon, occurring mostly in deeper water during summer. However, latent effects of hypoxia may appear where DO is in the normoxic range because effects of seasonal or periodic hypoxia may persist after normoxic conditions are restored (e.g. Pihl et al. 1991). In this dataset, DO itself

usually did not predict macrobenthic biomass when DO was observed to be greater than 2.34 mg l^{-1} (Fig. 5-4, Table 5-3). Exceptions were at nodes 12 and 22, for which likely explanations cannot be identified. Although the relative unimportance of DO at higher levels does not discount chronic sublethal effects (see Breitburg et al. 1997), it suggests that other factors were more important at the large scale. The most successful predictor of macrobenthic biomass among normoxic sites was total depth, whereas sites with depth >11 m (N=451) had a mean biomass of 1.8 g m^{-2} and shallower sites (N=971) had a mean biomass of 6.6 g m^{-2}. Among the shallower sites, those in the oligohaline region (salinity≤8.5) had the highest mean biomass (=27.1 g m^{-2}, N=234), while sites in the mesohaline region (8.5<salinity≤20.4, N=646) had intermediate biomass (=3.0 g m^{-2}) and polyhaline sites (salinity>20.4) had the lowest biomass (=0.1 g m^{-2}, N=91). The appropriate explanation for low biomass in shallow polyhaline sites is unclear, but could be partly due to an inadequate number of samples collected (N=26, Table 5-3).

Among the oligohaline sites, higher percent silt-clay was associated with higher biomass. When % silt-clay was >59%, mean biomass was 44.6 g m^{-2} (N=153), while sandier sites had a mean biomass of only 5.8 g m^{-2} (N=81). Among these sandier sites, nearly freshwater habitats (salinity≤0.37 ppt) had lower biomass than oligohaline habitats with slightly higher salinity. Among the siltier sites, 44 sites with DO>7.2 mg l^{-1} had much lower biomass (12.4 g m^{-2}) than the 26 sites with DO≤7.2 mg l^{-1} (95.1 g m^{-2}). Variables such as season, water temperature and depth were included in the model, but were found to be less effective predictors than DO in this

context. The correct explanation may involve a reversal of cause and effect, whereas high biomass causes decreased DO.

Macrobenthic biomass distributions among shallow (< 11 m) normoxic (DO > 2.34 mg l^{-1}) mesohaline sites (node 14, N=646, Fig. 5-4) were explained by total depth, salinity, percent silt-clay, and water temperature. Biomass was highest at the shallowest sites (node ≤7.65 m, node 15), but the 224 sandy sites (%silt-clay ≤ 3.6) among these had lower biomass (node T12, 3.2 g m^{-2}) than the sites with higher silt-clay content (node 17, 15.4 g m^{-2}). Finally, as long as the sediments were not sandy, the shallowest mesohaline sites (depth≤4.6m, node T13) had much higher biomass (31.0 g m^{-2}) than slightly deeper sites (5-11m, 10.4 g m^{-2}, node T14). Mid-depth mesohaline habitats (7.6-11m) had lower biomass (1.3 g m^{-2}, node 18, N=84) than the shallower habitats, especially at higher water temperatures characteristic of late summer (0.1 g m^{-2}, node 19). Interestingly, the analysis revealed that at both extremes of silt-clay contents (sand, mud), relatively more mixed sediment types were associated with higher macrobenthic biomass.

Deep (>11 m) normoxic (DO > 2.34 mg l^{-1}) sites (node 20, N=451) generally included only mesohaline and polyhaline sites. Percent silt-clay explained explained the most variation among these sites. When % silt-clay > 58%, biomass averaged 0.9 g m^{-2} (node 23), while biomass at less silty sites averaged 7.8 g m^{-2}. Among the less silty sites, biomass was higher among polyhaline (salinity>22 ppt) sites (10.7 g m^{-2}) than other sites (2.9 g m^{-2}). At siltier sites, average biomass was lower (0.4 g m^{-2}) during warmer seasons (>21°C) as compared to other times (1.0 g m^{-2})

The results of the CART analysis (Fig. 5-4, Table 5-3) strongly implicated several habitat factors as important determinants of macrobenthic biomass. The extent to which the observed correlations can be used to infer causation bears some consideration. Nearly all of the habitat factors that were identified as important are known to vary among regions of Chesapeake Bay (e.g. salinity, silt-clay content), while other factors also known to vary among regions were not included in the analysis. For example, water column stratification is often higher in the mid-Bay than elsewhere (e.g. Chapter 2), while physical disturbance during winter storms is probably more important in the lower Bay (Schaffner 2000). Net plankton production, an indicator of food resources potentially available to the benthos is much higher in the south Bay then elsewhere, while the upper Bay receives considerable allochthonous carbon inputs (Kemp et al. 1997). Thus, in another CART analysis, regional differences were investigated directly by adding latitude to the list of variables submitted.

Regional Characterizations Macrobenthic Biomass, Composition and Bioenergetics

A CART model including latitude as an explanatory variable confirmed the strong regional differences in macrobenthic biomass that have been previously reported (e.g. Diaz and Schaffner 1990, Weisburg et al. 1997) and suggested a regional segmentation scheme for Chesapeake Bay based solely on total macrobenthic biomass (Fig. 5-7). Theree main regions of the Bay, the upper Bay, mid Bay and lower Bay, were identified. The mid Bay was further divided into north and south halves and three depth zones (Fig. 5-7). Several analysis were completed for each of

the regions of the Bay and are described below. First, the computed species composition, biomass and production of the macrobenthos in each region are described. This is followed by an examination of regional differences in average body size. Finally, computations of the organic carbon requirements of the macrobenthos and the supply rate of organic carbon are described, addressing the potential for food limitation in each region. The discussion is prefaced by a brief discussion of the macrobenthic production models that were considered and the justification for choosing the model of Edgar (1990).

Macrobenthic Production Models. Because of the difficulty of measuring the production rates of diverse assemblages of macrobenthic organisms, several studies have suggested size-based approaches. This study compared the structure and predictions of three models, each of which are based on a meta-analysis of published production estimates (Banse and Mosher 1980, Edgar 1990, Tumbiolo and Downing 1994). The Banse and Mosher (1980) model is a univariate model relating annual P/B to body size. The Edgar (1990) model predicts daily production as a function of body size and water temperature. The Tumbiolo and Downing (1994) model predicts annual macrobenthic production from depth and annual mean biomass and water temperature. Comparison of these models reveals the primary importance of body size and temperature (Fig 5-8). Production declined more rapidly with body size according to the Banse and Mosher (1980) allometric relationship, a result disputed by Peters (1983). The differences between the two other models are small compared to other factors that may affect estimates of production, particularly variations in biomass. This is especially true for temperatures between 15 and 25°C and body sizes between

10^{-4} and 10^{-2} g (Fig 5-7), which encompasses much of the Chesapeake Bay macrobenthos. Blumenshine and Kemp (2000) utilized the Tumbiolo and Downing (1994) model in an analysis of benthic production in the middle Chesapeake Bay, citing closer agreement with a study that directly estimated benthic production in the mid-Chesapeake Bay (Holland et al. 1988). However, considering the close agreement between the two models, the Edgar (1990) model was selected for this study on the basis of its more appropriate scope of inference (e.g. seasonal production rather than annual mean production).

Upper Bay Biomass and Species Composition. Summer average benthic biomass was highest (59 g m^{-2}) in the upper Bay region, over 90% of which was due to the suspension-feeding bivalve, *Rangia cuneata*. Production in this region was the highest in the Bay, 0.49 g m^{-2} d^{-1}, or ~45 g m^{-2} for the summer. This estimate is somewhat higher than suggested for a healthy oligohaline estuarine habitat by Weisburg et al. (1997), possibly because it includes only the upper Chesapeake Bay, rather than oligohaline habitats throughout the Chesapeake Bay region. For example, intense tidally-driven resuspension of sediments causes reduced macrobenthic biomass in the oligohaline York River (Schaffner et al. 2000). Perhaps for similar reasons, the estimated total summer production in the upper Chesapeake Bay exceeds the annual production estimate of Diaz and Schaffner (1990) for oligohaline habitats in the Chesapeake Bay region.

Mid Bay Biomass and Species Composition. Shallow water habitats at the northern end of the mid Bay region had by far the highest summer biomass among mid Bay sites, about 12 g m^{-2}. This biomass was dominated by two suspension-feeding

bivalves, *Tagelus plebeius* and *Mya arenaria*, plus *Macoma balthica,* a facultative suspension-feeder. Shallow water habitats further to the south had much lower average biomass, 2.8 g m^{-2}. The assemblage there was more diverse, with the most abundant taxa being the small opportunistic bivalve *Mulinia lateralis* (20%). Mid-depth habitats in the mid-Bay were divided into two regions based on latitude. In the north region, nearly all the mid-depth habitat consists of a shelf flanking the main channel on the western shore between Cove Point and the South River. This region had an average biomass of 2.1 g m^{-2}, dominated by *M. balthica* (68%) and polychaetes of the genus *Leitoscoloplos*. Mid-depth habitats in the lower mid-Bay were located on both western and eastern flanks and had very low average biomass (0.64 g m^{-2}). This may have been due to the very low silt-clay content of the sediments (<5%). However, this habitat was also poorly sampled, with only 5 observations during June-August. The deep water habitat of the northern mid-Bay also had low average summer biomass (0.62 g m^{-2}) and was dominated by *M. lateralis* (55%), *M. balthica* (19%), and two polychaetes, *Nereis succinea* (10%) and *Paraprionospio pinnata* (7%). Biomass exceeded this average early in the summer, prior to the near-inevitable onset of complete anoxia by mid summer (Chapter 2). In contrast, the southern mid-Bay deep waters had an average biomass of 3.5 g m^{-2} and included many species more typical of the lower Bay, suggesting it is a transition habitat. Macrobenthic biomass in the mid-Bay as a whole averaged 2.9 g m^{-2}, approximately in the same range as suggested for degraded sites by Weisburg et al. (1997). Macrobenthic production in the mid-Bay overall was only 0.04 g m^{-2} d^{-1}, or 3.68 g m^{-2} $summer^{-1}$.

Lower Bay Biomass and Production. In the northern portion of the lower Bay, macrobenthic biomass computed from the Benthic Monitoring Program data was estimated to be 10 g m^{-2}, slightly lower than in the vicinity of the Bay mouth (14.2 g m^{-2}). However, Thompson (2000) estimated the biomass of the large, tube-dwelling polychaete *Chaetopterus variopedatus* to be ~10 g m^{-2}, making it the dominant species in terms of biomas in the lower Bay. Since this taxa accounted for only 3% of lower Bay biomass in the Chesapeake Bay Benthic Monitoring Program database, it seems likely that the biomass of this polychaete may have been greatly underestimated. Such an underestimate could have resulted from the sampling gears utilized by the Chesapeake Bay Benthic Monitoring Program, either due to insufficient penetration depth or cross-sectional area (Schaffner, pers. comm.). That possibility is supported by the fact that the mean size of *C. variopedatus* collected by the monitoring program was computed to be 0.068 g, the size of juveniles rather than the much larger and deeper-dwelling adults which are 0.2-0.3 g (Thompson 2000). Thus, the computed macrobenthic biomass for the lower Bay was amended by 10 g m^{-2} to account for the biomass of this polychaete, giving a total biomass estimate of 22 g m^{-2} for the lower Bay. In contrast to the middle and upper Bay, where bivalves were the largest contributors to macrobenthic biomass, polychaetes dominated the benthos in the lower Bay. Aside from *C. variopedatus*, there was a very diverse assemblage of polychaetes, with the head-down deposit feeder *Macroclymene zonalis* the most abundant taxa (see also Schaffner 1990).

Community production in the lower Bay was estimated to be 0.31 g m^{-2} d^{-1}. This includes a production estimate for *Chaetopterus variopedatus* of 0.18 g m^{-2} d^{-1}

derived from Thompson (2000), which includes production by juvenile cohorts, net somatic growth, reproductive effort by adults, and tube formation. At an average biomass of 10 g m^{-2}, P/B for this polychaete is ~0.018 d^{-1}. Although this is higher than suggested by the Edgar (1990) model for an organism as large as *C. variopedatus*, it reflects a substantial contribution from juvenile cohorts and tube formation, which may not be reflected well by Edgar (1990).

Body Size and Production/Biomass Ratios. The average body size of macrobenthos varied among the different regions of the Bay (Fig. 5-8, $p<0.05$). Differences among the means were tested using the Tukey-Kramer method due to the unequal numbers of observations in each group (Sokal and Rohlf 1995). Average body size was highest in the upper Bay where the benthic community was overwhelmingly dominated by the bivalve *Rangia cuneata*. The smallest average body size was found in the deep habitat at the north mid-Bay region where the most abundant taxa in summer was the small opportunistic bivalve *Mulinia lateralis*. The mid-Bay shallow water habitat and the lower Bay habitats had similar average body size. The south mid-Bay deep water habitat had slightly lower body size, but was not statistically distinguishable from several other regions (Fig. 5-8). Mean body size was lower in the south mid-Bay mid-depth habitat than anywhere other than the north mid-Bay deep habitat; however, due to a small number of observations in that region, the mean body size was not statistically different from any region other than the upper Bay.

The community production/biomass ratio (hereafter, P/B) was computed for Chesapeake Bay benthic communities as the quotient of total community production

and community biomass. Since production per individual was estimated as a function of water temperature and body size (eq. 1), P/B ranged from zero (e.g. winter) to 0.032 d^{-1} (95^{th} percentile), which represents a summer community dominated by very small individuals. This range includes the range of P/B as reviewed by Ulanowicz and Baird (1986) for a variety of taxa present in the Bay (e.g. *Nereis succinea*, *Heteromastus filiformes* and other polychaetes, 0.027 d^{-1}; *Macoma balthica*, 0.016 d^{-1}; Rangia *cuneata*, 0.011 d^{-1}). Average P/B during summer varied among the regions of the Bay (Table 5-4), from a low of 0.008 d^{-1} in the upper Bay to a high of 0.017 d^{-1} in the south mid-Bay deep water. Although the smallest average body size was found in the north mid-Bay deep water, biomass declined to negligible levels in this region by mid summer or earlier. Thus, much of the production was limited to early summer when water temperature was lower. In contrast, rapid summer growth of *Chaetopterus variopedatus* newly recruited to the lower Bay contributed to higher P/B in that region (Thompson 2000). While summer average P/B varied two-fold, summer average biomass varied among the regions by two orders of magnitude. Despite the recognized potential that relatively depauperate benthic communities could have higher than expected production due to the predominance of opportunists, these results suggested that in Chesapeake Bay production patterns largely reflected biomass patterns. These regional patterns are discussed in more detail below.

Potential Food Limitation and the Role of the Chesapeake Bay Benthos.

Bioenergetic budgets were developed for Chesapeake Bay benthic communities during summer, a major objective being to compare the carbon requirements of regional

benthic communities with available carbon sources (Tables 5-7). The results are presented first by region, then an overall evaluation and summary is provided.

The plankton community in the upper Bay is net heterotrophic (i.e. respiration exceeds photosynthesis) on an annual basis and modestly autotrophic in summer. Estimates of gross primary production vary among published studies but are between 680 mgC m^{-2} d^{-1} (based on Kemp et al. 1997) and 1236 mgC m^{-2} d^{-1} based on Harding et al. (2001) as modified according to suggestions of Smith (2000, see Chapter 5 Appendix). Summer average plankton respiration is 586 mgC m^{-2} d^{-1} based on Kemp et al. (1997) and assuming $\bar{z}$=4.5. Thus, net plankton production was estimated to be 94-650 mgC m^{-2} d^{-1} (Table 5-5). The upper Bay receives a daily input of organic carbon from the Susquehanna River, but exports a substantial fraction of the input as DOC to the mid Bay. The net advective influx of organic carbon, was computed to be 90 mgC m^{-2} d^{-1}. Thus, the total carbon potentially available to the benthos (Table 5) amounts to 184-740 mgC m^{-2} d^{-1}, probably sufficient to support the estimated respiration of the upper Bay macrobenthos (194-596), but not the consumption (294-1235). Thus, these estimates suggest that the upper Bay macrobenthos can only be sustained through recycling of unrespired (i.e. egesta, ungrazed production) organic carbon back into the food web (Table 5-5, see Chapter 5). Such recycling is known to be important in Chesapeake Bay (Baird and Ulanowicz 1989).

An analyses based on the suspension feeding computations described by Gerritsen et al. (1994) provided an alternative approach to estimating the carbon resources available to the upper Bay suspension feeding macrobenthos, which in the case of the upper Bay accounts for nearly all the biomass (Tables 6 and 7). According

to these computations, vertical mixing in the upper Bay is adequate to bring the entire volume of the upper Bay within reach of benthic suspension feeders one or more times each day (Table 5-6). The combined clearance of suspension feeders was estimated to be 11.5 $m^3\ m^{-2}\ d^{-1}$, clearing 92% of the upper Bay volume each day (Table 5-7). Given the concentration of particulate organic carbon in the upper Bay, the ration consumed would be unrealistically high. Gerritsen et al. (1994) approached this problem by assuming that at steady state actual clearance would be limited by the rate at which particles could be replaced in the water column. In other words, they assumed that the filtered fraction (V_F/V_T) estimates the fraction of daily primary production consumed, rather than the fraction of suspended particles consumed. Using this same assumption here, the ration available via suspension feeding is 747 $mgC\ m^{-2}\ d^{-1}$, sufficient to support consumption by suspension feeders toward the lower end of the estimated range (Table 5-7). By effectively neglecting the possibility that suspension-feeders could consume organic detritus, this is a conservative estimate of the possible organic matter flux to the suspension-feeding benthos.

On the other hand, the is the potential that *Rangia* refiltered water in areas where the bivalves were most densely populated. While eq. (9) addresses refiltration at the large scale, it does not address the possibility than a single water parcel could be filtered several times during a single "approach" to the bottom. At dense populations refiltration rates may be as high as 48% (O'Riordan et al. 1995), effectively halving the clearance rate of the suspension-feeding population. In this case, the computed cleared ration based on primary production alone would be insufficient to meet the minimum estimate of organic carbon demand. Thus, it would be required that some

allochthonous carbon or other suspended particles be included in the filtered ration to obtain the ration estimated to be required. Given the results of both the suspension-feeding and carbon budget computations, it appears likely that the organic carbon resources may be just sufficient to support the community, indicating the potential for food limitation.

Comparison of the estimated bioenergetic rates for the upper Bay macrobenthos with several aspects of the carbon budget suggests that consumption (and therefore respiration and egestion) by the macrobenthos must be toward the lower end of the estimated range. The range of macrobenthic respiration estimates for the upper Bay (Table 5-5) was 88-262% of sediment O_2 consumption (SOC) estimated by incubating benthic cores (Cowan and Boynton 1996, Table 5-8). Since metabolic rates for meiobenthos and benthic microbiota are not likely to be negligible (see Chapter 6), this implies that either the lower estimates of macrobenthic respiration are most appropriate, that macrobenthic metabolism was under-represented in SOC, or both. Although macrobenthic-rich cores were not avoided when making SOC (W. R. Boynton, pers. comm.), the relative rarity of high biomass sites makes it probable, or even likely, that the macrobenthos were under-represented. As with consumption, the respiratory demand of the macrobenthos appears to be a significant component of carbon flow in the upper Bay benthos.

Net plankton production (NPP) in the mid Bay was sufficiently positive during summer to support even the most generous estimate of consumption by the macrobenthic community (Table 5-5, Kemp et al. 1997). Assuming that vertically integrated rates of both gross production and plankton respiration per unit volume are

independent of depth (Kemp et al. 1997), NPP in the shallow water habitats of the mid Bay is much greater than the regional average (Table 5-5). Thus, even though macrobenthic biomass and production in these areas was greater than in deeper waters, NPP exceeds the estimated consumption of the shallow water benthos by a very large margin (see also Blumenshine and Kemp 2000).

Computations based on the particulate diffusion model of Gerritsen et al. (1994) show that horizontal and vertical exchange is sufficient to bring all of the littoral zone production and 16% of the pelagic surface mixed layer production to the littoral zone benthos of the mid Bay each day. From this perspective, the available primary production was estimated to be a minimum of 7-fold greater than the computed requirements of the suspension-feeding benthos. Actual clearance by suspension feeders was estimated to be <5% of the available volume, but was sufficient to support the requirements of suspension feeders (Table 5-7).

Although the available historical data is not extensive, data examined by Holland et al. (1987) suggested that stable populations of larger *M. arenaria* and *Macoma* spp. disappeared after the early 1970's. An abrupt decline in Maryland landings of *M. arenaria* from ~3000 tons yr^{-1} prior to 1972 to <1000 tons yr^{-1} thereafter suggests that the abundance of this species declined following floods due to tropical storm Agnes (June 1972) and never fully recovered (NOAA Landings Data). The bioenergetic results suggest that current primary production greatly exceeds the requirements of the macrobenthos, while the limited historical data point to higher suspension feeder populations in the past, when phytoplankton biomass (Harding and Perry 1997) and presumably production were lower. These results imply that

reductions in primary production as a result of nutrient loading reductions would probably not lead to food limitation of the shallow water benthos.

Unlike the shallow water zones, net plankton community production reaching the benthos at the average depths of the mid-depth and deeper mid Bay habitats was estimated to be negative and therefore was not sufficient to directly support the metabolic requirements of the benthos (Table 5-5). However, the high rates of aerobic and anaerobic metabolism in deep water sediments imply that a large quantity of organic matter is transported to these habitats (Cowan and Boynton 1996, Marvin-DiPasquale and Capone 1998). Lateral imports of carbon from shallower habitats are a likely source of carbon for the deeper areas, an explanation also invoked by Blumenshine and Kemp (2000) for the mid Chesapeake Bay and by Pearson and Rosenburg (1992) to explain a carbon imbalance in the Kattegat.

Deposition of fresh phytoplankton to mid Bay sediments at the conclusion of the spring bloom is a possible source of high quality organic matter, particularly for the early summer benthos. The average deposition of organic matter to mid Bay sediments during spring has been estimated to be ~27 gC m^{-2} (Chapter 4). Distributed over the duration of summer, this flux alone is sufficient to support at least a 10-fold increase in benthic respiration (Table 5-5), which would bring mid Bay biomass into the same range as elsewhere in the Bay (Table 5-4). Since summer benthic microbial metabolism in the mid Bay is on the order of 1200 mgC m^{-2} d^{-1} (Kemp et al. 1997), it is clear that there is a continual flux of organic matter across the pycnocline during summer, not just the residual biomass imported from spring. A sediment trap study in the mid Bay found that, despite the lack of excess net plankton production in the

deeper waters of the mid Bay, the vertical carbon flux inferred from the vertical chl-a flux at the pycnocline was about 500 mgC m^{-2} d^{-1}. The directly measured vertical carbon flux was ~1000 mgC m^{-2} d^{-1} (Boynton et al. 1993). The lower number, which may represent a more labile fraction of the sedimenting POC, and is less likely to included resuspended POC, would also be more than sufficient to support the macrobenthos. The higher number would be required to balance the total benthic metabolism (Table 5-8).

Like the shallow mid Bay, net plankton community production in the lower Bay was substantially positive. Despite the estimated net advective export of DOC onto the continent shelf computed from a box model (Table 5-5), one still obtains a surplus of organic matter production equal to 948 mgC m^{-2} d^{-1} (=1148-200, Table 5-5), sufficient to support macrobenthic consumption in the middle of the estimated range (Table 5-5). Thus, while the available carbon estimated via NPP was sufficient to support the lower Bay benthos, it was not vastly more than sufficient as in the mid Bay.

Suspension-feeding benthos accounted for slightly more than 50% of production (Table 5-4). According to computations based on the Gerritsen et al. (1994), physical mixing makes nearly all of the volume of the lower Bay available to the benthos each day, enabling suspension-feeders to have a substantial grazing impact. The lower Bay suspension-feeders were estimated to filter about half of the volume lower Bay volume each day (Table 5-7). Assuming that this means that they could consume the same fraction of daily primary production (see discussion for upper Bay), the ration obtained by suspension feeding could be 756 and 680 mg m^{-2} d^{-1} in

the north and south divisions of the lower Bay, respectively. These values are near the maximum that the suspension-feeding benthos in the lower Bay may require (Table 5-7), indicating food limitation is not likely.

Summary and Conclusions

Previous studies and reviews of benthic ecology have shown that the biomass and production of estuarine and marine macrobenthos can depend on many interacting factors, hypoxia being among them. Although benthic biomass and production within estuaries is known to be highly variable, this study developed empirical models that resolved the complex dependence of the Chesapeake Bay benthos on multiple habitat factors, providing a validated predictive capability and identifying which among the factors that were examined were the most predictive in which environmental context. Among these, hypoxia was found to be the most important factor affecting the biomass of the macrobenthos. Consistent with the findings of Diaz and Rosenburg (1995), benthic biomass was found to be reduced when dissolved oxygen (DO) was less than ~2 mg l^{-1}, with even lower biomass associated with lower DO (Fig 4, Table 5-2). However, depth and interactions between depth and salinity appeared as predictors of benthic biomass in a way that suggested hidden effects of periodic or episodic hypoxia in habitats that were normoxic at the time they were sampled. Most obvious was the depression of macrobenthic biomass at all depths in the mesohaline Chesapeake Bay relative to the upper and lower Bay. These patterns are put into a comparative context in Fig. 5-9, which reproduces the relationship between macrobenthic biomass and annual phytoplankton production reported by Herman et al.

(1999). Estimates from this study were added, showing that macrobenthic biomass in the lower Bay was consistent with expectations based on primary production. In contrast, benthic biomass was greater than expected in the upper Bay, perhaps due to either allochthonous organic matter sources or to reduced predation on the dominant clam, *Rangia cuneata*. Finally, the mid Bay, despite very high primary production, had a very depauperate macrobenthos compared to coastal systems with similar primary production. Based on this relationship, the macrobenthic biomass in the mid Chesapeake Bay could be expected to be as high as 40 gC m^{-2}, a 14-fold increase over the present average. A 10-fold increase would still be reasonable even if primary production was reduced significantly.

Aside from the possibility that episodic hypoxia is to blame, the reason for the depression of macrobenthic biomass and production in shallower habitats of the mid Bay was not resolved and would be a good area for further investigation. One hypothesis is that demersal predators may be concentrated into the areas where adequate benthos is present and thereby exert an exceptionally strong effect. This could be exacerbated by low oxygen events, which force burrowed animals to the surface where they are more vulnerable to predation (Diaz et al. 1992).

The results of this study suggest that the primary effect on the benthos of a reduction in organic matter inputs, as might be achieved through nutrient loading rate reductions, would be to benefit the community by reducing oxygen stress. This is particularly evident in the mid Bay. In contrast, reduced organic matter inputs to the benthos would most likely not limit benthic production, since these populations do not appear strongly food limited, if food limited at all. Moreover, the models of

suspension feeding indicate that the Chesapeake Bay benthos, except for in deeper waters of the mid Bay, may not rely on surplus organic matter from the plankton (i.e. positive net plankton production). Rather they obtain their ration from net phytoplankton production, not net plankton production, as needed, possibly to the detriment of the plankton. In this way, one may hypothesize that net plankton production results in part from benthic suspension-feeding and that, lacking significant suspension-feeding, the plankton will tend toward P/R=1. Although this argument would not apply directly to deposit-feeders, suspension-feeding can contribute to deposit feeding via biodeposition, extending this coupling mechanism to all the macrobenthic taxa. Considering the massive, but now absent, biomass of oysters that once filtered the waters of Chesapeake Bay (e.g. Newell 1988), it seems likely that such coupling was once an important aspect of the ecology of Chesapeake Bay. One may conclude that a management policy that avoids reducing primary production in order to maintain secondary production in the benthos would be misguided. Such a policy would neglect the demonstrable effects of habitat quality effects in favor of a hypothetical and, by this analysis, improbable food limitation effect, and would not be consistent with inferences that can be based on historical precedent and comparative ecology.

Because patterns in benthic biomass appeared to reflect known seasonal and spatial patterns in the frequency and intensity of hypoxia, benthic monitoring is supported as a means of assessing progress toward ecosystem restoration. Two regions in the mid Bay would be particularly valuable places to target benthic monitoring effort in order to develop indicators of ecosystem change in Chesapeake

Bay. Benthic communities in the mid depth zone (7.5-10m) in the mid Bay may be an effective integrator of periodic oxygen stress which results from upwelling of hypoxic or anoxic water from the channel. Similarly, variability in the extent of hypoxia is often manifest most dramatically as changes in the southern limit of hypoxia in the Bay, which changes both interannually and on the biweekly time scale resolved by the Chesapeake Bay Monitoring Program (Chapter 2). Therefore, the benthic community in deep waters at the southern limit of the mid Bay may also be a useful and sensitive indicator that could be targeted by monitoring efforts seeking to assess the progress of restoration.

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Table 5-1. Parameter estimates and F-table for a multiple regression (r^2=0.34) predicting log ash-free biomass per m^2 (recoded by adding 0.01 g m^{-2}) at locations in the mainstem Chesapeake Bay. Explanatory variables include bottom water dissolved oxygen (DISOXY), bottom water salinity (SALINITY), bottom water water temperature (WTEMP), % sediment silt-clay content (SILTCLAY), and all two-way interactions. A categorical variable representing seasons (Winter=December-February, Spring=March-May, Summer=June-August, Fall=September-November) was also included in the model. n.s. = not statistically significant (p>0.10).

Source	Estimate	DF	Type III SS	Significance
DISOXY	-0.2020	1	17.02	<0.01
SALINITY	0.0301	1	0.84	n.s.
WTEMP	-0.1056	1	20.48	<0.01
SILTCLAY	*-0.0022*	1	0.20	n.s.
DISOXY*SALINITY	*0.0016*	1	0.65	n.s.
DISOXY*WTEMP	0.0107	1	66.73	<0.01
DISOXY*SILTCLAY	0.0013	1	16.41	<0.01
SALINITY*WTEMP	*0.0002*	1	0.06	n.s.
SALINITY*SILTCLAY	-0.0011	1	68.14	<0.01
WTEMP*SILTCLAY	0.0005	1	11.03	<0.01
SEASON (W, Sp, Su, F)	0.28, 0.24, 0.30, 0.00	3	21.34	<0.01
Intercept	1.5977			<0.01
Model (r^2=0.34)		13	567.63	<0.01
Error		1571	1060.06	
Corrected Total		1584	1607.69	

Table 5-2. The importance of water quality and habitat variables as factors in a CART regression-tree model predicting biomass of mainstem Chesapeake Bay macrobenthic communities. Relative importance scores are included in the CART software output and reflect the total contribution of the variable to model predictions. The variable with the highest importance score is arbitrarily assigned a value of 100. When importance statistics are based on primary splitting rules only, other indicators of importance, such as appearance as a surrogate are discounted (Steinburg and Colla 1995).

Variable Name	Relative Importance	Relative Importance (primary splitting rules only)
Dissolved Oxygen	100	100
Salinity	71	49
Percent Silt-Clay	63	48
Total Depth	58	54
Month	39	24
Water Temperature	38	15
Percent Carbon	8	0
Percent Nitrogen	5	0

Table 5-3. Node detail for the regression-tree model shown in Fig. 5-4. DO=bottom dissolved oxygen (mg l^{-1}), MONTH=month of the year (1-12), TDEPTH=total depth (m), SALINITY=bottom salinity (ppt), SILTCLAY=% silt-clay content of sediments. For non-terminal nodes, an observation is directed to the left child node if the splitting rule is true. Log Mean biomass refers to the mean of macrobenthic biomass after log transformation by log(biomass+0.01) where biomass has units g AFDW m^{-2}. Mean biomass was computed by back-transforming using $B = 10^{B'+\sigma^2/2} - 0.02$, where B=mean biomass, B'=log mean biomass, and σ^2 is the variance of the log mean observations. The term $\sigma^2/2$ corrects for the bias due to log-transformation.

Node	Splitting Rule	Log Mean Biomass	Std. Dev.	Mean Biomass (g m^{-2})	N	Child Nodes (Left, Right)
1	DO≤2.34	0.095	1.017	4.1	1664	2,6
2	MONTH≤6.5	-0.955	1.008	0.3	242	T1, 3
3	TDEPTH≤10.4	-1.351	0.864	0.1	167	4, 5
4	DO≤1.1	-0.511	1.049	1.1	25	T2, T3
5	DO≤0.875	-1.499	0.734	0.0	142	T4, T5
T1		-0.075	0.703	1.5	75	
T2		-1.291	0.917	0.1	8	
T3		-0.145	0.895	1.8	17	
T4		-1.659	0.60	0.0	92	
T5		-1.204	0.857	0.1	50	
6	TDEPTH≤11.05	0.273	0.904	4.8	1422	7, 20
7	SALINITY≤8.545	0.470	0.835	6.6	971	8, 13
8	SILTCLAY≤58.78	0.936	0.998	27.1	234	9, 11
9	SALINITY≤0.370	0.351	0.912	5.8	81	10, T8
10	TDEPTH≤2.95	-0.092	0.958	2.3	31	T6, T7
11	SILTCLAY≤89.95	1.246	0.898	44.6	153	12, T11
12	DO≤7.17	1.000	1.037	34.5	70	T9, T10
T6		-0.778	0.515	0.2	11	
T7		0.285	0.936	5.3	20	
T8		0.625	0.762	8.2	50	
T9		1.622	0.844	95.1	26	
T10		0.632	0.961	12.4	44	
T11		1.454	0.698	49.8	83	

Table 5-3. Continued.

Node	Splitting Rule	Log Mean Biomass	Std. Dev.	Mean Biomass ($g\ m^{-2}$)	N	Child Nodes (Left, Right)
13	SALINITY≤20.4	0.322	0.716	3.8	737	14, T19
14	TDEPTH≤7.65	0.238	0.705	3.0	646	15, 18
15	SALINITY≤14.025	0.303	0.665	3.3	562	16, T15
16	SILTCLAY≤3.622	0.483	0.691	5.2	309	T12, 17
17	TDEPTH≤4.65	0.884	0.780	15.4	85	T13, T14
18	WTEMP≤24.880	-0.193	0.807	1.3	84	T16, 19
19	SILTCLAY≤86.68	-0.825	0.900	0.4	26	T17, T18
T12		0.330	0.585	3.2	224	
T13		1.321	0.585	31.0	24	
T14		0.712	0.780	10.4	61	
T15		0.083	0.560	1.7	253	
T16		0.090	0.567	1.8	58	
T17		-0.156	0.645	1.1	14	
T18		-1.606	0.371	0.0	12	
T19		-0.916	0.462	0.1	91	
20	SILTCLAY≤58.44	-0.150	0.900	1.8	451	21, 23
21	SALINITY≤21.95	0.644	0.706	7.8	103	22, T22
22	DO≤4.385	0.158	0.788	2.9	38	T20, T21
23	WTEMP≤20.60	-0.385	0.813	0.9	348	24, 26
24	TDEPTH≤22.85	-0.181	0.612	1.0	248	T23, 25
25	TDEPTH≤31.5	-0.529	0.634	0.4	69	T24, T25
26	SALINITY≤18.80	-0.891	1.005	0.4	100	T26, T27
T20		-0.674	0.869	0.5	8	
T21		0.379	0.594	3.6	30	
T22		0.928	0.456	10.7	65	
T23		-0.047	0.547	1.2	179	
T24		-0.787	0.517	0.2	45	
T25		-0.045	0.543	1.2	24	
T26		-1.323	0.729	0.1	58	
T27		-0.295	1.029	1.7	42	

Table 5-4. Regional area and summer (June-August) average biomass, daily production and daily P/B ratio, as estimated using the Edgar (1990) model. Means for combined regions (e.g. upper Bay, mid Bay, lower Bay, whole Bay) are weighted by the area of component regions. Biomass and production for the lower Bay include estimates for the polychaete *Chaetopterus variopedatus*, which were derived separately from Thompson (2000).

Region	Area (km^2)	Biomass ($g\ m^{-2}$)	Production ($g\ m^{-2}\ d^{-1}$)	% Susp Feeding	P/B (d^{-1})
Upper Bay	353	59.22	0.49	92	0.008
N Mid Bay, <7.6 m	303	11.72	0.13	35	0.011
S Mid Bay, <7.6 m	890	2.77	0.03	29	0.012
N Mid Bay, 7.6-10 m	172	2.07	0.03	8	0.013
S Mid Bay, 7.6-10 m	408	0.64	0.01	10	0.017
North Mid Bay, >10 m	783	0.63	0.01	50	0.014
South Mid Bay, >10 m	532	3.51	0.04	17	0.012
N Lower Bay	1009	20.05	0.30	67	0.015
S Lower Bay	1011	24.18	0.33	60	0.013
Upper Bay	353	59.2	0.49	92	0.008
Mid Bay	3089	2.9	0.04	29	0.012
Lower Bay	2019	22.1	0.31	63	0.014
Whole Bay	5461	13.7	0.17	46	0.012

Table 5-5. Estimated ranges for summer (June-August) average consumption (C), respiration (R), and excretion plus egestion (U) by macrobenthic communities in Chesapeake Bay, computing using net growth efficiency=0.3 or 0.56 and assimilation efficiency=0.4 or 0.6, resulting in gross growth efficiency=0.12 or 0.34. Bioenergetic rates are compared to summer (June-August) average net plankton production, recomputed for each region using data from Kemp et al. (1997), and the net external TOC exchange, computed using physical transport estimates computed using a box model (Chapter 2). Net input of TOC is available only for regions as a whole. n.e. = not estimated. All units are mgC m^{-2} d^{-1}.

Region	C	R	U	NPP	Ext. Src.
Upper Bay	735-2058	194-576	294-1235	94-650	90
North Mid Bay - Shallow	193-539	51-151	77-324	2279	n.e
South Mid Bay - Shallow	51-142	13-40	20-85	2298	n.e
North Mid Bay - Middle	39-110	10-31	16-66	-91	n.e
South Mid Bay - Middle	16-45	4-13	6-27	-50	n.e
North Mid Bay - Deep	14-38	4-11	5-23	-532	n.e
South Mid Bay - Deep	63-178	17-50	25-107	-484	n.e
North Lower Bay	446-1249	118-350	178-750	907	n.e
South Lower Bay	485-1359	128-380	194-815	1388	n.e
Upper Bay	735-2058	194-576	294-1235	94-650	90
Mid Bay	52-146	14-41	21-88	656	-10
Lower Bay	466-1304	123-365	186-782	1148	-200
TOTAL	249-698	66-195	100-419	801	-80

Table 5-6. The parameters describing mixing characteristics of 5 segments of Chesapeake Bay, leading to estimates of the fraction of the water volume available to suspension feeders each day. t_V =the mean time for a water parcel to encounter the benthos, P_V=the probability that a water parcel in the littoral zone will encounter the bottom within 1 day.

Region	Mean Depth (m)	t_V (hours)	P_V	Fraction Available
Upper Bay	4.50	1.9	1.00	1.00
North Mid Bay	5.69	2.9	1.00	0.43[1]
South Mid Bay	5.33	2.6	1.00	0.51[1]
North Lower Bay	9.90	9.1	0.93	0.93
South Lower Bay	8.19	6.2	0.98	0.98

[1] refers to the fraction of littoral volume plus pelagic SML volume available, computed using eqs. 4, 5, 6 and 7 from Gerritsen et al. 1994.

Table 5-7. Computations based on the models of Gerritsen et al (1994) showing the relationship between potential ratio available via suspension feeding and the range of estimated carbon requirements of the suspension feeding macrobenthos. V_B=volume of water approaching the benthos, V_T=volume of water in the littoral zone and adjacent pelagic surface mixed layer. V_F=volume filtered by suspension feeders. PP=Summer Net ^{14}C-Primary Production (Harding et al. 2001). C demand differs from the values in Table 5-5 because these values are for suspension feeders only.

Region	Clearance $m^3\ m^{-2}\ d^{-1}$	V_B/V_T	V_F/V_T	PP $mgCm^{-2}d^{-1}$	Filt. Ration $mgC\ m^{-2}\ d^{-1}$	C Demand $mgC\ m^{-2}\ d^{-1}$
Upper Bay	11.46	100%	92%	811	747	667-1889
N Mid Bay	1.02	36%	4%	2300	226	101-287
S Mid Bay	0.25	48%	1%	1945	71	20-57
N Lower Bay	6.78	93%	48%	1571	756	295-835
S Lower Bay	6.65	98%	55%	1240	680	288-816

Table 5-8. Average total benthic metabolic rates for three regions of Chesapeake Bay during June-August. Sediment oxygen consumption (SOC) estimates were obtained from Cowan and Boynton (1996). Benthic sulfate reduction (SR) estimates were obtained from Marvin-DiPasquale and Capone (1998). Total benthic respiration (R_b) was computed as SR plus half of SOC (after Kemp et al. 1997), which reflects the likelyhood that some SOC resulted from chemical oxygen demand due to SR. SOC was converted to C assuming RQ=1. SR was converted to C by assuming $S:O_2=2$ and RQ=1.

	SOC ($g\ O_2\ m^{-2}\ d^{-1}$)	SR ($mmol\ S\ m^{-2}\ d^{-1}$)	Total R_b ($g\ C\ m^{-2}\ d^{-1}$)
Upper Bay	0.58	4.64	0.22
Mid Bay	0.18	50.2	1.24
Lower Bay	0.72	26.4	0.77

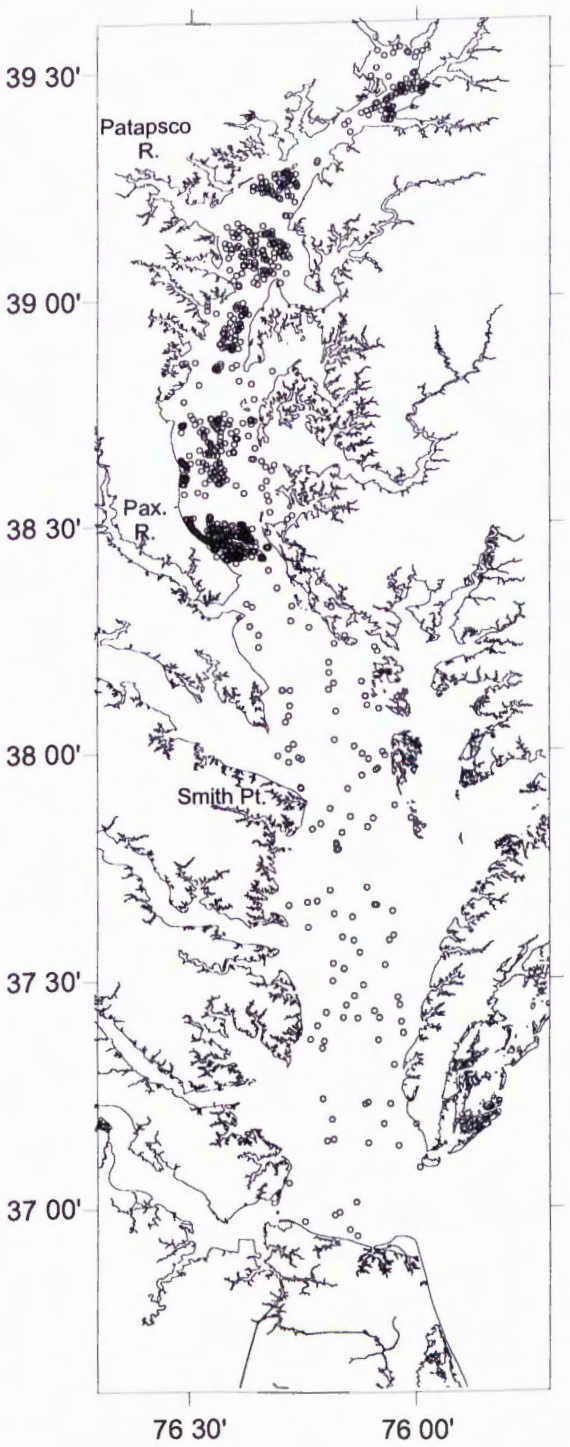


Fig. 5-1. The locations where cores were collected by the Chesapeake Bay Benthic Monitoring Program in the mainstem Chesapeake Bay from 1984-1999. Samples south of Patuxent River (Px. R) accounted for 22% of the total, more than suggested here, but reflecting less intensive sampling effort in the southern portion of the Bay. Greater use of random station locations in the middle and upper Bay reduced overplotting of repeatedly sampled locations, exaggerating the difference.

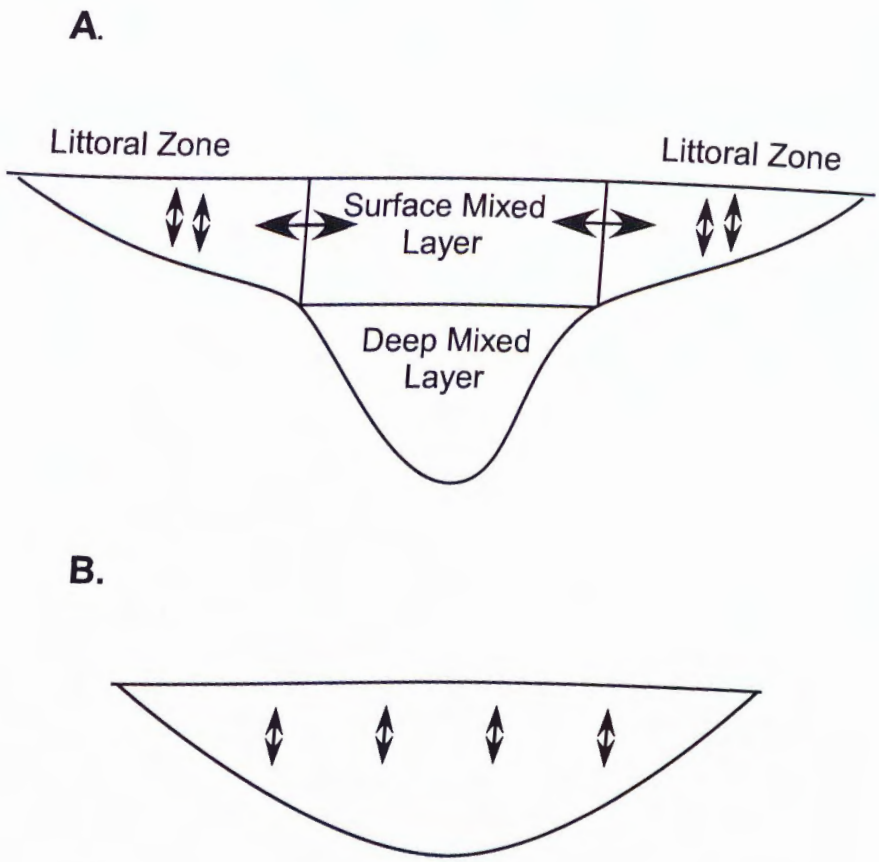
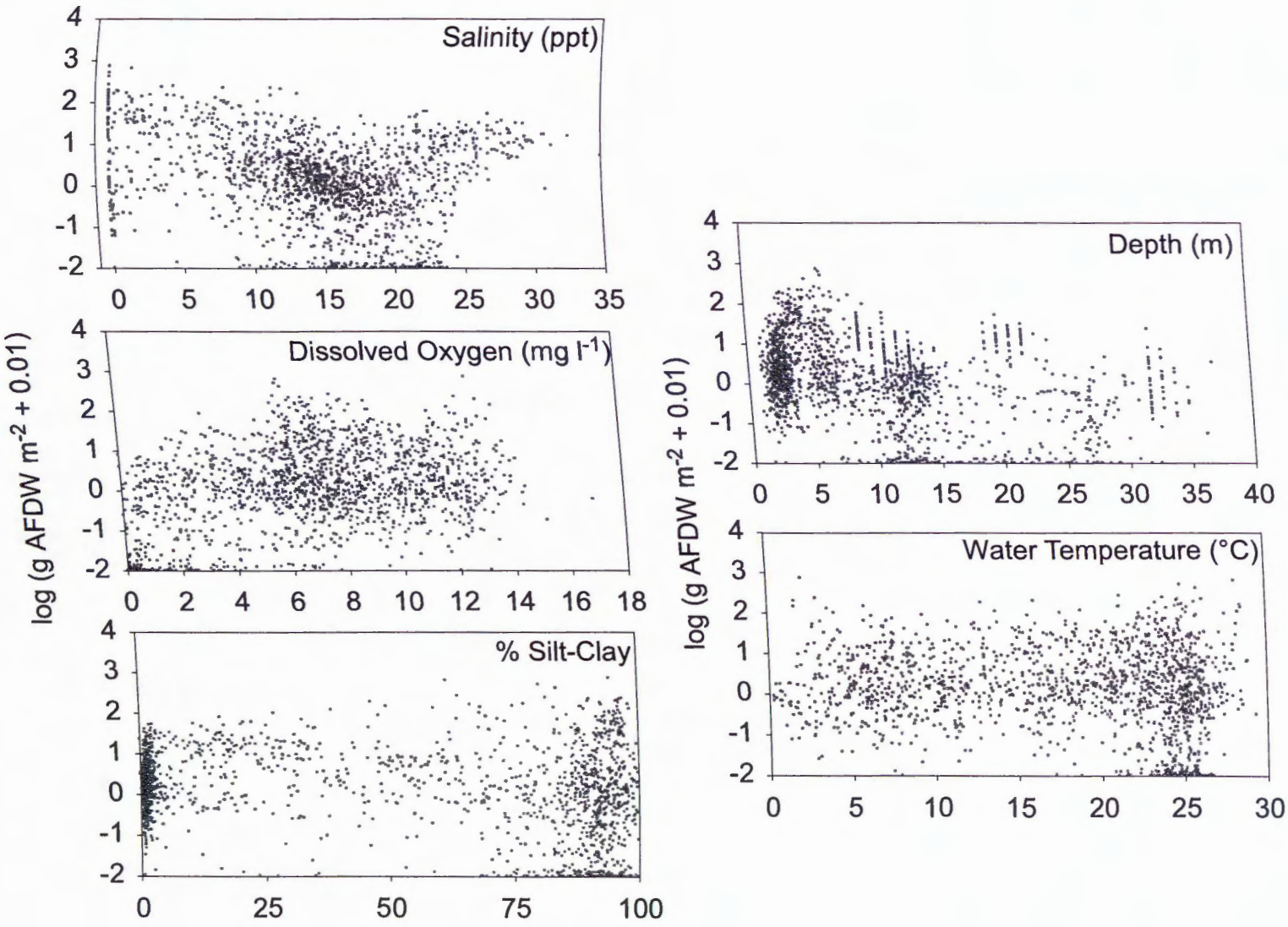


Fig. 5-2. (A) The partitioning of the mid Chesapeake Bay into regions for computation of potential filtration by suspension feeders using the approach of Gerritsen et al. (1994). (B) A collapsed model in the case where it is assumed that there is not a pelagic zone, efffectively isolated from the bottom by water column stratification. This scheme was used for the upper and lower regions of the Bay, while the scheme in (A) was used for the mid Bay.

Fig 5-3. Univariate plots relating macrobenthic biomass in Chesapeake Bay to key variables expected to affect macrobenthic biomass. Macrobenthic biomass (g AFDW m^{-2}) was recoded by adding 0.01 g m^{-2} then log-transformed. Biomass was computed from data reported by the Chesapeake Bay Benthic Monitoring Program. Water quality was concurrently measured in bottom water. Percent silt-clay content of sediment was also measured concurrently. Water quality and sediment properties were both collected by the Chesapeake Bay Benthic Monitoring Program.


Salinity (ppt)
Dissolved Oxygen (mg l-1)
% Silt-Clay
Depth (m)
Water Temperature (°C)
log (g AFDW m-2 + 0.01)
log (g AFDW m-2 + 0.01)

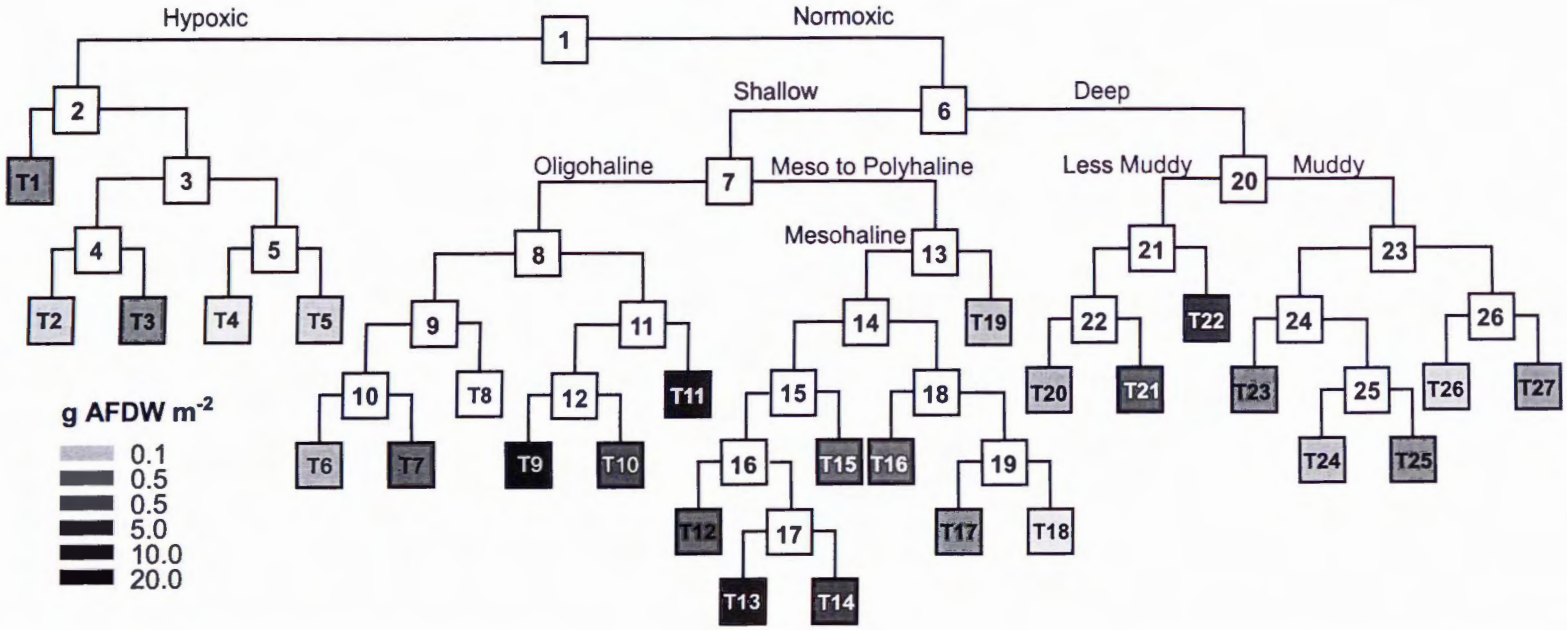


Fig. 5-4. A regression-tree predicting macrobenthic biomass in Chesapeake Bay. Splitting rules and node detail are provided in Table 5-2. Descriptive terms indicate major regions of the tree-structure defined on the basis of primary splitting rules. Terminal nodes, denoted by "T" before the terminal node number, are shaded according to the geometric mean biomass for observations classified to the node. The distribution of values in the terminal nodes is also shown in Fig. 5-5.

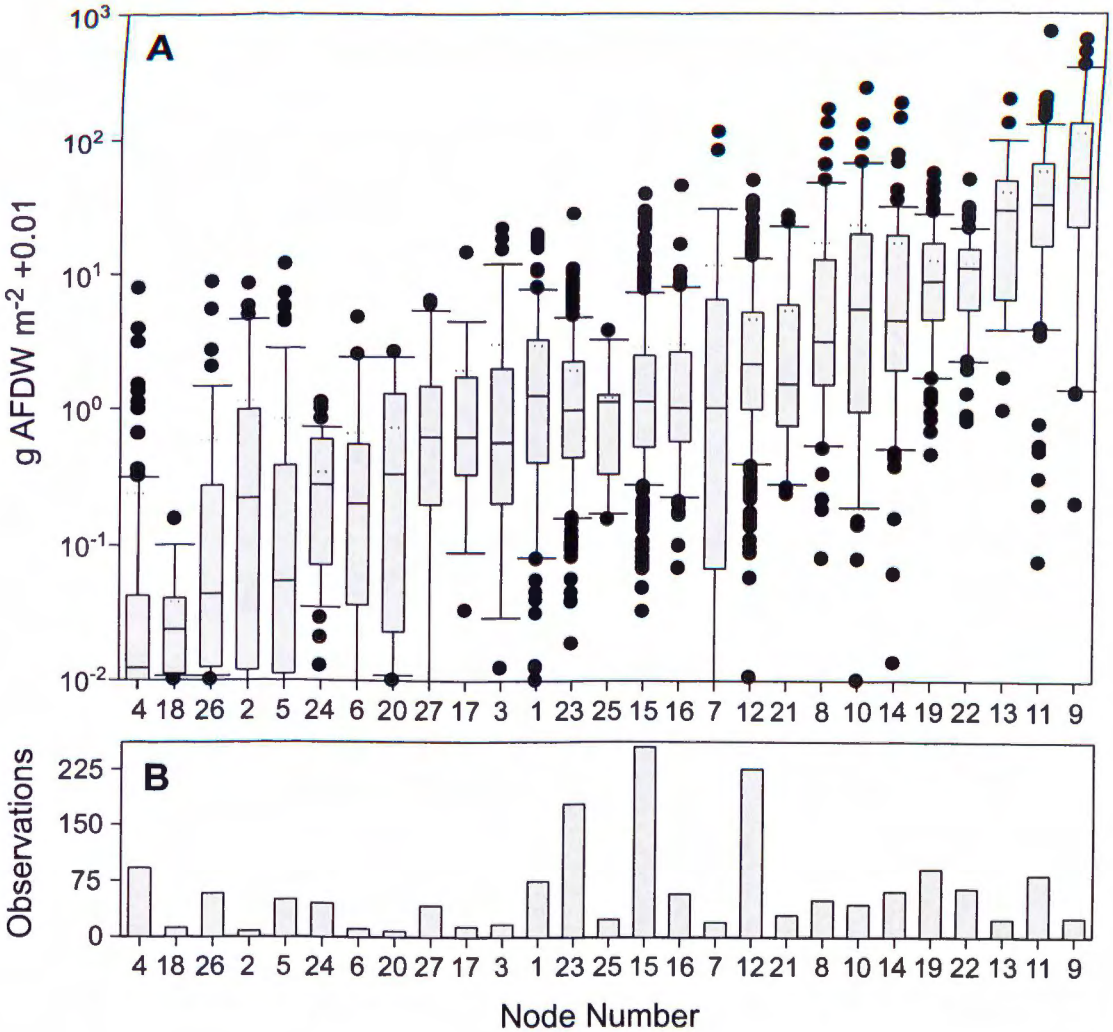


Fig. 5-5. (A) The distribution of macrobenthic biomass among observations classified into the 27 terminal nodes of the regression tree in Fig. 5-3. To facilitate plotting on the log scale, 0.01 g m^{-2} was added to all values; therefore, 10^{-2} g m^{-2} is equal to zero biomass. Boxes indicate the quartiles and median, while the whiskers indicate the 5th and 95th percentiles. Observations outside the 5th and 95th percentiles are plotted individually (B) The number of observations classified into each node.

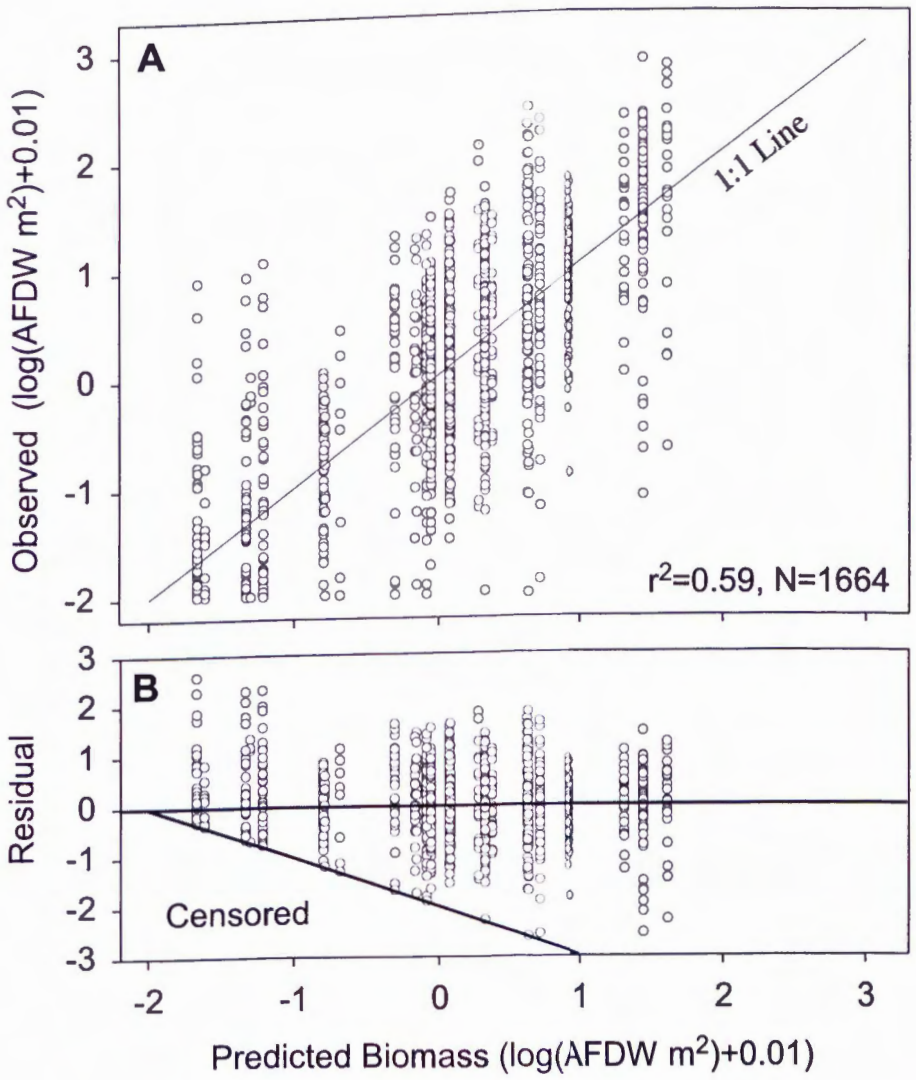


Fig. 5-6. (A) Observed vs. predicted macrobenthic biomass at sites in mainstem Chesapeake Bay. Predictions result from a regression tree model relating macrobenthic biomass to habitat factors (Fig. 5-3). Biomass values were recoded by adding 0.01 g AFDW m^{-2} then log transformed. This resulted in left-censoring of the data at -2 on the log scale. (B) A plot of predicted vs. residuals (observed-predicted). Because of left-censoring of observed values at -2, the sum of the predicted value and associated residualcannot be less than -2.

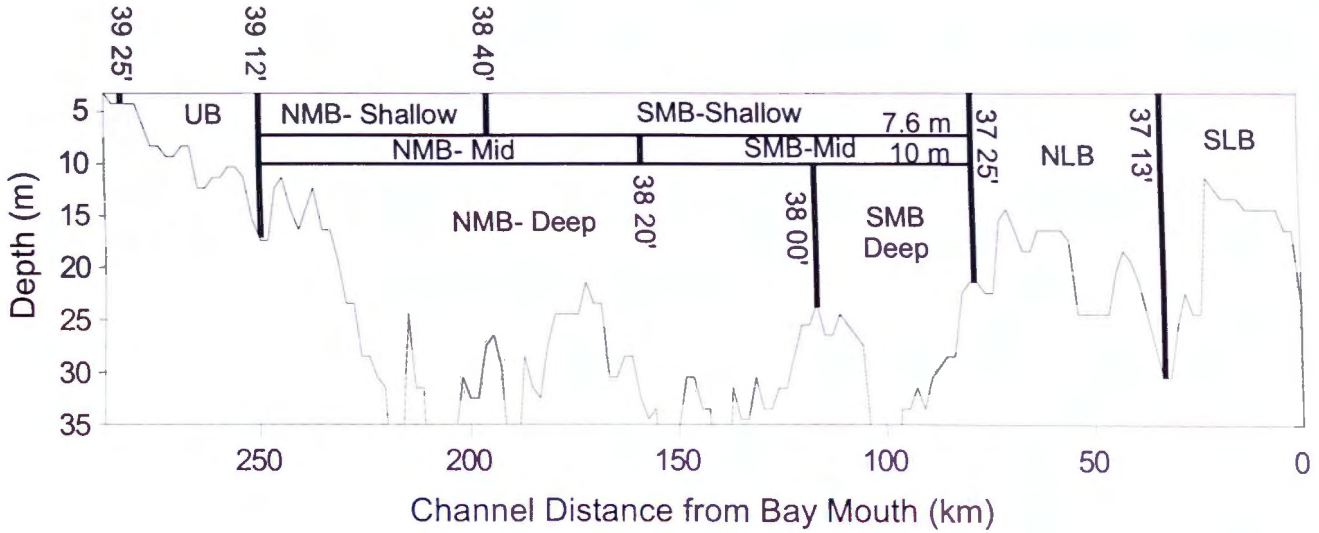


Fig. 5-7. A cross-section of the mainstem Chesapeake Bay indicating the maximum depth profile up to 35 m. Depth and axial distance boundaries are shown for regions identified by a regression tree-model predicting macrobenthic biomass from latitude and depth. The regression-tree algorithm finds regions within which the variance of biomass is minimized.

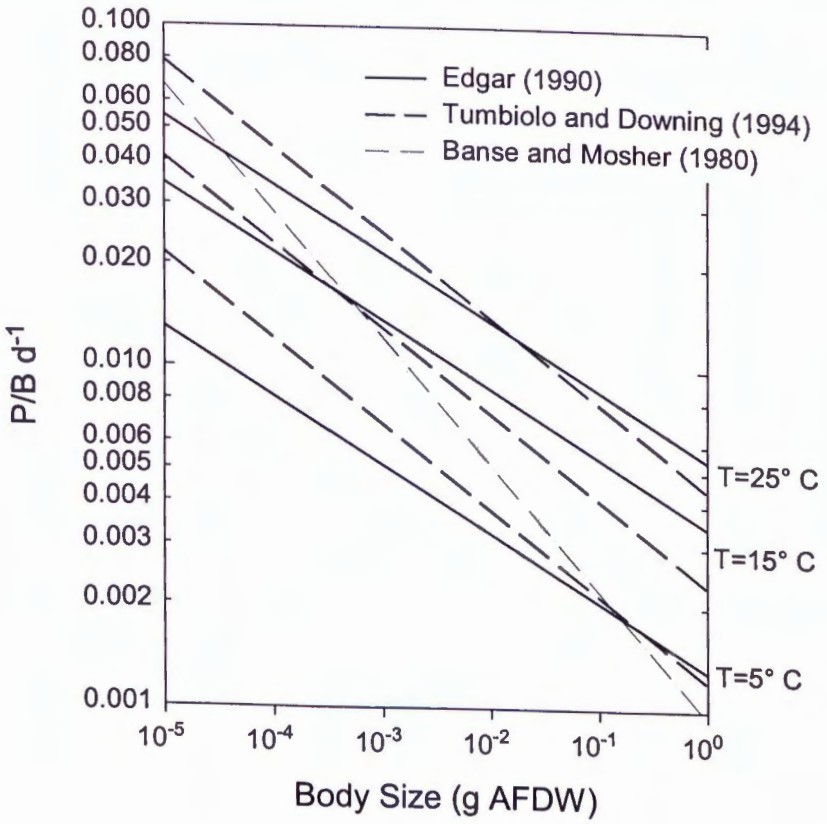


Fig. 5-8. A comparison of three statistical models predicting production/biomass ratios for macrobenthic animals. For the Tumbiolo and Downing (1994) model, a depth of 10 m has been assumed.

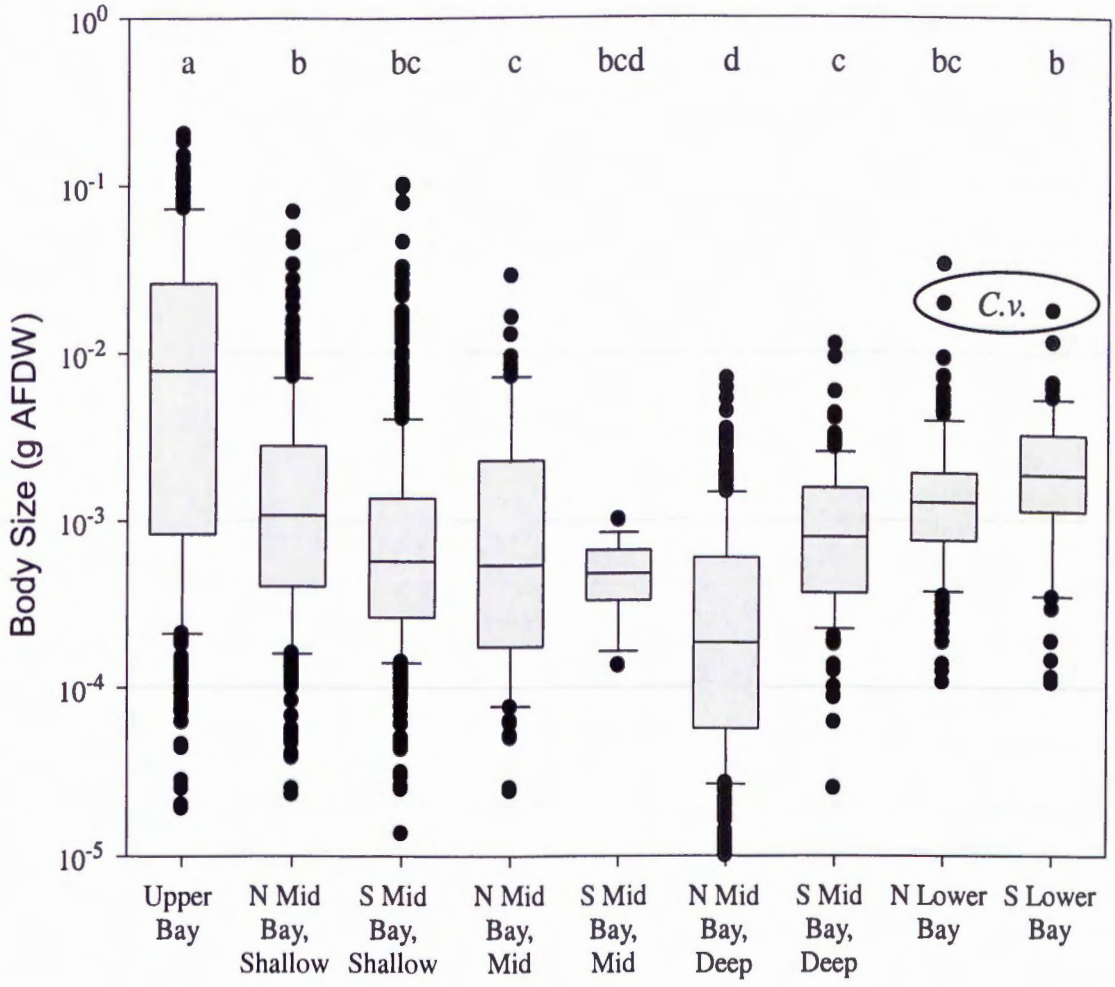


Fig. 5-9. Mean body size of macrobenthos in 9 regions of Chesapeake Bay computed from the Chesapeake Bay Benthic Monitoring Program data. Regions not sharing the same letter at the top of the graph have significantly different mean body size (Tukey-Kramer adjusted $p<0.05$). "*C.v.*" indicates the approximate size of the large polychaete *Chaetopterus variopedatus*, whose abundance is under-represented in the Benthic Monitoring data and is estimated to account for ~50% of the biomass in the lower Bay (Thompson 2000).

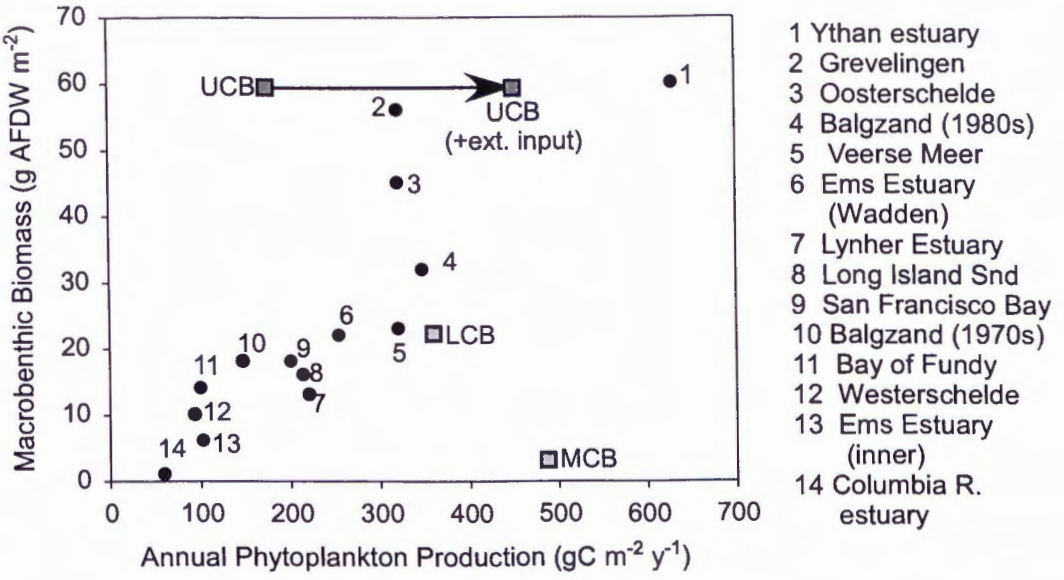


Fig. 5-10. The relationship between annual phytoplankton production and macrobenthic biomass is estuaries and coastal systems as shown in a review by Herman et al. (1999). Three observations have been added reflecting macrobenthic biomass and annual phytoplankton production in three regions of Chesapeake Bay. Macrobenthic biomass estimates are from this study. Phytoplankton production estimates were computed from data in Harding et al. (2001) and are means of spring, summer and fall regional mean production. UCB=Upper Chesapeake Bay, MCB=middle Chesapeake Bay, LCB=Lower Chesapeake Bay. The upper Bay observation is translated to the right by adding the estimated 266 mgC m^{-2} d^{-1}, which is the approximate annual subsidy due to allochthonous organic matter inputs to the region.

Chapter 6:

A NETWORK ANALYSIS OF MAINSTEM CHESAPEAKE BAY FOOD WEBS DURING SUMMER: EUTROPHICATION EFFECTS ON CARBON TRANSFER EFFICIENCY TO FISH

Abstract

Time-invariant trophic-flow networks were constructed for three regions of the Chesapeake Bay during summer. The trophic flow networks nominally represent the period from 1985-1999, for which most of the data were obtained. A trophic flow network was also described to characterize the mid Bay following successful nutrient reductions sufficient to reduce phytoplankton biomass and production to levels observed in the 1950's and early 1960's. The network parameters other than for phytoplankton were characterized using a combination of comparative ecological studies (bacteria and benthos) and the mass balance constraints of network analysis. Rather than attempting to estimate changes in the biomass and production of fish, potential changes in fish production were evaluated in term of the available production of prey items.

The trophic flow networks were evaluated to determine how trophic transfer efficiency and major patterns of carbon flow differed among the regions and between the modern and restored mid Bay networks. The most dramatic differences pertained to the relative role of bacterial processing of organic matter, which was much greater in the mid Bay than elsewhere in the Bay as well as in other coastal systems. The mid Bay macrobenthos was found to be degraded as compared to the other regions of the

Bay and similarly productive coastal systems. Benthic production was sufficient to support the demands of demersal predators, but with little surplus available. The macrobenthos outside the mid Bay and in the restored mid Bay was sufficient to support a much larger biomass of demersal predators than was present, possibly indicating overfishing.

Trophic transfer efficiency was estimated to average 30%, but was not a sensitive indicator of efficient trophic transfers to fish. Gross elemental transfer efficiencies and total contribution coefficients, analogous measures of transfer along particular trophic pathways, were more informative. A combination of informational indices that has been proposed as a quantitative definition of eutrophication also proved to be insensitive in practice to indicators of change and may be overly sensitive to investigator bias. Effective food web connectance is proposed as a useful indicator of a healthy estuarine ecosystem.

Introduction

Eutrophication, defined here as an increase in the rate of organic input (Nixon 1995), is a growing global problem in estuaries and coastal systems. One frequently observed consequence of eutrophication is habitat degradation and loss. In Chesapeake Bay, as in many other estuaries, loss of vegetated habitats (Orth and Moore 1984) and increased frequency, extent and impact of hypoxia and anoxia (e.g. Officer et al. 1984, Chapter 3, Chapter 5) are two major consequences of eutrophication. The combined effects of organic enrichment and habitat loss on the ecosystem are likely to be complex. For example, eutrophication could have direct

beneficial effects, whereas increased organic inputs increase production by food limited consumer organisms (i.e. secondary production). On the other hand, habitat degradation could change the absolute and relative magnitudes of the trophic transfers that collectively describe the "food web" of the estuarine ecosystem, potentially negating any direct beneficial effects of enrichment. An understanding of these food web effects is an important element of our understanding of ecological changes associated with eutrophication, particularly when we seek to describe the effects of eutrophication on fish and shellfish resources in estuaries.

Production of fish and shellfish is one of the important functions of estuarine ecosystems. In part due to their high primary productivity, estuaries contribute a much greater fraction of global fish production than would be expected from their surface area (Houde and Rutherford 1993). While Chesapeake Bay is no exception, degradation of critical habitats (e.g. SAV) and water quality raise the concern that fish production in the Bay could be threatened. Interestingly, even though some fisheries (e.g. American oyster, *Crassostrea virginica* and American shad *Alosa sapidissima*) have declined dramatically, total landings from Chesapeake Bay remain high, buoyed by substantial landings of blue crab and menhaden (Houde et al. 1999). Whether eutrophication has enabled total landings to be maintained in the face of large declines in landings of several historically important species is an important question. A similar question is whether a reversal of eutrophication via decreases in nutrient loading rates could have deleterious effects on fisheries in the Bay by decreasing prey abundance.

The concept of trophic transfer efficiency (TTE) is central to the questions introduced above. TTE is defined here as the fraction of organic matter consumed at one trophic level (gross production for primary producers) that is consumed at the next higher trophic level. For the i^{th} trophic level, this is $TTE_i = C_{i+1}/C_i$. Consumption at trophic level n can be expressed as $(C_2/C_1)(C_3/C_2)\ldots(C_n/C_{n-1})$, or equivalently as $TTE_1 \cdot TTE_2 \ldots TTE_n$. The average TTE for a series of trophic transfers is the geometric mean of the efficiencies at each trophic transfer, namely $\overline{TTE} = \left(\prod_{i=1}^{n} TTE_i \right)^{1/n}$. Trophic transfers over pathways of length n steps can therefore be computed as $C_{i+n} = C_i \cdot \overline{TTE}^n$, which is the same basic expression commonly used to predict potential fish yields for marine systems (e.g. Ryther 1969, Iverson 1990, Houde and Rutherford 1993). Accordingly, it is clear that a decrease in consumption at upper trophic levels, concurrent with an increase in organic inputs, entails either a decrease in average TTE or an increase in the number of trophic transfers. Conversely, maintaining or increasing secondary production while organic inputs decline requires either increased TTE or a lower average number of trophic levels. Recognizing that this latter possibility, a desired outcome of ecosystem restoration and management efforts (e.g. EPA 2000), implies changes in either food web structure (i.e. number of transfers) and/or increased average TTE, it is important to understand if such changes are likely, and if so, what specific changes are most likely involved.

This study examined TTE and food web structure by constructing and analyzing time-invarient, quantitative trophic flow networks. A time-invarient

modeling approach was selected rather than dynamic simulation models because the additional information provided by dynamic simulations was not needed to address the specific questions of interest. Equally important is the fact that the time-invarient modeling approach makes maximal use of the unprecedented data resources now available to examine Chesapeake Bay food webs. Baird and Ulanowicz (1989), introducing a landmark application of time-invarient trophic flow models to Chesapeake Bay, suggested that "more emphasis should be placed on new methods of interpreting the mass of data at hand." However, their work, which was based on data collected through the mid 1980's, largely preceded the 15-year accumulation of detailed biological and physical data by the Chesapeake Bay Monitoring Program. Their research effort also preceded 12 years of intensive investigation of the Chesapeake Bay ecosystem under the auspices of two 6-year NSF-sponsored Land-Margin Research Program (LMER) programs. The first LMER program, "Processes of Recycling, Organic Transformations and Exchanges between the Upland and the Sea" or PROTEUS, investigated primary production, nutrient cycling and major organic matter transformations, primarily involving the plankton and benthic microbiota. The second LMER program, "Trophic Interactions in Estuarine Systems," or TIES, focused on processes leading to secondary production in the plankton and nekton. Thus, the comments of Baird and Ulanowicz (1989) are even more apropos today.

Specifying and analyzing such time-invarient trophic flow networks has commonly been referred to as "network analysis." Network analysis provides a valuable framework for data synthesis and, once networks have been quantified, a

powerful suite of algorithms for analyzing them. The algorithms were principally developed and described by R. E. Ulanowicz and colleagues (Ulanowicz and Kemp 1979, Ulanowicz 1986, Szyrmer and Ulanowicz 1987, Ulanowicz and Puccia 1990) and were later embodied in software packages available from Ulanowicz (NETWRK, Ulanowicz 1999). Another software package, ECOPATH with ECOSIM, (Christensen and Pauly 1992, Christensen et al. 2000) was built on the basic model of Polovina (1984) and later incorporated some of the algorithms of NETWRK, plus many additional functions. The power of both the network analysis approach and the breadth of questions that can be addressed are underscored by the substantial impact of the first study to investigate Chesapeake Bay food webs using network analysis (Baird and Ulanowicz 1989). Although the goals of Baird and Ulanowicz (1989) differed from those of most interest here, the model structure that they described and their initial parameter estimates were a valuable point of departure.

Using the methods introduced above (see "Methods" for detailed description), this study examined change in TTE and food web structure associated with eutrophication. The ideal manner in which to do this would be to independently describe trophic flow networks as they changed with eutrophication over time. However, it was realistically possible to specify only a time-averaged network addressing the food web in recent years. This problem was addressed in two separate ways. First, because eutrophication has affected different regions of Chesapeake Bay to differing degrees and in different ways (i.e. phytoplankton biomass, Harding and Perry 1997; hypoxia, Chapter 3; macrobenthic biomass, Chapter 5) food webs in three regions of Chesapeake Bay were contrasted. Since the mid Bay is most dramatically

affected by increased hypoxia, this study contrasted the mid Bay food web with that of other regions of the Bay, hypothesizing that TTE would be lower in the mid Bay than in the other regions of the Bay. A second approach that was used to examine eutrophication-related changes in the food web was to develop an empirically-based description of a food web for a restored Chesapeake Bay. For brevity, this analysis was limited to the mid Bay. The analysis was based on available historical data and a series of specific "rules" derived from comparative ecological studies and mass balance and other constraints afforded by network analysis. As with the comparative approach, the hypothesis here was that the restored Bay network would show that despite lower primary production, secondary production could be maintained through higher average TTE.

Study Area and Scope of the Analysis

Chesapeake Bay is a large, partially mixed estuary on the mid-Atlantic coast of the United States. The spatial scope of research was limited to the mainstem Bay, excluding the major tributaries and major embayments such as Eastern Bay and Tangier Sound (Fig. 6-1). This choice reflects known ecological differences between the mainstem and corresponding salinity zones in these adjacent environments. Extending ~300 km from the head of the estuary at the Susquehanna River in Maryland to its mouth between the capes of Virginia, the mainstem Chesapeake Bay is commonly divided into three functionally distinct regions, the upper Bay, mid Bay and lower Bay. For the purposes of this study, the boundaries were determined by the segmentation scheme of the box model used to estimate physical transport among the

regions (Chapter 2). Surface areas of the respective regions are 472, 2338, and 2661 km^2 with mean depths of 4.4, 10, and 9 m. Bathymetric values were computed from data reported by Cronin and Pritchard (1975).

The summer season was examined because this is the time of the year when hypoxia, one of the major effects of eutrophication in Chesapeake Bay, is most developed (Chapter 2). Summer was defined as June 1 to August 31, which has a duration of 92 days. Carbon was selected as the currency for the model due to the fact that more information is available to describe exchanges involving carbon relative to other elements. Depending on the questions at hand, investigation of trophic exchanges of other elements such as nitrogen or phosphorus may also be appropriate (e.g. Ducklow 1983). One could also examine flows of energy rather than elemental flows. From this perspective, carbon flow approximates energy flow more than some other currencies (i.e. wet weight). Changes in energy content per unit carbon depend on the relative importance of carbohydrates, proteins and lipids. These changes were implied throught the carbon-specific assimilation and growth efficiencies.

Methods

Use of trophic network models requires explicit identification of the elements or nodes that comprise the food web. For this study, the food webs of the upper, mid and lower Bay were conceived to consist of 34 nodes (Fig. 6-2). These include 3 detrital pools, 4 types of primary producers, 9 planktonic consumers, 5 benthic consumers, and 13 nektonic consumers.

Network analysis requires estimates of all the flows between the nodes, the dissipation of carbon via respiration, and the net input minus export. The latter can occur equivalently in time (i.e. biomass accumulation or depletion), space (immigration or emigration), or due to harvest. For the i^{th} node these flows are constrained by the requirements that

$$C_i = P_i - R_i - U_i \tag{1}$$

and

$$EE_i = \frac{Y_i + E_i + BA_i + M2_i \cdot B_i}{P_i} \leq 1 \tag{2}$$

where the terms of which are defined in Table 6-1. The flow of carbon from node i to node j can be represented as T_{ij}. If the network has n nodes, The n x n matrix of T_{ij} describes all the internal flows in the network and is called the diet matrix. Network analysis also requires an estimate of the external flows, which can be specified as a input and outputs vectors, each with n elements. One approach to specifying the network, called inverse analysis, is to estimate some of the flows, then solve for the remaining subject to constraints (eq. 1, 2). Some elements of the diet matrix can be estimated using inverse analysis (e.g. Vézina 1989). It is also possible to estimate all the flows independently via the so-called *a priori* method (Field et al. 1989), in which all or nearly all the estimates are computed directly from field data or the published literature. This study used this latter approach.

Quantifying the Networks

The network models were quantified using a large volume of unpublished data, including all the data that comprise the different elements of the Chesapeake Bay Monitoring Program. In addition, ~180 published studies were utilized. Every effort was made to utilize research and data that pertain directly to the biota and ecosystem processes of Chesapeake Bay. As a result, all the unpublished data sources and 56% of the published studies pertained directly to Chesapeake Bay. The basic approach for computing the model inputs is described below. In the interest of brevity, the description omits many important details, including appropriate citations of data sources. Instead, all the citations for data sources are summarized in a Table (Table 6-2). A complete discussion is provided as a substantial appendix which makes appropriate reference to the sources of data, describes how they were used, what assumptions were made, and on what basis the assumptions were justified.

Publications from the widely available peer reviewed literature were used preferentially over other sources and account for the majority of references cited. Many of the unpublished data that were used were freely available to the public, often published via the Internet. For example, data were obtained from the web sites of the US Environmental Protection Agency's Chesapeake Bay Program, the US Geological Survey, and the National Oceanographic and Atmospheric Administration. Particularly useful for many computations related to finfish was the FishBase database (Froese and Pauly 2001).

Three detrital compartments in each region were dissolved organic carbon (DOC), suspended particulate organic carbon (POC) and sediment organic carbon

(Fig. 6-2). The abundance of DOC and POC was computed from Chesapeake Bay Water Quality Monitoring Program data. Allochthonous input of POC into the mainstem Bay was assumed to come only from the Susquehanna River and was computed from loading rates reported by the USGS. Inputs of DOC were computed from USGS estimates, plus contributions from major tributaries, which were computed as the product of average surface water concentration and net freshwater outflows. Transport of POC among the regions was assumed to be negligible, while transport of DOC was computed as the product of concentration and box model-estimated flows (Chapter 2). The flux of organic matter from the water column to sediments was not computed directly but was estimated as the unutilized fraction of aggregate flows to POC. Phytoplankton and bacterial biomass was subtracted from measured POC pool to compute the non-living detrial fraction of POC. Similarly, the biomass of bacteria and meiobenthos was subtracted from the total sediment organic carbon to estimate the non-living carbonbiomass in sediments.

Regional average rates of gross phytoplankton production were computed from studies that employed ^{14}C uptake and net oxygen evolution methods and were partitioned into net plankton and picoplankton as reported by size-fractionated production studies. Production of SAV was computed as the product of SAV coverage area and production rates of Chesapeake Bay SAV beds. SAV production was not utilized directly, but instead was directed entirely through sediment POC. Benthic microalgal production was computed from published estimates of light saturated benthic microalgal production and photosynthesis-irradiance relations.

Extrapolation to the whole system scale was accomplished via available estimates of light attenuation and bathymetry in each region.

The food web included three bacterial nodes, free-living, particle-attached, and benthic bacteria (Fig. 6-2). Biomass and production of free-living and particle attached bacteria in the plankton were obtained from published studies employing acridine-orange direct counts and radiolabeled thymidine uptake techniques. Benthic bacterial metabolism was computed by subtracting the metabolic rate of meiofauna from the total sediment flux measurement, which incorporated O_2 consumption and sulfate reduction. The biomass of benthic bacteria was estimated from respiration via assumed growth efficiency and biomass turnover rates.

The zooplankton community was divided into three components, the microplankton, mesozooplankton and gelatinous plankton. The microplankton community included heterotrophic microflagellates, ciliates, rotifers and meroplankton (Fig. 6-2). Biomass for these nodes was obtained primarily from literature sources, but also from the Chesapeake Bay Microzooplankton Monitoring Program when the methods employed were deemed adequate. Energetic rates were derived entirely from literature sources. The mesozooplankton, which were defined to include all life stages of copepods (nauplii, copepodid, adult) were described using data from the Micro- and Mesozooplankton components of the Chesapeake Bay Monitoring Program. Bioenergetic rates were derived from literature sources as reconciled with field data via an age-structured zooplankton production model. The gelatinous zooplankton community was represented as two nodes, ctenophores and sea nettles. The biomass of these organisms was derived from the Chesapeake Bay Monitoring Program

(ctenophores only) and from unpublished data collected by the TIES program (ctenophores and nettles). Diet and energetics were derived using literature data and the relevant *in situ* conditions for Chesapeake Bay (e.g. prey density).

The zoobenthos, other than bacteria, were represented by five nodes, the meiofauna, deposit-feeding benthos, suspension-feeding benthos, oysters and blue crab (Fig. 6-2). The biomass and energetics of meiofauna were estimated from published sources, except that biomass was assumed to be reduced in the anoxic regions of the mid Bay due to the exclusive presence of anaerobic meiofauna. The biomass and energetics of deposit-feeding and suspension-feeding benthos were derived from the Chesapeake Bay Benthic Monitoring Program data, except for the polychaete *Chaetopterus* as described in Chapter 5. After examining the available data, the biomass of oysters in Chesapeake Bay was found to be insignificant except in the tributaries. Blue crab biomass and bioenergetics were derived from published sources, which included a stock assessment based on fisheries methods. Fisheries removals from the mainstem Bay were estimated via fisheries landings data for the crab pot fishery only and migration of biomass, principally from the tributaries to fishing areas in the mainstem, was inferred by mass balance.

The fish community, like the zoobenthos, included a diverse assemblage and was generally represented as a collection of nodes for individual species, following the practice of most applications of network analysis (Fig. 6-2). An exception was the herrings and shads, an assemblage of anadromous species. The fish taxa that were included are bay anchovy, menhaden, herrings and shads, spot, croaker, hogchoker, American eel, catfish, white perch, striped bass, bluefish, and weakfish (Table 6-3).

The procedure for estimating the abundance, energetics and trophic relationships varied by species. The most detailed information was available for bay anchovy, the abundance and bioenergetics of which was computed via an age structured approach based on published studies. Adult abundance was obtained from published estimates based on egg production models. The biomass of menhaden was estimated from a published virtual population analysis and from Chesapeake Bay landings by the purse-seine fleet. The biomass and production of other species of fish was estimated via age-structured computations based on growth rates, natural and fishing mortality rates, predator demand, and commercial and recreational landings. Where possible, both the weight and size structure of landings were used to infer the age-structured exploitation rate, from which biomass was computed. The diets and bioenergetics of striped bass, bluefish, and weakfish were based on the published results of a detailed age-structured investigation for these species in the mid Bay. The estimated biomass and ecological role of fish in the Bay is most likely a minimum estimate due to the fact that an unknown number of less abundant or little studied species were not included in the model.

Balancing the Networks

The systematic estimation of biomass, bioenergetic rates and approximate diet composition provided a first estimate of the biomasses and flows comprising the trophic flow networks. Although these initial estimates were remarkably commensurable, some adjustments were needed to satisfy eq. (1) and eq. (2). The

initial estimates were entered into ECOPATH with ECOSIM software (Christensen et al. 2000), which provided an interactive platform for making the needed adjustments.

In most cases, the adjustments that were needed were to the diet composition. While the basic diet composition was often known *a priori*, the proportions contributed by each diet were usually not known exactly, if at all. Thus, these were adjusted in accordance with several conditions. First, the diet compositions must result in EE_i consistent with eq. (2). If $EE_i > 1$, then one can infer that one or more species must obtain a smaller fraction of its diet from the i^{th} node than originally estimated. Thus, diet compositions were modified in small increments from initial values, but within reasonable limits suggested by the available *a priori* data, until eq (2) was true for each node. In making adjustments, it was also assumed that EE_i close to zero was probably incorrect in most cases (the sea nettle is a counter-example). A transformed version of the Chesson (1983, cited in Christensen et al. 2000) forage ratio was also used to assist in making these adjustments. The forage ratio expresses the consumption of a particular prey relative to its availability in the environment. These values were examined to ensure that indicated prey preferences were consistent with expectation based on published accounts.

In a few cases (e.g. spot), eq. (2) was also used to derive minimum biomass estimates when other means for making such estimates were not sufficient. By assuming EE_i=1, BA_i=0, and E_i=0, and rearranging, one obtains $P_i = Y_i + M2_i \cdot B_i$. The quantity $M2_i \cdot B_i$ is the sum of all flows to predators, while P_i can be expressed as the product of the specific growth rate and biomass. Rearranging gives an estimate of

the minimum biomass required to balance combined fishing removals and predation losses.

Equation (2) also applies to detritus. Specifically, internal flows to detritus, plus external inputs and any net decrease in biomass, must equal or exceed utilization of detritus. Total flows to detritus associated with each node can be represented as $P_i(1-EE_i)+U_i$. Depending on the species in question and the means by which inputs were estimated, these flows can represent many different processes. For example, these could include egestion, excretion, partial consumption of prey (i.e. "sloppy-feeding", Moller and Nielsen 2001), pseudo-feces production, and mortality. The fraction of detritus production from each node allocated to each of the three detritus pools was specified based on an assessment of the most likely processes involved. As a default, it was assumed that unutilized DOC was exported, that unutilized POC was deposited to sediment POC, and that unutilized sediment POC was exported via burial. In practice these assumptions were not always consistent with mass balance constraints.

The "Restored Bay" Scenario

A trophic flow network was constructed to examine likely differences in carbon flow between the modern mid Bay and the mid Bay if it were restored to conditions approximating 1950-1965 by adjusting primary production rates. To ensure that the network was not arbitrary, it was constructed by following a series of consistently applied "rules" and assumptions:

1. Phytoplankton production is 50% less than present as suggested by historical chlorophyll-a concentrations (Harding and Perry 1997).
2. Submersed aquatic vegetation extends to the 2 m depth contour. Light attenuation was assumed to be reduced to permit this distribution based on known SAV/light relationships (Batiuk et al. 1992).
3. Production by microphytobenthos is a function of bathymetry and light penetration.
4. Macrobenthic biomass is consistent with estuaries having similar trophic status (i.e. organic inputs, Herman et al. 1999, Chapter 5).
5. Ratio of benthic to non-benthic metabolism consistent with other estuaries (Nixon 1982).
6. Planktonic bacterial uptake/net phytoplankton production consistent with lower Bay and other studies (e.g. Cole et al. 1988)
7. Subsequent changes were the minimum needed to satisfy eq. (1) and eq. (2), i.e. balance the network.

The same approach that was used to balance the trophic flow networks for the three regions of the modern Bay were used to balance the restored mid Bay network. This included maintaining diet compositions that are consistent with the literature and ensuring that diet electivities based on the Chesson (1983) forage ratio were reasonable.

Network Analysis

Balanced trophic flow networks for each of the three regions of the Bay were exported from ECOPATH into SCOR format (Ulanowicz 1999). For each network, the suite of outputs available in ECOPATH and NETWRK software were used to make inferences about the trophic flow networks. These specifically included apportionment of activity of omnivores to integer trophic levels (Ulanowicz and Kemp 1979, Ulanowicz 1995), quantification of mixed trophic impacts (Ulanowicz and Puccia 1990), evaluation of total trophic dependency (Szyrmer and Ulanowicz 1987), and computation of indices based on information theory, which describe the flow network overall (Ulanowicz 1986). Descriptions of many of the relevant procedures and equations and their appropriate interpretations are provided by Christensen et al. (2000), Kay et al. (1989), Baird and Ulanowicz (1989), and Ulanowicz (1986, 1997, 1999).

Numerical Precision and Rounding Errors

Some propagation of error due to rounding occurred as the result of conversions among rates, biomass specific rates, efficiencies, daily rates versus seasonal total rates, etc., as well as the exchange of data between ECOPATH and NETWRK. Rounding errors are revealed in small inconsistencies between some numbers that are presented.

Results and Discussion

The major results obtained directly by the process of parameterizing the networks include biomass and production estimates for each node (Table 6-4, Table 6-5), trophic flow (T_{ij}) matrices (Tables 6a,b,c), respiration (Table 6-7), and summer fishery landings (Table 6-8). Estimates of average trophic level and ecotrophic efficiency were obtained through network analysis (Table 6-5). A general description of the food webs in each of the three regions follows.

Upper Bay

The upper Bay region had a low rate of gross primary production (1487 mgC m^{-2} d^{-1}) compared to the other regions of the Bay (Table 6-5). Heterotrophic activity was subsidized by allochthonous inputs of organic matter, principally from the Susquehanna River, plus an import of sediment POC via depletion of detritus accumulated during spring, which was the larger of the two detrital sources. Primary production plus inputs of detritus totaled 1854 mgC m^{-2} d^{-1} (Fig. 6-3).

A substantial biomass of suspension-feeders, principally the introduced bivalve *Rangia cuneata*, consumed the largest fraction of both phytoplankton and particulate detritus; however, mesozooplankton, ciliates, and menhaden were also important herbivores, as in other regions of the Bay (Table 6-6a). Free-living bacteria consumed a large quantity of dissolved organic carbon (DOC) and were consumed themselves by heterotrophic microflagellates and microphagous ciliates. Ciliates consumed 67% of heterotrophic microflagellates (Table 6-5, Table 6-6a). The largest fraction of ciliate production was consumed by the mesozooplankton; however meroplankton, rotifers,

and even young-of-the-year bay anchovy also consumed ciliates. The average trophic level (TL) for mesozooplankton was 2.6, despite the fact that they obtained 63% of their diet at TL 2. The high TL estimate reflects consumption at TL 3, 4 and even 5 (22%, 7%, 7%, respectively) due to predation on ciliates and rotifers (Table 6-5, Table 6-6a). Bay anchovy consumed 70% of mesozooplankton production in the upper Bay and were the most important link between the zooplankton and nekton (Table 6-6a). Also important as links from the zooplankton to the nekton were the menhaden, and herrings and shads, which consumed an additional 17% of the mesozooplankton production. Menhaden, which were primarily phytoplanktivorous, were the largest and most efficient link from plankton to nekton, producing 53 $mgCm^{-2}d^{-1}$ (Table 6-5), about 2-fold greater than bay anchovy. Because of the zooplankton diet of bay anchovy, however, they required the equivalent of 6-fold more organic matter inputs. Ctenophores were a minor presence in the upper Bay, consuming only a small fraction of the mesozooplankton.

The suspension feeding benthos in the upper Bay consumed more organic matter than any other node. Principally through egestion, they also accounted for about half of the organic matter fluxed to upper Bay sediment POC. Accounting for the large removal of seston by benthic suspension-feeders required a significant flux of sediment POC back to suspended POC, which was assumed to occur via resuspension of sediments. Resuspension has been identified as a key mechanism in the sediment dynamics of the upper Bay in general and the estuarine turbidity maximum zone in particular (Sanford 1994). The upper Bay was the only region of the Bay where resuspension appeared to be important as a source of suspended POC.

The microphytobenthos contributed 6.3% of total primary production in the upper Bay and was most important for the meiofauna and the deposit feeding benthos. The upper Bay macrobenthos was consumed by an array of demersal feeding predators, which included hogchokers, blue crab and spot, which accounted for a combined 87% of predatory consumption of the benthos. Despite the high benthic production in the upper Bay, demersal feeding accounted for only 8% of trophic transfers to the nekton (20% excluding menhaden). This small fraction is reflected in the low ecotrophic efficiencies for the macrobenthos (Table 6-5), and may reflect the apparent resistance of larger individuals of the biomass dominant, *Rangia cuneata*, to predation by the blue crab and potentially other predators (Ebersole and Kennedy 1994). Overfishing may have reduced the biomass of American eels, which may at one time have exerted greater predation pressure on the upper Bay benthos. If not controlled by predation, the biomass of *Rangia* may be controlled in part by periodic mass mortality. For example, a major decrease in biomass occurred early in 1996, possibly associated with the record January flood, and biomass increased slowly in subsequent years (Chesapeake Bay Benthic Monitoring Program data).

Thirteen fish species (or groups), plus the blue crab, were included in the upper Bay network. Total fish production was 89 mgC m^{-2} d^{-1} (Table 6-5). Menhaden had the highest estimated biomass and production. After menhaden, bay anchovy were most productive, but the relatively slow-growing catfish had higher biomass (Table 6-4, Table 6-5). The most productive demersal feeder was the rapidly growing hogchoker. Of the three major piscivores included in the network, weakfish were estimated to be most productive, although the biomass of long-lived striped bass was

greatest. Commercial fishery landings in the upper Bay exceeded the recreational catch due to blue crab landings, which accounted for 83% of all summer landings (Table 6-8). Many finfishes are landed primarily in spring and fall rather than summer. Recreational fishing accounted for 64% of summer finfish landings. The dominant species in the catch were bluefish and catfish (Table 6-8).

Total respiration by the upper Bay food web averaged 1803 mgC m^{-2} d^{-1} (Table 6-7, Fig. 6-4), exceeding gross production by 318 mgC m^{-2} d^{-1}, or 21% (Table 6-7). Summertime net heterotrophy exceeded the estimated advective input of detritus from the Susquehanna River and was supported to a larger extent by sediment POC accumulated during spring and stored in sediments. Organic matter exports were dominated by emigrating menhaden (48 mgC m^{-2} d^{-1}). Other studies have estimated that, on an annual basis, a substantial quantity of organic carbon is buried in the upper Bay (Kemp et al. 1997). While this observation is not disputed here, this study found that the summer food web completely utilized the available carbon resources, leaving little surplus for burial. Other than to assume that carbon was not buried in summer, this discrepancy cannot be resolved here.

Mid Bay

Gross primary production in the mid Bay was the highest among the three regions, averaging 3515 mgC m^{-2} d^{-1} (Table 6-5). Phytoplankton production accounted for 93% of total production (Table 6-5). The accumulated sediment POC from spring (Fig. 6-3), which was estimated to be 27.8 gC m^{-2} (302 mgC m^{-2} d^{-1}), accounting for about half of total detritus inputs (Fig. 6-3). The remaining 298 mgC

m^{-2} d^{-1} was required to balance the carbon demands of the food web and was input to sediment POC from unknown sources (Fig. 6-3). Inputs at upper trophic levels were a small fraction of total inputs, about 9 mgC m^{-2} d^{-1}, and were obtained principally through depletion of macrobenthic biomass (i.e. input from spring). Such depletion of the benthos was not indicated outside the mid Bay, where seasonal changes in abundance were less pronounced (Chesapeake Bay Benthic Monitoring Program Data).

The most important herbivores were the ciliates and mesozooplankton, which each consumed about 17% of net primary production (Table 6-6b). As in the upper Bay, the mesozooplankton were mostly herbivores, obtaining 73% directly from phytoplankton (Table 6-6b). Only 12% of carbon flows to the mid Bay mesozooplankton passed through DOC (i.e. via the microbial loop), with the remainder obtained from phytoplankton through ciliates. The menhaden were the only substantial herbivore other than the zooplankton. About half of gross phytoplankton production in the mid Bay passed to detritus, either via excretion of DOC or as ungrazed net production (Table 6-5, Table 6-6b).

Despite the abundance of bay anchovy and ctenophores, the major consumers of mesozooplankton, 32% of the zooplankton production was not consumed by any predator (i.e. ecotrophic efficiency = 0.68, Table 6-5). To the extent that carbon flow alone supports such inference, this suggests that mesozooplankton were neither controlled by predators nor by food-limitation. An alternative hypothesis, consistent with the "foraging-arena theory" (Walters 2000) is that zooplankton occupied the lower water column to the extent permitted by hypoxia (Roman et al. 1993), perhaps

to avoid predation by bay anchovy, a visual predator (Luo et al. 1996). In doing so, they may have been food-limited, even as they left a considerable fraction of primary production ungrazed. Spatial and temporal heterogeneity may play a role in preventing effective herbivore control of primary production as well. For example, if a phytoplankton bloom developed on time scales shorter than generation times for the principal consumers, it might be underexploited. The existence of excessively large or otherwise unpalatable phytoplankton species could also result in ungrazed primary production.

Ctenophores were the second largest consumer of mesozooplankton in the mid Bay, behind bay anchovy. They consumed a quantity equal to 42% of consumption by bay anchovy (Table 6-6b). In this capacity they may divert a substantial flow of organic carbon away from piscivores production. Ctenophores were both a direct competitor for bay anchovy and a minor predator, consuming a small fraction of eggs. As a result, the adverse trophic impact on bay anchovy (Ulanowicz and Puccia 1990) was the largest effect arising from ctenophores and the second largest affecting bay anchovy (behind menhaden). Surprisingly, the reciprocal competitive effect of bay anchovy on ctenophores was approximately equal in magnitude to the effect of sea nettle predation. Thus, while sea nettles have high clearance rates for bay anchovy eggs and larvae (see Appendix), they were overall a beneficial predator (Ulanowicz and Puccia 1990) on bay anchovy. In their limited abundance in the mainstem Bay, they may serve a useful ecological function. Evidence for sea nettles as a beneficial ecological presence was provided by recent observations. Low salinity due to high river flow in 1996 limited reproduction of sea nettles (Purcell et al. 1999).

Concurrently, a massive bloom of ctenophores (6-fold more abundant than average; J. Purcell, unpublished data) developed in that summer; bay anchovy recruitment levels in that summer were the lowest recorded (North 2001, S. Jung, unpublished data).

The benthos of the mid Bay was depauperate compared to both the upper Bay and lower Bay, where biomass was >10-fold greater (Chapter 4). Despite low production by the benthos, production was sufficient to support the requirements of the demersal feeding fish and crabs. However, demersal predators consumed ~80% of benthic production, a much larger fraction than elsewhere in the Bay. This high ecotrophic efficiency suggests that predation may have a greater detremental effect on the benthos in the mid Bay, exacerbating the effects due to water quality (e.g. hypoxia). In fact, poor water quality may interact with predation pressure to enhance the vulnerability of the benthos to predation (Diaz et al. 1992).

The fish community of the mid Bay was similar to that of the upper Bay, except that biomass of low salinity species such as catfish, white perch and eel was reduced. Total fish production in the mid Bay was slightly higher than in the upper Bay, 93 mgC m^{-2} d^{-1}. As elsewhere, menhaden and bay anchovy accounted for most trophic transfers from plankton to the fish community, as well as most fish production. Other than these forage species, spot and croaker had the highest biomass and production, followed by blue crab. Blue crab accounted for 86% of summer landings from the mid Bay, reflecting the aggressive crab pot fishery (Table 6-8). Bluefish was second most important followed by weakfish, spot and croaker. A significant component of the already small landings of Menhaden by the pound net fishery in Maryland were assumed to be contributed by tributary landings. Therefore, these

landings were neglected. The striped bass fishery, an important fishery in the mid Bay, was closed during much of the study period, and remained closed during summer at least through 1994 (EPA 1994). Although the recreational fishery is now open in summer, striped bass production was assumed to accumulate during summer with no landings.

Total respiration for the mid Bay food web averaged 4049 mgC m^{-2} d^{-1}, the highest of the three regions (Fig. 6-4), exceeding gross primary production by 538 mgC m^{-2} d^{-1} (15%). The mid Bay was more heterotrophic than the upper Bay in absolute terms, but the deficit was smaller as a fraction of primary production.

Lower Bay

Lower bay primary production averaged 2,956 mgC m^{-2} d^{-1} (Table 6-5) of which 89% was due to phytoplankton production (Fig. 6-3). The lower Bay food web heavily utilized the available organic carbon, including the accumulated sediment POC left from spring (21 gC m^{-2}) and an approximately equal quantity of DOC which was required from unknown sources to balance the food web.

The most important herbivore in the lower Bay was the mesozooplankton, which consumed 14% of gross primary production (GPP). Ciliates consumed an additional 9% of GPP. As in the upper Bay, the suspension feeding benthos also consumed a substantial fraction, about 10% of GPP. Only 39% of GPP was not consumed directly by herbivores, which, accounting for algal respiration (~20%, Fig. 6-4) and excretion of DOC indicates that phytoplankton production in the lower Bay was nearly fully exploited.

Mesozooplankton biomass was higher in the lower Bay than elsewhere, although mesozooplankton P/B was estimated to be lower. Thus, both production of mesozooplankton and consumption by mesozooplankton was comparable to rates in the mid Bay. The average trophic level of mesozooplankton in the mid Bay was estimated to be 2.4, slightly lower than in the mid Bay and reflecting only a slightly decreased consumption of protozooplankton. As in the mid Bay, mesozooplankton production was not fully exploited by predators (Table 6-5). Bay anchovy consumed 35% of zooplankton production and was by far the largest consumer (Table 6-5, Table 6-6c). Ctenophores, which were less abundant in the lower Bay than in the mid Bay, consumed 13% of production, while cannibalism by mesozooplankton accounted for a similar fraction. Ecotrophic efficiency for lower Bay mesozooplankton was 62%, leaving a significant fraction of production unexploited (Table 6-5).

The macrobenthos of the lower Bay includes a diverse assemblage of taxa, dominated by polychaetes. The deep-burrowing tubicolous polychaete *Chaetopterus variopedatus* is the biomass-dominant among the suspension-feeders and accounts for about half of the macrobenthos (Chapter 4). While total macrobenthic biomass in the lower Bay was only 37% of upper Bay biomass, benthic production in the lower Bay was 65% of upper Bay rates due to the presence of more rapidly growing taxa in the lower Bay (Table 6-5). Predators consumed about 50% and 25% of deposit-feeder and suspension-feeder production in the lower Bay, respectively (Table 6-5). Although larger *Chaetopterus* are resistant to predation due to their deep burrows (L. Schaffner, personal communication), this low ecotrophic efficiency suggests that increased predation could be supported.

Fish production was estimated to be higher in the lower Bay than in the other regions. Eight of the most abundant fish species were included. As in the other regions of the Bay, menhaden and bay anchovy accounted for most (84%) of the total fish production. The purse-seine fishery in the lower Bay accounted for most of the fisheries landings in the lower Bay, and Bay-wide as well (Table 6-8). Spot, croaker and hogchokers were also productive, accounting for 75% of the remaining fish production (Table 6-5). The number of fish species represented in the lower Bay network is less than in the other regions, probably an artifact of data limitations. Therefore, the estimates of the role of the fish community here are minimum estimates (S. Jung, unpublished data)

Total respiration in the lower Bay was 3204 mgC m^{-2} d^{-1}, exceeding gross primary production by 247 mgC m^{-2} d^{-1} or 8% (Fig. 6-4). Of the three Bay regions, the lower Bay was the least heterotrophic during summer, in both absolute terms and as a fraction of primary production. Net heterotrophy was approximately balanced by detrital input due to the spring accumulation of sediment POC (Fig. 6-3). However, an additional net detrital input (DOC) of 61 mgC m^{-2} d^{-1} was needed from unknown sources to balance fisheries landings and biomass accumulation in fish.

Examining Eutrophication Effects

Given the primary description provided above, several means of analyzing the trophic flow networks were utilized to examine possible effects due to eutrophication. A hypothesis of this study was that compared to elsewhere in the Bay, the mid Bay trophic network would exhibit more substantial eutrophication effects. Specifically, it

was hypothesized that degradation of critical habitats via eutrophication decreased trophic transfer efficiencies, thereby limiting secondary production despite high rates of primary production. Trophic transfer efficiency is defined as the fraction of organic matter consumed at one trophic level (TL) that is subsequently consumed at the next TL. These efficiencies are difficult to examine in a food web, but can be readily computed by projecting the food web into a linear chain of canonical flows (Fig. 6-5a,b; Ulanowicz and Kemp 1979, Ulanowicz 1995, see also Baird and Ulanowicz 1989) and then combining primary production and detrital flows to produce a "Lindeman Spine" (Fig. 6-6). In order to combine these flows, it was necessary to extract the cyclic flow from primary producers directly to detritus (Fig. 6-6). Utilizing the algorithms of NETWRK, inflows due to immigrating biota were distributed over the canonical food chain according to apportioned activity at each trophic level. A similar allocation was applied for emigration, exploitation, other exports and respiration (Fig. 6-5a,b).

Trophic transfer efficiencies for TL 1 were ~85% in all three regions. This high efficiency reflects little more than the loss due to algal respiration from combined gross production and detritus flow. For trophic levels 2-5, efficiencies were 20-30%, not differing systematically with increasing trophic level or among the regions. Trophic transfer efficiency declined precipitously for trophic levels greater than 6, as illustrated by the retreat of flows at these levels below the log-linear decline in flows to trophic levels 1-5 (Fig. 6-7). Although one might assume that this reflects decreased growth efficiency and biomass of top predators (see Appendix, Table A-13), this is incorrect. The carbon flow at these high concatenations was principally due to

ctenophores, bay anchovy and sea nettles, which obtain a fraction of their diet via the microbial food web.

Average trophic efficiency over n trophic levels can be computed as the geometric mean (see Methods), namely $TTE_n = \left[\prod_{i=1}^{n} TTE_i\right]^{1/n}$, where TTE_i is the trophic transfer efficiency for the i^{th} trophic level. While n can be set to the highest canonical trophic level, which was 10 in the mid Bay, this appears to be arbitrary if presented as a property of the system. At n=8, the "average efficiency" is less than the true mean for almost all the trophic transfers that occur (Fig. 6-7). For the Chesapeake Bay, n=5 may be most relevant, since none of the taxa obtained more than 5% of their diet above this level. By this measure, the upper Bay was slightly more efficient than the other regions, with TTE_5=0.30 versus 0.27 for both the mid Bay and lower Bay. This efficiency is higher than the rule-of-thumb figure of 10% and is comparable to the higher rates suggested by Iverson (1990). While *TTE* is usually computed on the basis of internal flows only, this decreases *TTE* artificially when fisheries remove a large fraction of the production. Eliminating this artifact increased TTE the most for trophic levels higher than 5 where other flows were small, but did not have a significant effect otherwise.

Because the lower Bay fish community was probably under-represented, an alternative scenario was examined to see if this may have affected the trophic transfer efficiency estimates for the lower Bay. Fish biomass was artificially increased in three feeding guilds: planktivores, benthivores, and piscivores. Surprisingly, the effect on trophic transfer efficiency of even a dramatic increase in fish biomass was small, even

though the effect of this change on some other parameters was more substantial. For example, the ecotrophic efficiencies for mesozooplankton and the benthos were increased. These results suggest that far from a sensitive indicator of ecosystem performance, overall trophic transfer efficiency may be a biologically-regulated property that is more likely to be conserved, even across systems in which the structure of trophic flow differs.

Alternate Pathways of Trophic Transfer

In view of the apparent inconclusiveness of average trophic efficiency as an indicator of ecosystem performance and degradation, the trophic flow networks were used to contrast differences in the major pathways of trophic transfer among the regions. For such flows, the efficiency of transfer to a particular endpoint can be examined via the gross carbon transfer efficiency, which is simply the ratio of production at a particular endpoint to gross carbon input (i.e. gross production plus detrital imports). Here, substantial differences were found.

The most dramatic difference was the prevalence of bacterial processing of organic matter in the mid Bay. Bacterial respiration (i.e. dissipation by bacteria) in the mid Bay was 4-fold greater than in the upper Bay and 27% greater than in the lower Bay. Bacteria accounted for 76% of consumption at trophic level II in the mid Bay, compared to 33% and 61% in upper and lower Bay, respectively. Due to the high net growth efficiency of bacteria compared to most herbivores and detritivores, trophic transfer efficiency at TL 2 was 30% in the mid Bay compared to 20% elsewhere (Fig. 6-7). However, this did not translate to increased efficiency beyond TL 2 due to

inefficient transfer to mesozooplankton via the heterotrophic flagellates and microphagous ciliates (Table 6-5). Despite the enormous bacterial processing of organic matter in the mid Bay, the mesozooplankton there were estimated, using the total dependency matrix (Szyrmer and Ulanowicz 1987), to obtain only 12% of their diet via the microbial food web. The same analytical procedure reveals that the top predators such as striped bass, bluefish and weakfish obtained about 9% of their diets by pathways involving DOC and bacteria. While these values may seem large if one is accustomed to thinking of the microbial loop as primarily a "sink," they still represent an enormous amount of energetic dissipation. Moreover, energetic dissipation via the microbial loop occurs as high as the fourth trophic level, explaining why low average TTE was not a symptom of eutrophication in the mid Bay. As a final note, despite the smaller contribution of bacteria system activity in the upper and lower Bay, their contribution to upper trophic levels was similar or greater. In the upper Bay, pathways involving DOC accounted for 15% of carbon flow to mesozooplankton, more than in the mid Bay, while 12% of carbon flow to mesozooplankton in the lower Bay passed through DOC.

Trophic flow through the gelatinous zooplankton is another feature that, though not unique to the mid Bay, was most pronounced there and has been hypothesized to divert organic matter from pathways leading to fisheries production (Berdnikov et al. 1999). Ctenophores were the second largest consumer of mesozooplankton in the mid Bay, and their effect on their competitors, predators and prey has already been discussed. The relative rarity of ctenophores in the upper Bay most likely reflects a salinity effect, rather than a eutrophication effect. Because

ctenophore abundance in the lower Bay was 85% of the mid Bay abundance, their trophic impact there was estimated to be comparable. Thus, while it is clear that ctenophores divert carbon flow from bay anchovy and, to a lesser degree, from their predators, it is not clear that ctenophore abundance is enhanced significantly by hypoxia. Moreover, since mesozooplankton production was not fully consumed (Table 6-5) and Klebasco (1991) has noted that bay anchovy were not usually food limited, it is difficult to envision how the activity of ctenophores, at their average abundance, could substantially limit fish production. However, blooms of ctenophores have been identified around the world as a possible consequence of eutrophication. Their increase may reflect their enormous capacity to increase consumption when prey is very abundant, while their absence in less eutrophic environments could reflect their high prey density requirements (>8 l^{-1}, Kremer and Reeve 1989). Chesapeake Bay may have been spared the extreme *Mnemiopsis* abundances (300 m^{-3}) that have occurred in the Black Sea (Zaitsev 1992) because of the presence of sea nettles.

Carbon Flow Through The Benthos

The most dramatic difference between the regional food webs is in the role of the macrobenthos. Compared to the mid Bay, the upper and lower Bay macrobenthos consumed 30-fold and 10-fold more organic matter, respectively. Despite lower rates of primary production in these regions compared to the mid Bay, this level of macrobenthic production was easily accommodated and was in fact comparable to similarly productive coastal systems elsewhere (Herman et al. 1999, Chapter 4).

Except for menhaden, demersal feeding species contribute the bulk of fisheries

landings from Chesapeake Bay during summer (Table 6-8). In the upper Bay, blue crab was the largest fishery and along with American eel and catfish accounted for 67% of summer landings. Spot and croaker also contributed to fish production in the mid Bay. Along with the other demersal feeding species, they contributed 69% of mid Bay landings in summer. In the lower Bay, demersal feeding fish accounted for 78% of landings other than menhaden. The role of the benthos in supporting these demersal feeders is clear. For example, 78% of the diet of blue crab in the upper Bay passes along pathways involving the deposit and suspension feeding macrobenthos (Table 6-6a). Similar fractions apply for the other demersal feeders. Hartman and Brandt (1995a) noted that the major piscivores sustain much of their growth during fall, when they are voracious feeders on planktivores, mainly menhaden. In this regard, the major piscivores depend mainly on plankton. However, their summer diets include substantial fractions of spot and croaker (Hartman and Brandt 1995a), giving them a strong indirect dependence on the benthos. Their dependence on the benthos is especially apparent in June-July, before their diets begin to switch to more menhaden (Hartman and Brandt 1995a). As a result, 29%, 50% and 34% of trophic flows to striped bass, bluefish, and weakfish, respectively, passed through the macrobenthos.

Given the substantial dependence of fisheries on the highly degraded benthic community, it was surprising that the gross carbon transfer efficiency to fish in the mid Bay was only marginally lower there (0.019) compared to the other regions (0.047 and 0.028, Table 6-5). The small size of this difference reflects at least three factors. First, the Bay-wide abundance of bay anchovy and menhaden provides a link to the nekton that does not involve the benthos. Secondly, the population dynamics of

demersal feeders may not depend on the mid Bay environment because individuals migrate among regions as well as offshore. Finally, the diet of the demersal feeders is supported by the mid Bay benthos, but not with significant unused production. In fact, to maintain ecotrophic efficiency below unity, it was necessary to account for the decline in macrobenthic biomass during summer, a decline which was not evident outside the mid Bay region (Chesapeake Bay Benthic Monitoring Program Data). An increase in the abundance of demersal feeders, perhaps due to a particularly successful recruitment, would likely result in food limitation. Demersal feeders have already been estimated to be more abundant outside the mid Bay than within (Table 6-4). Based on the current degree of utilization of benthic production, one may infer that this pattern would be exacerbated to accommodate the demands of the diet if total biomass of demersal feeders increased.

The observation that degraded benthos may be a trophic bottleneck in the mid Bay does not hold elsewhere. In the upper Bay, ecotrophic efficiency for the deposit feeding benthos was only 34% (Table 6-5). Only 8% of suspension feeder production was consumed by predators, although some fraction may be invulnerable to predation. The same was true for the lower Bay. In order to exploit the lower Bay macrobenthos fully in a hypothetical scenario, it was necessary to increase the biomass of demersal feeding fish (assuming growth and energetics similar to spot and croaker) by 86%. Some of this additional fish biomass may be present, but was overlooked. Nonetheless, these results seem to suggest that while fish production in the mid Bay is limited by poor habitat quality and degraded macrobenthic communities, overfishing is the more likely culprit elsewhere in the Bay.

A Restored Middle Chesapeake Bay

In restoring an ecosystem, it is both informative and motivating to examine what the restored system might "look" like. In a limited way, we know exactly. For example, a series of aerial photographs of the area around Solomons Island, MD, dating as far back as the 1930's shows submerged aquatic vegetation (SAV) growing in an extensive bed out to several meters depth. These compelling photographs suggest that not long ago Chesapeake Bay was probably very different from the present. Hints of what the Bay was like at the time Europeans first arrived are provided by historical accounts, but it was assumed here that the so-called "John Smith" Bay was not only impossible to imagine with any certainty, but also irrelevant from the perspective of restoration. Rather, an attempt was made to describe the carbon flow networks for the Bay based on certain documented features of the Bay in the 1950s and early 1960's (i.e. SAV, algal biomass, hypoxia), but otherwise looking forward to ask not what the Bay was like, but what it might become. The questions are related, but the latter is both more relevant and, fortunately, less challenging.

The parameterization of the restored Bay network began with the the historical distribution of SAV, which has been inferred from pictures and accounts (e.g. Orth and Moore 1987). The true extent of historical SAV coverage is not known, but a conservative estimate is that at some time in past 50-years, SAV probably extended to 2 m depth. This encompasses about 10% of the mid Bay bottom area (Cronin and Pritchard 1975) and 7-fold more area than present SAV coverage. Since SAV requires about 20% of incident light to survive (Batiuk et al. 1992), one may infer that water

clarity in the Bay was once much greater than at present. To obtain 20% light at 2 m depth requires that light attenuation (k_d) in nearshore waters be 0.8 d^{-1}, or less. Since k_d in nearshore waters tends to be about 0.4 m^{-1} greater than in open water (W. M. Kemp, personal communication), k_d for open water might have been 0.4 m^{-1}, about 50% of the present mid Bay average (Harding et al. 2001). Given k_d=0.4, the maximum depth of the euphotic zone (1% of I_0) would be 11.5 m, sufficient to illuminate 60% of the mid Bay bottom. Perhaps as important, the pycnocline in much of the Bay would be within the euphotic zone, possibly altering the vertical distribution of phytoplankton (and oxygen) in the water column.

Historical data show that lower surface chlorophyll-a concentrations accounted for part of the apparently greater water clarity (Harding and Perry 1997). In the 1960's, the seasonal pattern of chlorophyll-a in the mid Bay featured a substantial spring phytoplankton bloom (as today), followed by summer chlorophyll-a reduced by about 50% compared to the present (Harding and Perry 1997). Phytoplankton production was probably also lower, although this need not be the case. As an initial suggestion, phytoplankton production might have been lower by 50% as well. An effort to apply a more sophisticated approach to estimating historical rates of primary production is planned (L. Harding, personal communication).

At the same time that historical accounts imply that Bay waters were clearer and that SAV beds were larger, fisheries outputs were evidently as large or larger than present (Houde et al. 1999). Fisheries outputs included oysters and soft-shelled clams, the landings of which have declined to relative insignificance in recent years (NOAA landings data, also see Appendix). The optimist might imagine a restored Bay

teeming with fish, similar to the exuberant descriptions of the early European arrivals. Realistically, this cannot be assured since it is difficult to separate pollution impacts from the effects of fishing and overfishing (Boreman 1997). Controversially, Jackson et al. (2001) noted that the first human impacts on ecosystems, and some of the most devastating, have been due to overfishing. The approach of this study was to examine how ecological changes associated with reversal of eutrophication might affect the prey resource and what possible fish production that might support. The question of whether the fish community would actually fully exploit the resource was left unanswered.

Specification of a trophic flow network for a "restored" mid Bay began with the estimated 50% reduction in phytoplankton biomass and production, noted above, and the expansion of SAV coverage to the 2 m depth contour. As the area of SAV expands to the 2 m depth contour, it would cover about 10% of the bottom. Therefore, the average biomass would be 13500 mgC m^{-2} and average production would be 122 mgC m^{-2} d^{-1}, a 7-fold increase from the present. While SAV may not grow in some areas due to factors other than light (Koch 2001, see also Orth and Moore 1984), this was neglected, assuming that SAV also grows to greater depth in some more favorable areas.

A change in light attenuation, as discussed above, from 0.8 m^{-1} to 0.4 m^{-1} would increase the light-dependent production rate of microphytobenthos. Asssuming unchanged light-saturated gross production, the average production would increase with the light field (Fig. 6-8) to 447 mgC m^{-2} d^{-1}, a 91% increase. Because benthic microalgae grow as epiphytes on SAV, the vegetated area was not assumed to lack

microphytobenthos. Thus, total gross primary production in the "restored" mid Bay would be 2212 mgC m^{-2} d^{-1}, 63% of the present day estimate. Benthic microalgal production would account for 20% of production, up from 6% in the modern mid Bay.

If the level of phytoplankton production approximates levels in the 1950's to 60's, one may suspect that hypoxia will be reduced as well (Chapter 3) allowing the benthos to increase to levels consistent with comparative ecological relationships (Herman et al. 1999, Chapter 5). Based on organic inputs, total macrobenthic biomass should be ~20 g AFDW m^{-2}, equivalent to 10,000 mgC m^{-2} or a 7-fold increase over the present. In most of the modern Bay, suspension-feeding biomass is 2-fold greater than deposit feeding biomass and it was assumed that this ratio would remain unchanged.

Without further changes in the food web, there was clearly insufficient organic matter to support consumption. Mass balance constraints, therefore, dictate that other flows would likely change as the Bay is restored. Again these changes were made in accordance with the predetermined procedure (see Methods). In the lower Chesapeake Bay, free-living bacteria consume 89% of net phytoplankton production, lower than the modern mid-Bay, but still higher than the average fraction consumed by bacteria in marine systems (Cole et al. 1988). Assuming that this fraction would apply to the restored mid Bay in summer, but that bacterial growth effiiciency also decreases from 0.5 to 0.4 (del Giorgio and Cole 1998), bacterial consumption of DOC would decrease to 50% of the present level, or 1425 mgC m^{-2} d^{-1}. Decreased free-bacterial production requires commensurate reduction in the production of heterotrophic flagellates, the primary bactivores. Assuming that ecotrophic efficiency

for free-bacteria is 90%, one can compute that the biomass of heterotrophic flagellates must decrease to 55 mgC m^{-2} d^{-1}. Although production by heterotrophic flagellates must decrease, the production remains sufficient to support the consumption by ciliates.

Decreased phytoplankton production also limits herbivory (i.e. not just detritivory). If one assumes that menhaden consumption is unchanged and that suspension-feeding increases as stipulated, consumption by other herbivores must be decreased. Meroplankton might be expected to increase in abundance, rather than decrease, due to the increased abundance of macrobenthos (Table 6-9). Of the two remaining planktonic herbivores, it was assumed that ciliate biomass would decrease. Accordingly the mesozooplankton must shift their diet slightly from ciliates to phytoplankton. These adjustments achieve balanced carbon flows within the plankton. While the exact changes are somewhat speculative, it is clear that a decrease in phytoplankton production and the associated decrease in bacterial productivity require a cascade of reductions in the role of the microplankton (Cole et al. 1988).

The benthos can also be expected to change as a result of decreased primary production, as is commonly seen on an interannual basis in response to river flow variations (Boynton and Kemp 2000). Nixon (1982) observed that across systems with a wide range of total organic input, total benthic mineralization consumed a nearly constant proportion of the input, about 24%. Nixon's (1982) relationship approximates the modern condition the upper and lower Chesapeake Bay with remarkable, perhaps serendipitous, precision (within 5% error). However, the benthos in the present-day mid Bay consumes about 25% less than predicted (Table 6-5, Table

6-7). This may reflect the minimal suspension-feeding activity in the mid Bay compared to other regions of the Bay, perhaps due to anoxia and/or the near elimination of oysters by overfishing and parasitic diseases. In a restored mid Bay, respiration due to meiofauna and macrobenthos (based on Herman et al. 1999 model) was estimated to total 254 mgC m^{-2} d^{-1}, slightly less than half of the total metabolism predicted by the Nixon (1982) model. Thus, benthic bacterial metabolism might be as low as 277 mgC m^{-2} d^{-1}. Although this is 35% of the present rate, it may not be unreasonably low, as bacterial metabolism in the modern upper Bay was even less than this reduced value.

Remarkably, no additional changes were needed to bring the carbon budget of the mid Bay into approximate balance, despite the significant decrease in phytoplankton production (Table 6-9). The exception was that the supply of dissolved organic carbon was deficient by 12%, even as some sediment POC was exported by burial (see later discussion). This does not imply that no other changes would or could occur. However, this exercise showed how it is possible to support the upper trophic levels of the mid Chesapeake Bay food web with a significantly decreased level of primary production, without departing from widely observed relationships among the components of the lower food web. Moreover, decreased primary production was clearly commensurable with even a dramatic increase in the biomass and production of macrobenthos.

The increased macrobenthos production provides an increased prey resource for demersal fish. Since the macrobenthic biomass increased 7-fold, the prey resource and biomass that can be supported in the mid Bay increases commensurately. As

previously noted, it is difficult to imagine what form such an increase might take, or if it would occur at all. however, since it is contrary to the propensities of ecosystems to leave a substantial and available prey resource unutilized, production of demersal feeding fish such as spot and croaker could increase. In addition, or perhaps alternatively, production of non-targeted competitors such as hogchokers or skates and rays (e.g. cownose ray, *Rhinoptera bonasus*), already present in the Bay, could increase.

Because the "restored" Bay is a hypothetical construct, caution is needed in interpreting analyses of the network. Without resorting to complex computations, some major conclusions can be reached simply because it has been shown that the network can exist in balance, without resorting to unreasonable assumptions. For example, if fish production does not decrease, but primary production decreases, then the gross transfer efficiency to fish is greater. If benthic macrofauna increase in biomass and production, at the expense of plankton and benthic bacteria, then the role of bacteria is reduced. Oddly, but consistent with regional differences noted before, decreased bacterial production in the water column did not decrease the relative importance of the microbial loop as a link to upper trophic levels. The fraction of carbon flow passing through DOC to the mesozooplankton increased from 0.12 in the modern mid Bay, to 0.15 in the restored Bay. This increase reflects an assumed shift in the diet of ciliates, due to decreased phytoplankton abundance, toward more consumption of heterotrophic flagellates. Thus, the accuracy of conclusions regarding the role of the microbial loop hinges on the validity of that assumption.

The average trophic transfer efficiency, computed from the "Lindeman Spine" for the restored mid Bay, was greater than for the modern mid Bay (Fig. 6-9). For example, average efficiency for trophic levels (TL) 1-5 was 27% in the modern mid Bay and 32% in the restored mid Bay (Fig. 6-9). The increased efficiency was a surprising result considering the apparent lack of differences in average trophic transfer efficiency among the upper, mid and lower Bay. The differences could be traced mainly to a few changes in the flows among the plankton. The trophic transfer efficiency for TL 2 was lower in the restored Bay, reflecting the decreased activity of the highly efficient bacteria. On the other hand, the efficiencies for TL 2-5 increased due to increased ecotrophic efficiencies for heterotrophic microflagellates and ciliates (Table 6-9). These changes were responsible for both the increased dependency of the mesozooplankton on DOC and the increased average efficiency for the canonical food chain (Fig. 6-9). Nonetheless, because of the relative uncertainty of the trophic transfers among the microplankton, other measures of the response to eutrophication may be more compelling.

As with the inter-regional comparisons, the fraction of primary production passed to desired endpoints in the food web revealed the most substantial differences, as qualitatively described above. The matrix of total contribution coefficiency, a basic output of NETWRK, describes this quantitatively. In the modern mid Bay food web, 0.125% of the production by net phytoplankton was passed to striped bass, while in the restored network, 0.237% eventually reached striped bass (Fig. 6-10). Although picoplankton production reached striped bass with lower efficiency than for net phytoplankton, the efficiency of contribution to striped bass increased similarly in the

restored Bay network. Conversely, benthic bacteria (for example), consumed a smaller fraction of production from all sources. Interestingly, the fraction of SAV production reaching striped bass increased, while the fraction of microphytobenthos reaching striped bass decreased. This reflects increased meiobenthic consumption of microphytobenthos in the restored Bay, which effectively added an intermediate trophic transfer slightly and decreased the overall efficiency. Despite decreased efficiency, the total flow from microphytobenthos to striped bass along all paths increased from 24 to 39 mgC summer^{-1}.

This analysis shows that reasonable adjustments to the modern food web of the mid Chesapeake Bay permit sustained or even increased fish production, even as phytoplankton production decreases by 50%. Although the network description for the restored Bay was not based entirely on direct observation, it was based on sound relationships which have been observed to hold for coastal ecosystems around the world. The networks also conform to the mass balance constraints imposed by a network analysis approach (e.g. Nixon 1982, Cole et al. 1988). In retrospect, it might have been far more challenging to correctly envision what might happen to a system like the restored Bay if phytoplankton production were doubled and the system departed from the norm. Indeed, the food web of the modern mid Bay, in devoting such a large fraction of production to bacteria, has become extraordinary among its peers.

Informational Indicators of Eutrophication

Interest has been growing in recent years of developing objective indicators of ecosystem status and health. Toward that end, Ulanowicz (1997) defined eutrophication in terms of a series of indices, each based on information theory, which describe aspects of a trophic flow network in its entirety (Ulanowicz 1986). Total system throughput (TST) is the sum of all the flows and effectively measures ecosystem size. Average mutual information (AMI) defines the "determinacy" of the flows. To use an analogy from baseball, the flow of base runners has a high AMI. In contrast, should the runners choose to run among the bases not in order, but at random, AMI would be low. The product of AMI and TST defines "ascendency." (Ulanowicz 1986, 1997). Ulanowicz (1997) defined eutrophication in terms of these information indices: an increase in system ascendancy, due to a rise in total systems throughput that more than compensates for a concomitant fall in average mutual information.

Analysis of the four networks constructed for Chesapeake Bay provided a natural test for this definition. TST was indeed found to be much greater in the modern mid Bay ($1.5\ 10^6$ mgC m^{-2} $summer^{-1}$) compared to either the restored mid Bay ($1.1\ 10^6$ mgC m^{-2} $summer^{-1}$) or other regions of the Bay. Similarly, AMI was lower in the modern mid Bay (2.06) compared to the restored network (2.08). While the index technically passes the test, the difference is not compelling. The similarity of the estimates may reflect the largely unchanged topology of the two networks, which may be biased by the perceptions, knowledge or even goals of the investigator. For example, Monaco and Ulanowicz (1997) compared Chesapeake Bay (annual, not summer), Delaware Bay and Narragansett Bay, finding the AMI for these three

systems was 1.2, 1.3 and 1.3, respectively. Johnson et al. (1995) compared coral dominated and algae dominated regions of the Great Barrier Reef, Australia, observing that AMI was 1.877 and 1.878. Even when systems as different as a coral-dominated vs. algal-dominated reefs and Chesapeake Bay vs. Narragansett Bay are included, most differences in AMI can be related to the investigator.

Given the constraints of investigator bias, connectance may be a more useful indicator of change. Topologically connectance refers to the average number of connections involving a node. Social network scientists refer to the number of nodes flowing into a node as the "in degree" and the number of emerging connections as the "out degree." All the Chesapeake Bay networks were similar, having effective topological connectance of ~4 connections per node. Effective connectance decreases relative to topological connectance as a smaller number of flows come to dominate throughput. "Food web connectance," which examines only flows involving living compartments, varied in Chesapeake Bay from 1.89 in the mid Bay to 2.34 in the restored mid Bay. The upper Bay (2.26) and lower Bay (2.31) food webs varied between the two mid Bay scenarios. The differences most likely reflect the greater degree of balance among the different sources of organic matter as well as the fates. Whereas 68% of throughput involving living nodes in the modern mid Bay could be attributed to phytoplankton and bacteria, this figure was reduced to 53% in the restored mid Bay. Although connectance does not reveal changes in TST, which are clearly characteristic of eutrophication, it may be more sensitive than AMI to quantitative changes in flows when the network topology is fixed, by investigator bias or otherwise.

Research Issues and Needs

One of the often noted ancillary benefits of synthesis research is that it may reveal weaknesses or inconsistencies in the base of scientific knowledge, suggesting directions for future research. In assembling the trophic networks for Chesapeake Bay, quantifying the role of the free-living bacteria and especially the sources of the DOC that they require was a constant source of consternation. Consistent with the findings of Baines and Pace (1991), extracellular release of DOC by phytoplankton could not reasonably support the DOC requirements of the bacteria. The advective flux of DOC through the estuary was very large, and recent research indicates that this pool is not entireely recalcitrant (Raymond and Bauer 2000). However, advective inputs cannot reasonably provide the DOC required by the mainstem food web because the estuary appears to export as much DOC, or more, than it imports (Appendix A). To account for the required input to bacteria, DOC was assumed to be released as part of the egesta from almost every trophic interaction. Although this may in fact be reasonable, the sources and fate of detritus within the network was a major source of uncertainty. While organic matter cycling was not a major focus of this study, the nature of cycling was computed by NETWRK and was found here to be profoundly different than seggested by Baird and Ulanowiocz (1989). This difference may have resulted primarily from the fate of detritus, including flows among the detrital pools. Thus, continued study of bacterial metabolism and the sources and fate of detritus, in its various forms, would be warranted and helpful.

Trophic interactions within the microplankton were another source of significant uncertainty. While studies addressing trophic interactions involving the microplankton of Chesapeake Bay were not lacking, the emergent message was that many trophic interactions are possible and that, moreover, heretofore unappreciated interactions may not only occur, they may be important. These studies would be more useful for constructing trophic flow models if, in addition to addressing novel interactions, they also addressed where and under what circumstances different types of interactions were more or less prevalent. Such results would be useful for future food web models.

The data available to characterize the fish community, though more plentiful than expected, were often frustratingly disconnected, perhaps reflecting the multiple objectives of studies addressing fisheries. Frustratingly, it often appeared that the data needed for network analysis were present somewhere, perhaps collected for tactical fisheries management, but were never organized sufficiently to be utilized for research purposes. Therefore, enhanced integration of fisheries data into a broadly accessible databases would be very valuable. Fish may also be valuable integrators of ecosystem function. This study relied on many published studies of fish growth and diet, often accessed via FishBase (Froese and Pauly 2001). While extremely valuable, local studies would be valuable in assessing how fish utilize the resources within the ecosystem of interest. Given the difficulty of estimating absolute abundance of fish, diet requirements of better known and exploited predators proved to be a useful means of estimating the abundances of their prey.

Finally, additional work is needed to address seasonal and interannual variation. This study examined a long term average for summer only. It would be very valuable to expand this analysis to include coupled seasonal and regional models. Seasonal comparisons should be made similar to the analyses of Baird and Ulanowicz (1989), but the models should explicitly account for seasonal changes in biomass such that biomass is at steady state only on an annual basis. Significant interannual variations are known to occur in primary production as well as fish biomass and production. This food web described by this study is composite of many years, providing a useful baseline scenario based on the best data available. However, additional and possibly important insights could probably be gained by addressing alternative food web configurations associated with natural variability.

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Table 6-1. Definitions of parameters in equations.

Parameter	Definition	Units
B_i	Average biomass	mgC m^{-2}
C_i	Consumption	mgC m^{-2} d^{-1}
P_i	Production	mgC m^{-2} d^{-1}
R_i	Respiration	mgC m^{-2} d^{-1}
U_i	Unassimilation = Egestion plus Excretion	mgC m^{-2} d^{-1}
T_{ij}	Trophic transfer from i^{th} to j^{th} node	mgC m^{-2} d^{-1}
I_i	Immigration or importation of biomass	mgC m^{-2} d^{-1}
E_i	Net Emigration minus Immigration, or net export of biomass via advection or other process.	mgC m^{-2} d^{-1}
Y_i	Fisheries removals of biomass from i^{th} node	mgC m^{-2} d^{-1}
BA_i	Accumulation or depletion of biomass	mgC m^{-2} d^{-1}
$M2_i$	Biomass specific mortality rate due to predation.	d^{-1}
EE_i	Ecotrophic efficiency (defined in eq. 2)	unitless

Table 6-2. Sources of published and unpublished data for defining the trophic flow networks.

Node	References
DOC and POC	Schubel and Carter (1977), Biggs and Howell (1984), Hobbs et al. (1992), Chapter 1, Chapter 3, Chapter 4
Phytoplankton	Tang and Peters (1995), Baines and Pace (1991), Malone et al. (1991), Kemp et al. (1997), Smith (2000), Harding et al. (2001), Smith and Kemp (2001)
Microphytobenthos	Jassby and Platt (1976), Rizzo and Wetzel (1985), Macintyre et al. (1996), Miller et al. (1996), Boynton et al. (1999), Kemp et al. (1999), Harding et al. (2001)
Vascular Plants	Wetzel and Penhale (1983), Kemp et al. (1984), Kemp et al. (1986), Orth and Moore (1986), Orth et al. (1997), Duarte and Chiscano (1999).
Bacteria	Ducklow and Shiah (1993), Shiah and Ducklow (1994), del Giorgio and Cole (1998), Smith (1998), Choi et al. (1999), Smith (2000), Raymond and Bauer (2000)
Protozoa and Microzooplankton	Loftus et al. (1972), Fenchel (1982), Linley et al. (1983), Stemberger and Gilbert (1985), Verity (1985, 1991), Børsheim and Bratbak (1987), Heibokel et al. (1988), Dolan and Coats (1990), Dolan (1991a,b), Dolan and Gallegos (1991), Ducklow (1991), McManus (1991), Gaedke and Straile (1994), EPA (2000), Gifford and Caron (2000), EPA Chesapeake Bay Monitoring Program Data.
Mesozooplankton	Heinle (1966), Kiørboe et al. (1985), Kimmerer (1987), Berggreen et al. (1988), White and Roman (1992), Kiørboe and Nielsen (1994), Roman et al. (2001), Chesaepake Bay Microzooplankton and Mesozooplankton Monitoring Programs

Table 6-2 (continued).

Node	References
Gelatinous Zooplanton	Larson (1986), Kremer and Reeve (1989), Reeve et al. (1989), Nemazie (1991), Purcell (1992), Purcell and Nemazie (1992), Purcell et al. (1994, 1999, 2001), Houde et al. (1994), Purcell and Cowan (1995), J. Purcell, personal communication, EPA Chesapeake Bay Zooplankton Monitoring Program.
Benthic Bacteria	Cowan and Boynton (1996), Kemp et al. (1997), Marvin-DiPasquale and Capone (1998)
Meiobenthos	Gerlach (1971), Fenchel (1978), Banse and Mosher (1980), Schroeder (1981), Widbom (1984), Smol et al. (1994), Montagna et al. (1995), Sundbäck et al. (1996), Flach et al. (1999), Carlsen et al. (2000).
Macrobenthos	Sagasti et al. (2000), Chesapeake Bay Benthic Monitoring Program Data, Chapter 3.
Oysters	Newell (1988), Hargis and Haven (1994), Jordan et al. (1994), Rothschild et al. (1994), Tarnowski et al. (1994), Smith (2001)
Blue crab	Miller (1975), Virnstein (1977), Schroeder (1981), Laughlin (1982), Hines et al. (1990), Ebersole and Kennedy (1994), Prager (1996), EPA (1997), Ricciardi and Bourget (1998), Rugolo et al. (1998), Ju et al. (1999), NOAA Landings Data
Bay anchovy	Schroeder (1981), Tucker (1989), Klebasco (1991), Luo and Brandt (1993), Wang and Houde (1994), Wang and Houde (1995), Rilling and Houde (1999a, b), Jung and Houde (2000), Kimura et al. (2000).
Menhaden	Durbin and Durbin (1981), Friedland et al. (1989), Luo et al. (2001), Vaughn et al. (2001), NOAA Landings Data
Herrings and Shads	Schroeder (1981), Hoenig (1983), EPA (1989), Froese and Pauly (2001), S. Jung, unpublished data, NOAA Landings Data

Table 6-2 (continued).

Node	References
Striped Bass	Hollis (1952), Mansueti (1961), EPA (1994, 1995), Hartman and Brandt (1995a, b,c), Froese and Pauly (2001), NOAA Landings Data
Bluefish	EPA (1990), Barger (1990), Hartman and Brandt (1995a, b,c), Froese and Pauly (2001), NOAA Landings Data
Weakfish	Hoenig (1983), EPA (1990b), , Hartman and Brandt (1995a,b,c), S. Jung, unpublished data, NOAA Landings Data
Atlantic Croaker and Spot	Pacheco (1962), Schroeder (1981), Hoenig (1983), Ross (1988), EPA (1991), Froese and Pauly (2001), S. Jung, unpublished data, NOAA Landings Data
White Perch	Mansueti (1961), St. Pierre and Davis (1972), Schroeder (1981), Sadzinski et al. (1999), Webb and Zlokovitz (1999), Froese and Pauly (2001)
Catfish	Hoenig (1983), Poe et al. (1991), Sadzinski et al. (1999), Froese and Pauly (2001), S. Jung, personal communcation, NOAA Landings Data
Hogchoker	Dovel et al. (1969), Peters and Boyd (1972), Derrick and Kennedy (1997), S. Jung, unpublished data
American eel	Wenner and Musick (1975), EPA (1991b), Froese and Pauly (2001), S. Jung, unpublished data

Table 6-3. Scientific names of species or groups of species referred to in the text. UB=upper Bay, MB=mid Bay, LB=lower Bay

Common Name or Description	Scientific Name(s) of Taxa or Most Abundant Taxa
Mesozooplankton	*Acartia tonsa, Eurytemora affinis*(UB, MB), *Bosmina longirostris* (UB)
Suspension-feeders	*Rangia cuneata* (UB), *Mya arenaria* (soft-shelled clam, MB), *Mulinia lateralis* (MB), *Macoma balthica* (UB,MB), *Chaetopterus variopedatus* (LB)
Deposit feeders	*Nereis succinea, Macroclymene zonalis* (LB)
Ctenophores	*Mnemiopsis leidyi, Beroe ovata* (LB)
Sea nettle	*Chrysaora quinquecirrha*
Oyster	*Crassostrea virginica*
Blue crab	*Callinectes sapidus*
Bay anchovy	*Anchoa mitchilli*
Menhaden	*Brevoortia tyrannus*
Herrings and Shads	*Alosa* spp., *Dorosoma* spp.
Spot	*Leiostomus xanthurus*
Croaker	*Micropogonias undulatus*
Hogchoker	*Trinectes maculatus*
American eel	*Anguilla rostrata*
White perch	*Morone americana*
Channel catfish	*Ictalurus puctatus*
Striped bass	*Morone saxatilis*
Bluefish	*Pomatomus saltatrix*
Weakfish	*Cynoscion regalis*

Table 6-4. Estimated biomass (mgC m^{-2}) for each node in the summer trophic flow networks for the upper, mid and lower Chesapeake Bay. Below, biomass composition summarized by major groupings. The table is continued on the next page.

Node	Description	Upper Bay	Mid Bay	Lower Bay
1	Net Phytoplankton	1356	3326	2112
2	Picoplankton	239	587	373
3	Free Bacteria	649	2415	1258
4	PA Bacteria	36	73	39
5	Heteroflagellates	30	149	43
6	Ciliates	66	147	87
7	Rotifers	14	23	0
8	Meroplankton	3.2	18	38
9	Mesozooplankton	282	526	1073
10	Ctenophores	17	126	108
11	Chrysaora	0	6.3	0
12	μ-phytobenthos	293	265	293
13	SAV	2086	1952	1986
14	Benthic Bacteria	30	298	220
15	Meiobenthos	700	494	700
16	DF Benthos	2368	1030	4089
17	SF Benthos	27232	421	6962
18	Oyster	0	0	0

Table 6-4. (Continued)

Node	Description	Upper Bay	Mid Bay	Lower Bay
19	Blue Crab	610	390	342
20	Menhaden	2136	2136	2136
21	Bay anchovy	287	381	381
22	Herrings/Shads	212	0	0
23	White Perch	282	29	0
24	Spot	195	222	570
25	Croaker	50	226	236
26	Hogchoker	100	50	100
27	American eel	35	9.0	0
28	Catfish	450	45	0
29	Striped Bass	172	172	172
30	Bluefish	68	68	68
31	Weakfish	67	67	211
32	DOC	12504	28207	26915
33	Sediment POC	201670	201607	76080
34	POC	5249	10324	8309
Living Biomass		40065	15651	23597
susp POC+DOC		17753	38531	35224
Primary Producers		3974	6130	4764
Bacteria		715	2786	1517
Zooplankton		412	995	1349
Benthos		30300	1945	11751
Fish and Crabs		4664	3795	4216

Table 6-5. Estimated trophic level (TL), production (P, mgC m^{-2} d^{-1}) and ecotrophic efficiency (EE) for each node in each region of the Bay. Production by primary producers is net primary production (i.e. production minus respiration). Total gross primary production for each region is indicated at the bottom of the table. The ratio of total production in several groupings of nodes to total organic input (O.I.) to each region is shown at the bottom. The table is continued on the next page.

		Upper Bay			Mid Bay			Lower Bay		
	Description	TL	P	EE	TL	P	EE	TL	P	EE
1	Net Phytoplank	1.0	719	99	1.0	1962	0.47	1.0	1704	0.61
2	Picoplankton	1.0	186	63	1.0	511	0.36	1.0	426	0.36
3	Free Bacteria	2.0	350	100	2.0	1425	0.94	2.0	742	0.66
4	PA Bacteria	2.0	28	80	2.0	82	0.02	2.0	41	0.60
5	Heteroflagellates	3.0	99	67	3.0	417	0.35	3.0	142	0.61
6	Ciliates	2.6	165	59	2.6	366	0.48	2.6	218	0.79
7	Rotifers	2.3	4.2	54	2.4	6.9	0.56	2.4	0.0	0.00
8	Meroplankton	2.6	1.6	64	2.5	9.0	0.89	2.4	19.0	0.73
9	Mesozooplankton	2.6	107	99	2.5	263	0.68	2.4	268	0.62
10	Ctenophores	3.6	2.4	0	3.5	16.4	0.22	3.4	14.0	0.00
11	Chrysaora	4.6		0	4.4	0	0.00			0.00
12	µphytobenthos	1.0	176	67	1.0	159	0.48	1.0	234	0.66
13	SAV	1.0	17	0	1.0	18	0.00	1.0	18	0.00
14	Benthic Bacteria	2.0	34	72	2.0	337	0.12	2.0	249	0.37
15	Meiobenthos	2.1	49	63	2.3	35	0.70	2.3	49	0.95
16	DF Benthos	2.4	19	34	2.5	14	0.76	2.3	57	0.49
17	SF Benthos	2.0	218	8	2.1	6	0.86	2.1	97	0.24
18	Oyster			0			0.00			0.00
19	Blue Crab	3.1	2.4	78	3.2	1.6	0.98	3.0	1.4	0.85

Table 6-5. (Continued).

		Upper Bay			Mid Bay			Lower Bay		
	Description	TL	P	EE	TL	P	EE	TL	P	EE
20	Menhaden	2.1	53	97	2.1	53	0.97	2.1	53	0.74
21	Bay anchovy	3.6	23	41	3.4	31	0.34	3.4	31	0.32
22	Harrings/Shads	3.6	2.1	88			0.00			0.00
23	White Perch	3.4	0.6	88	3.4	0.1	0.17			0.00
24	Spot	3.1	2.0	96	3.2	2.2	1.00	3.2	5.7	0.98
25	Croaker	3.1	0.5	48	3.2	2.3	1.00	3.2	2.4	1.00
26	Hogchoker	3.1	2.5	13	3.2	1.3	0.00	3.2	4.0	0.00
27	American eel	3.1	0.1	99	3.3	0.0	0.99			
28	Catfish	3.2	0.5	37	3.3	0.0	0.38			0.00
29	Striped Bass	3.6	0.3	78	3.6	0.3	0.78	3.5	0.3	0.78
30	Bluefish	4.1	0.5	44	4.2	0.5	0.44	4.2	0.5	0.49
31	Weakfish	4.0	0.6	78	3.9	0.6	0.78	3.6	1.9	0.78
32	DOC	1.0		99	1.0		1.00	1.0		1.00
33	Sediment POC	1.0		49	1.0		0.99	1.0		0.91
34	POC	1.0		101	1.0		0.17	1.0		0.65
	Gross Primary Prod.		1487			3515			2956	
	Detritus Input		367			600			426	
	Bacterial P/O.I.		.22			.37			.29	
	Protozoa/O.I.		.14			.16			.10	
	Mesozoo P/O.I.		.057			.053			.074	
	Benthic P/ O. I.		.13			.004			.043	
	Fish P/ O.I.		.047			.019			.028	

Table 6-6a. The matrix of organic carbon flows (T_{ij}, mgC m^{-2} d^{-1}) among the nodes of the upper Chesapeake Bay summer trophic flow network. The matrix is partitioned into plankton (node 3-10), benthos (node 14-19), nekton (node 20-31) and detritus (node 32-34). S=Sum.

i	Node *j*															
	3	4	5	6	7	8	9	10	14	15	16	17	19	20	21	
1				165	11	2.6	119					223		192		
2				33	1.4	.53	26					56				
3			283	66												
4												22				
5				66	.70											
6					1.4	1.9	90								4.2	
7						.05	1.3								.84	
8									.12						.84	
9							7.7		5.5					11	75	
10																
12											98	19				
13																
14											20	5				
15												29		.73		
16														.73		
17														4.4		
19																
20																
21									.12					.73		
22																
23																
24																
25																
26																
27																
28																
29																
30																
31																
32	811															
33											113	78	44		.73	
34				66				.27	13					815		11 2.5
S	811		66	283	330		14	5.3	257	5.8	113	196	97	1117	7.3	214 84

Table 6-6a. (continued)

i	Node j													
	22	23	24	25	26	27	28	29	30	31	32	33	34	Total
1											4.6	.57	1	719
2											56		14	186
3											.78		1	350
4											2.9		3	28
5											76		76	218
6	.4										68		68	234
7	.08										3.8		4	9.8
8	.08										1.4		1.4	3.7
9	7	.10									58		58	223
10											2.3		2.3	4.6
12											29	29		176
13												17		17
14												9.4		34
15		.20	.70	.18								116		147
16		.41	2.8	.72	6.0	.19		.22		.36		94	10	116
17		.61	2.8	.72	7.5	.19	1.2	.22		.36	379		379	776
19								.22			1.8		1.8	3.8
20								2.15	1.0	.7	15		15	33
21		.51					.36	.65	1.4	1.7	20		20	45
22								.43	1.2	.23	1.3		1.3	4.6
23								.13		.23	.4		.36	1.1
24								.22	1.0	.68	1.2		1.2	4.2
25									.24		.4		.42	1.1
26								.09		.23	3.5		3.5	7.3
27											.06		.06	0.12
28											.4		.4	.9
29											.41		.41	.8
30											.55		.55	1.1
31											.46		.46	.9
32														811
33							.18				95		155	487
34	.23	.20	.70	.18	1.5									910
S	7.6	2.0	7.0	1.8	15	0.39	1.8	4.3	4.8	4.6	822	487	906	5862

Table 6-6b. The matrix of organic carbon flows (T_{ij}) among the nodes of the mid Chesapeake Bay trophic flow network. The matrix is partitioned into plankton (node 3-10), benthos (node 14-19), nekton (node 20-31) and detritus (node 32-34). Nodes with zero biomass are omitted. S=Sum.

i	Node *j*															
	3	4	5	6	7	8	9	10	11	14	15	16	17	19	20	21
1				293	16	18	379						16		192	
2				147	1.2	1.5	32						1.5			
3			1192	147									1.5			
4																
5				147	1.2											6
6					4.6	7.5	159									1
7						.15	3.2									7
8								.8							11	94
9						1.5	32	40	.20							
10									3.5							
11											69	7.1				
12																
13											35	7.1				
14												21		.47		
15														1.4		
16														1.9		
17														.47		
19																
20								.83	.20							
21																
23																
24																
25																
26																
27																
28																
29																
30																
31																
32	2850									673	35	36		.47		
33													10		11	3.3
34		165				1.5	32			673	138	71	29	4.7	214	111
S	2850	165	1192	734	23	30	636	42	3.9							

Table 6-6b (Continued)

i	Node *j*												
	23	24	25	27	26	28	29	30	31	32	33	34	Total
1										524		524	1962
2										262		66	511
3										43		43	1425
4										57		24	82
5										539		231	918
6										172		172	520
7										6.1		6.1	16
8										6.5		6.5	21
9										186		186	549
10										14.3		14	32
11										1.8		1.8	3.6
12										41	41		159
13											18		18
14										148	148		337
15		.80	.81		.75				.36	7.8	80		104
16	.06	4.8	4.9	.05	4.5	.05	.43		.36	3.1	31		55
17	.06	1.6	1.6	.05	1.5	.07	.22				12		23
19							.22				2.0		2.7
20							2.2	.39	1.1		5.9		9.6
21	.05					.02	.86	1.5	1.7	27		27	59
23										.06		.06	.11
24						.02	.43	.72	1.0	1.3		1.3	4.7
25								2.2		1.3		1.3	4.8
26													.00
27										.016		.016	.032
28										.04		.04	.09
29										.41		.41	.81
30										.55		.55	1.1
31										.46		.46	.92
32													2850
33	.02	.8	.8		.8	.02							746
34										812	271		1305
S	.21	8.0	8.1	0.1	7.5	.18	4.3	4.8	4.6	2854	910	1305	12023

Table 6-6c. The matrix of organic carbon flows (T_{ij}) among the nodes of the lower Chesapeake Bay trophic flow network. The matrix is partitioned into plankton (node 3-10), benthos (node 14-19), nekton (node 20-31) and detritus (node 32-34). Nodes with zero biomass are omitted. S=Sum.

i	Node *j*											
	3	4	5	6	8	9	10	14	15	16	17	19
1				174	38	360					278	
2				87	4.4	46					15	
3			405	87								
4											24	
5				87								
6					15	151						
8							.7					
9						33	35					
10												
12									98	57		
13												
14									49	43		
15										43		.21
16												2.1
17												1.0
19												
20												
21												
24												
25												
26												
28												
29												
30												
31	1900											
32								829	49	143		.82
33		105			6.3	65					171	
S	1900	105	405	435	63	655	36	829	196	286	487	4.1

Table 6-6c. (Continued)

i	Node j											
	20	21	24	25	26	28	29	30	31	32	33	Total
1	192								530		132	1704
2									219		55	426
3									200		50	742
4									13		3.3	41
5									180		45	312
6		5.5							111		28	309
8	5.3	7.8							15		15	44
9	5.3	94							198		198	563
10									14		14	28
12									39	39		234
13										18		18
14									78	78		249
15			1.0	.43	2.1					100		147
16			12	5.1	7.4	.43		.72	34	138		200
17			7.2	3.0	12	.22		.72	63	254		341
19						.22				1.9		2.1
20						2.15	.39	6.5	8.3	25	8.3	51
21						.86	1.5	2.2		52	13	70
24						.43	.72	4.3	3.3		3.3	12
25							2.2		1.4		1.4	4.9
26									5.4		5.4	1.7
28									.41		.41	.81
29									.54		.54	1.1
30									1.4		1.4	2.9
31												1900
32												1022
33	11	3.3								213		574
S	214	111	21	8.5	21	4.3	4.8	14	1916	1146	574	9435

Table 6-7. Respiration (mgC m^{-2} d^{-1}) for each node in the three summer trophic flow networks (UB=upper Bay, MB=mid Bay, LB=lower Bay) and the fraction of total respiration contributed by each of 5 major groups. Missing entries indicate nodes with zero biomass. The table is continued on the next page.

Node	Description	UB	MB	LB
1	Net Phytoplankton	271	665	422
2	Picoplankton	60	147	93
3	Free Bacteria	461	1425	1157
4	Particle Attached Bacteria	37	82	64
5	Heteroflagellates	65	274	93
6	Ciliates	96	213	126
7	Rotifers	4.2	6.9	
8	Meroplankton	1.6	9.0	19
9	Mesozooplankton	34	87	92
10	Ctenophores	1.2	9.4	8.1
11	Chrysaora		0.27	
12	Microphytobenthos	59	53	59
13	SAV			
14	Benthic Bacteria	79	787	581
15	Meiofauna	49	35	49
16	DF Benthos	50	21	86
17	SF Benthos	340	8.6	146
18	Oysters			
19	Blue Crab	1.8	1.2	1.0

Table 6-7. (Continued).

Node	Description	UB	MB	LB
20	Menhaden	132	156	132
21	Bay anchovy	35	46	36
22	Herrings and Shads	3.07		
23	White Perch	0.82	0.08	
24	Spot	2.82	3.22	8.25
25	Croaker	0.72	3.27	3.42
26	Hogchoker	7.70	3.85	10.28
27	American eel	0.16	0.04	
28	Catfish	0.71	0.07	
29	Striped Bass	3.25	3.25	3.25
30	Bluefish	3.53	3.53	3.53
31	Weakfish	3.18	3.18	10.02
	TOTAL	1803	4047	3203
	Algae/Total	0.22	0.21	0.18
	Bacteria/Total	0.32	0.57	0.56
	Zooplankton/Total	0.11	0.15	0.11
	Macrobenthos/Total	0.24	0.02	0.09
	Fish/Total	0.11	0.06	0.06

Table 6-8. Estimated summer fisheries landings in each of three regions of the mainstem Bay. Landings exclude estimated landings in tributaries as well as landings outside of summer. R=Recreational Landings, C=Commercial Landings. BC=blue crab, MH=menhaden, SP=spot, CR=croaker, AE=American eel, CF=catfish, BF=bluefish, WF=weakfish. Tot=Total.

	Upper Bay			Mid Bay			Lower Bay			
	R	C	Total	R	C	Total	R	C	Total	Total
					mgC m^{-2} d^{-1}					
BC		1.82	1.82		2.09	2.09		1.09	1.09	
MH								30.6	30.6	
SP				.021	.018	.039	.089	.163	.252	
CR				.02	.012	.032	.05	0.08	0.13	
AE		.126	.126		.032	.032				
CF	.146	.038	.184	.015	.004	.019				
BF	.197	.009	.206	.197	.009	.206	.21	.02	0.23	
WF	.036	.002	.038	.036	.002	.038	.359	.059	0.418	
Tot	0.38	2.00	2.37	0.29	2.17	2.46	0.71	32.01	32.72	
					tons WW $summer^{-1}$					
BC		988	988		5619	5619		3336	3336	9943
MH								74912	74912	74912
SP				45	39	84	218	399	617	701
CR				43	26	69	122	196	318	387
AE		55	55		69	69				124
CF	63	17	80	32	9	41				121
BF	57	3	60	282	13	295	343	33	375	730
WF	13	1	13	62	3	65	703	116	819	897
Tot	133	1062	1195	465	5778	6243	1386	78991	80377	87815

Table 6-9. Estimated trophic level (TL), biomass (B, mgC m^{-2}), production (P, mgC m^{-2} d^{-1}), ecotrophic efficiency (EE), and respiration (R, mgC m^{-2} d^{-1}) for the restored mid Chesapeake Bay trophic flow network. Gross production for primary producers is the sum of the indicated P and R.

Node	Description	TL	B	P	EE	R
1	Net Phytoplankton	1.0	1663	981	0.855	333
2	Picoplankton	1.0	294	256	0.659	74
3	Free Bacteria	2.0	503	568	0.874	855
4	PA Bacteria	2.0	37	42	0.55	42
5	Heteroflagellates	3.0	55	154	0.746	101
6	Ciliates	3.0	57	142	0.893	83
7	Rotifers	2.5	23	6.90	0.503	6.9
8	Meroplankton	2.5	120	60	0.568	60
9	Mesozooplankton	2.5	316	158	0.96	52
10	Ctenophores	3.5	126	16	0.215	9.4
11	Chrysaora	4.5	6.3	0.126	0	0.265
12	Microphytobenthos	1.0	559	335	0.429	112
13	SAV	1.0	13500	122	0	0
14	Benthic Bacteria	2.0	163	184	0.391	277
15	Meiofauna	2.3	700	49	0.306	49
16	DF Benthos	2.2	3333	47	0.443	68
17	SF Benthos	2.1	6666	93	0.093	137
18	Oysters	2.0	0			
19	Blue Crab	3.1	390	1.56	0.976	1.15
20	Menhaden	2.1	2176	54	0.95	135
21	Bay anchovy	3.5	381	31	0.342	46
22	Herrings and Shads	3.5	0			
23	White Perch	3.4	29	0.058	0.172	0.084
24	Spot	3.0	316	3.16	0.7	4.58
25	Croaker	3.0	322	3.22	0.7	4.66
26	Hogchoker	3.0	50	1.25	0	3.85
27	American eel	3.0	9	0.027	0	0.04
28	Catfish	3.2	45	0.045	0.376	0.07
29	Striped Bass	3.5	172	0.344	0.775	3.25
30	Bluefish	4.1	68	0.476	0.439	3.53
31	Weakfish	3.8	67	0.603	0.777	3.18
32	DOC	1.0	28207		1.001	
33	Sediment POC	1.0	201607		0.939	
34	POC	1.0	5162		0.739	
	Gross Primary Prod.			2213		2465
	Net Ecosys. Metabolism					-253
	Detrital Inputs					350

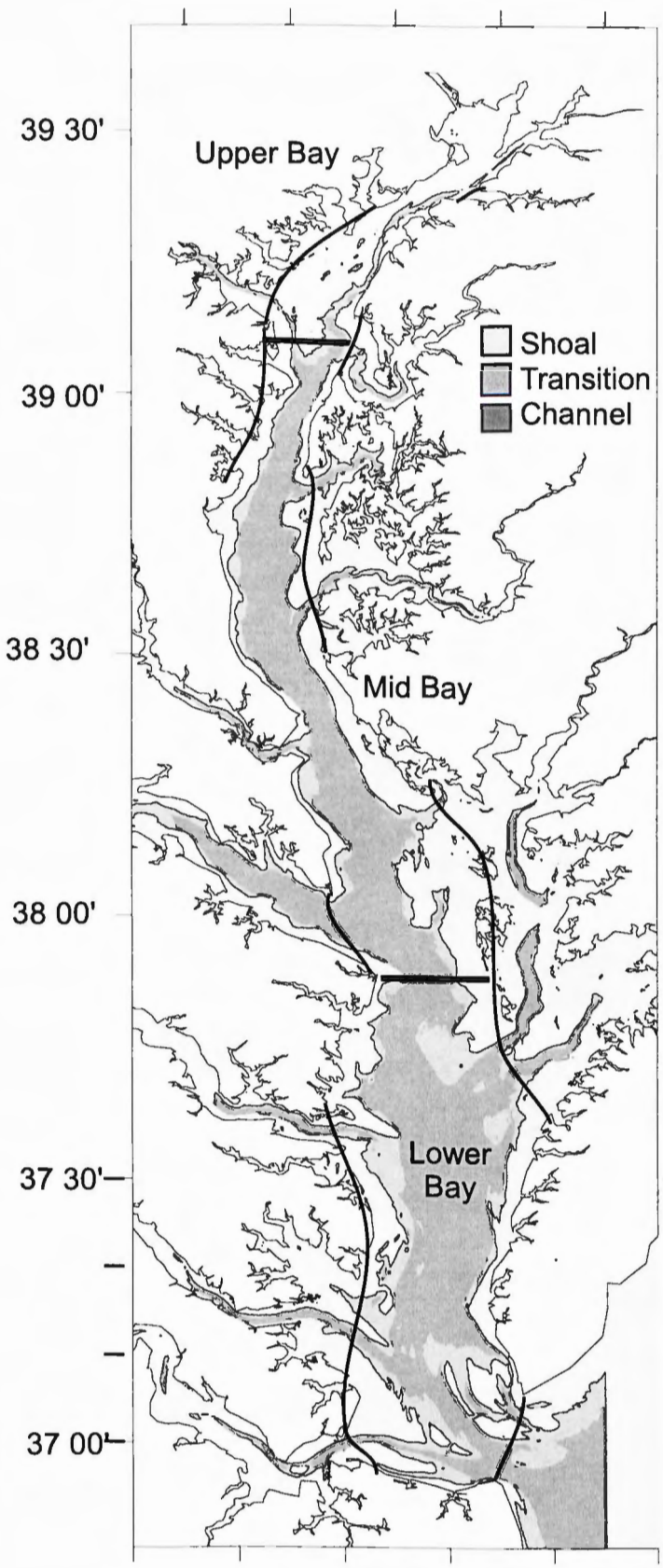
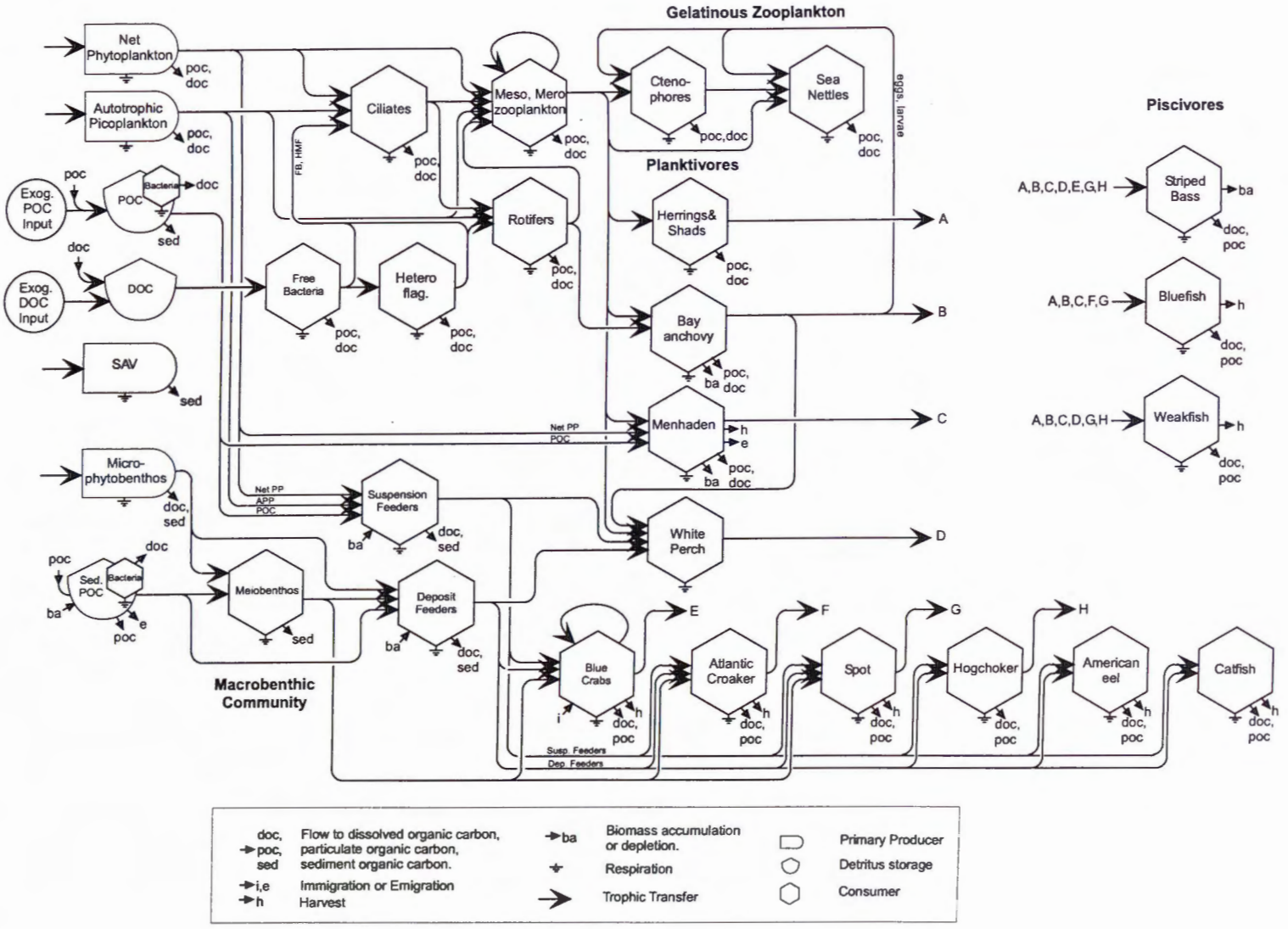


Fig. 6-1. A map of Chesapeake Bay showing the boundaries of the mainstem Bay regions for which trophic flow networks were computed. Depth contours indicate the distribution of shoal (<7m), transition (7-10m) and deep water (>10m) habitats in each region.

Fig. 6-2. A diagram of the basic model structure for the Chesapeake Bay trophic flow networks. All the nodes are present in the upper Bay network, while some nodes have zero biomass in the mid Bay and lower Bay networks. Non-living storages of organic matter, primary producers, and consumers are indicated via separate symbols. As indicated on the key, large arrows indicate trophic transfers. Labelled small arrows indicate flows to detritus, which are represented as collected flows returning to the respective detrital pools. Labelled small arrows also indicate biomass imports and exports due to net changes in biomass, immigration or emigration, physical processes (principally advection and burial), and biomass exports due to fisheries harvests. Respiration is indicated by electrical "ground" symbols. Capital letters are used to simplify the representation of flows from a large number of prey species to the three major piscivores. For simplicity, mesozoooplankton and meroplankton are represented as one node, even though they are separate in the network models. Oysters were found to have insignificant biomass and are therefore not included in the diagram. Also for simplicity, some very small flows were not included in the diagram. All the flows are accurately and quantitatively represented in the diet matrices (Tables 6-6a,b,c).


Gelatinous Zooplankton
Net Phytoplankton
Autotrophic Picoplankton
Exog. POC Input
Exog. DOC Input
SAV
Micro-phytobenthos
Sed. POC
Bacteria
POC
DOC
Ciliates
Meso, Mero zooplankton
Rotifers
Free Bacteria
Hetero flag.
Suspension Feeders
Meiobenthos
Deposit Feeders
Macrobenthic Community
FB, HMF
Net PP
APP
POC
Ctenophores
Sea Nettles
eggs, larvae
Planktivores
Herrings& Shads
Bay anchovy
Menhaden
White Perch
Blue Crabs
Atlantic Croaker
Spot
Hogchoker
American eel
Catfish
Susp. Feeders
Dep. Feeders
Piscivores
Striped Bass
Bluefish
Weakfish
A,B,C,D,E,G,H
A,B,C,F,G
A,B,C,D,G,H
doc, poc, sed Flow to dissolved organic carbon, particulate organic carbon, sediment organic carbon.
i,e Immigration or Emigration
h Harvest
ba Biomass accumulation or depletion.
Respiration
Trophic Transfer
Primary Producer
Detritus storage
Consumer

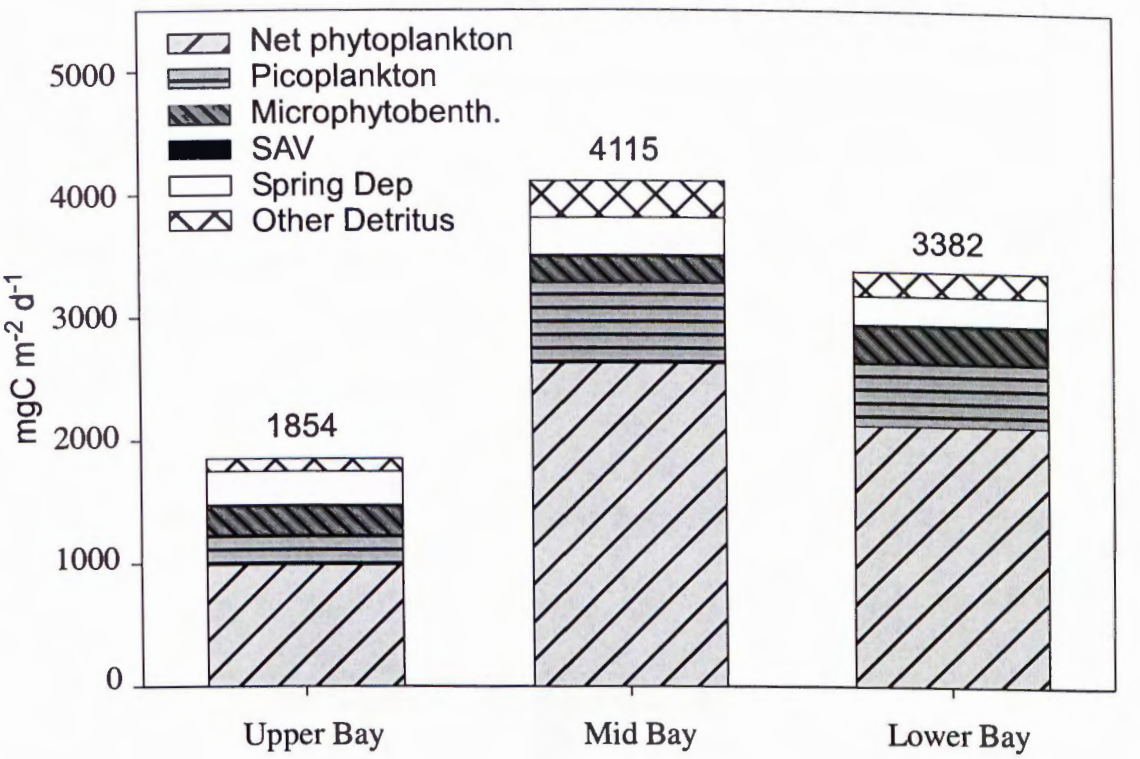


Fig.6-3. Estimates of organic matter inputs to the summer food webs in the three regions of Chesapeake Bay from net phytoplankton (>3 μm), autotrophic picoplankton (<3 μm), microphytobenthos, submersed aquatic vegetation, phytoplankton deposited to sediments during winter-spring, and other detritus. In the mid Bay, there was an additional input of 9 mgC m^{-2} d^{-1} at trophic levels >1 which was largely due to summer depletion of macrobenthic biomass accumulated during spring. In the other regions, this input was <1 mgC m^{-2} d^{-1}.

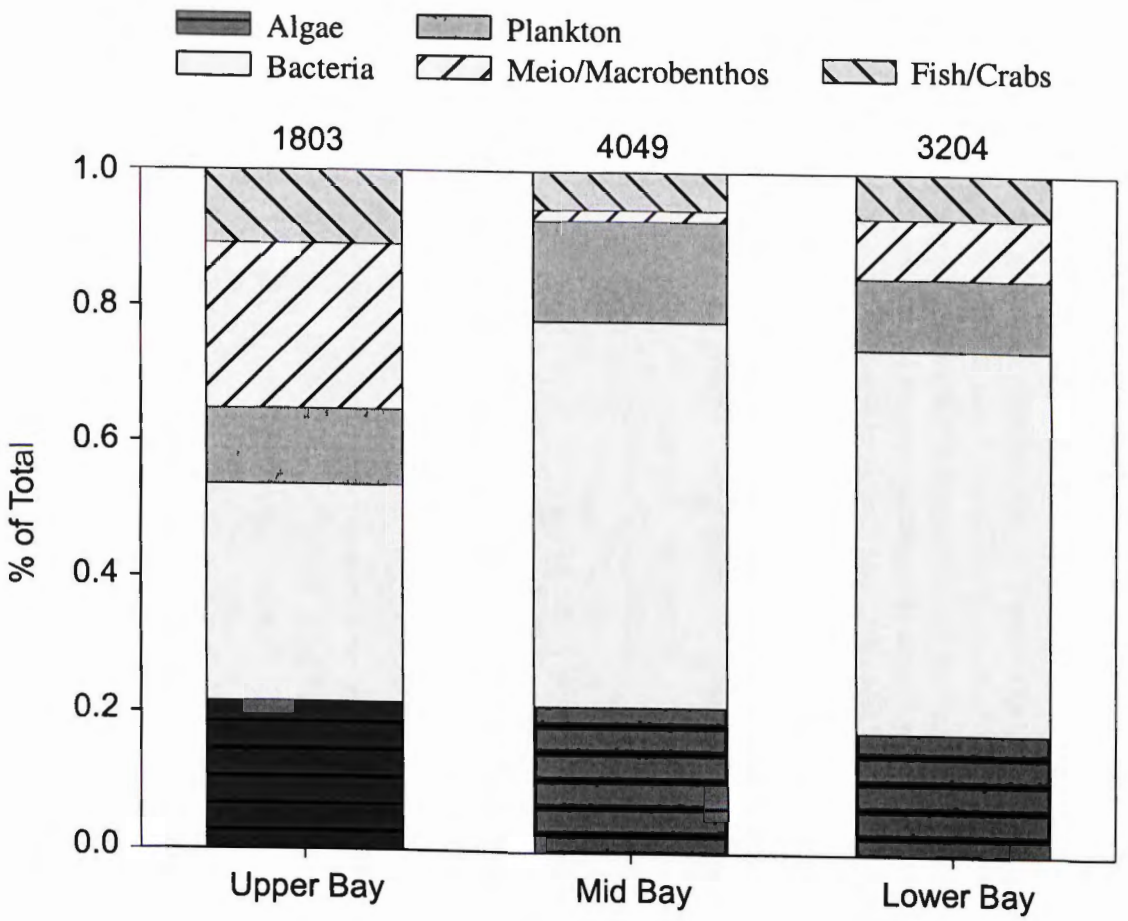


Fig. 6-4. The fraction of total respiration due to algae (including microphytobenthos), bacteria (including benthic bacteria), meiobenthos and macrobenthos, and fish and crabs. Total respiration (mgC m^{-2} d^{-1}) is indicated at the top of each bar.

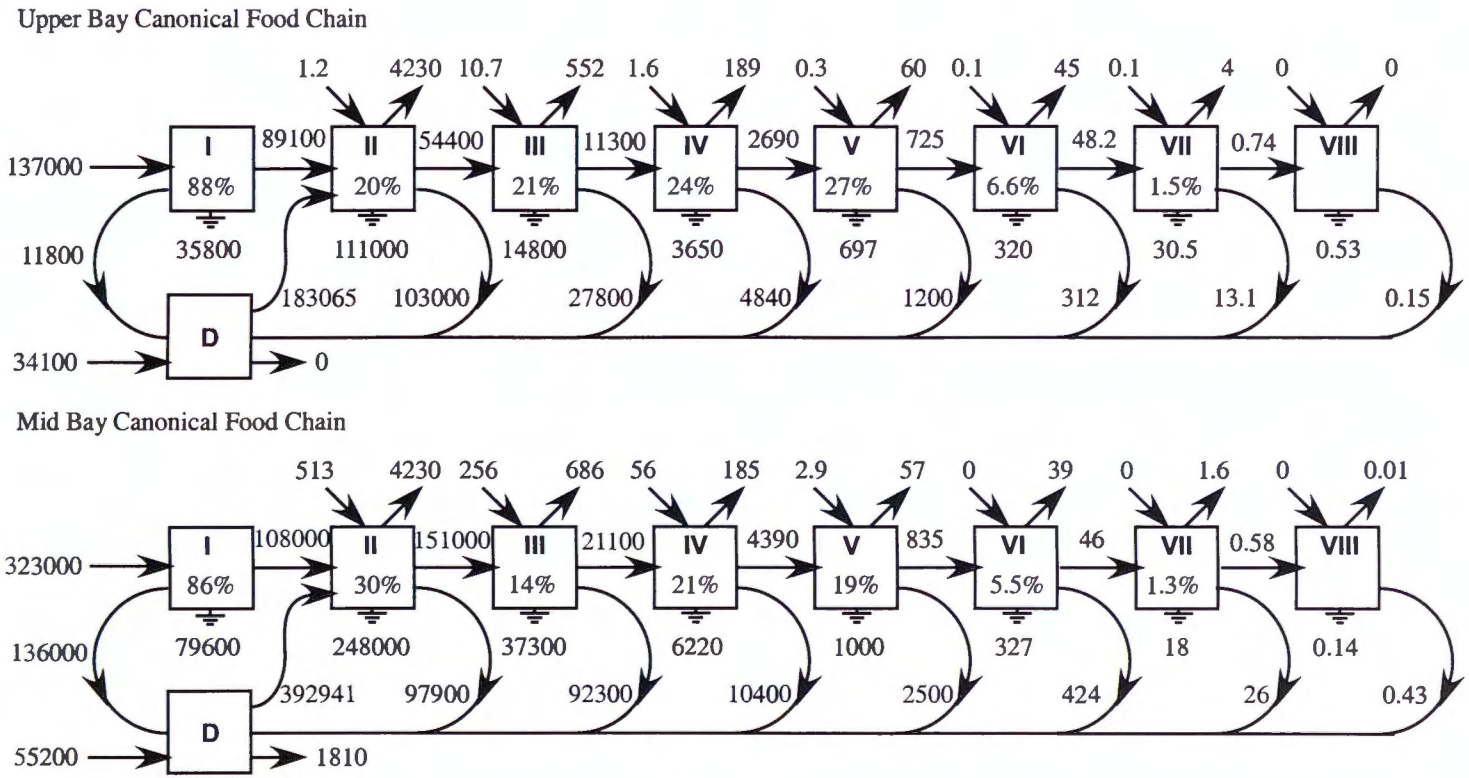


Fig. 6-5a. The trophic flow networks for the upper and mid Chesapeake Bay projected into a linear chain of canonical trophic levels indicated by Roman numberals. The aggregated detritus pool is indicated by "D." The projection was computed using the algorithm of Ulanowicz and Kemp (1979) as modified by Ulanowicz (1995) and implemented in NETWRK software. Arrows not originating froma box, or not pointing to a box indicate exogenous inputs and exports, respectively. All flows were converted to total summer (92 day) flows, with units mgC m^{-2} $summer^{-1}$.

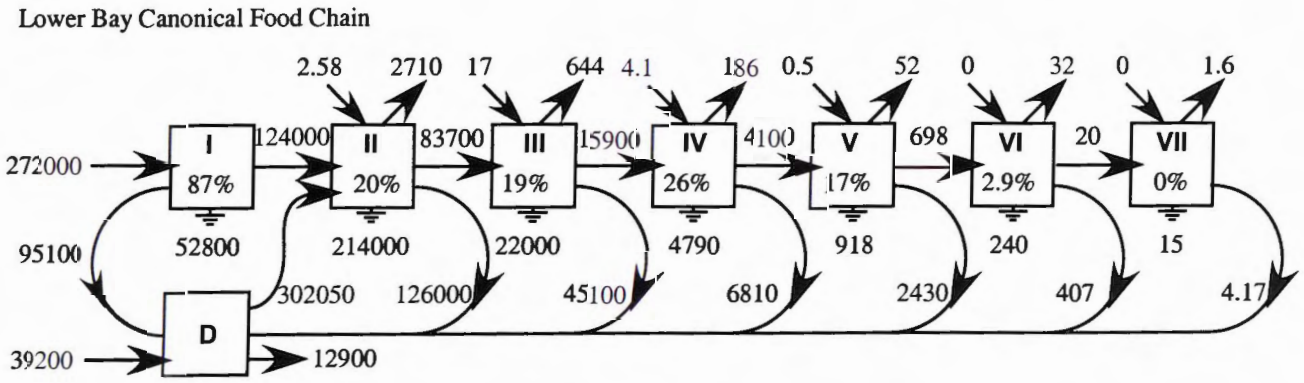


Fig. 6-5b. Linear chains of canonical flows for the lower Chesapeake Bay food web during summer. For a full description see Fig. 6-5a.

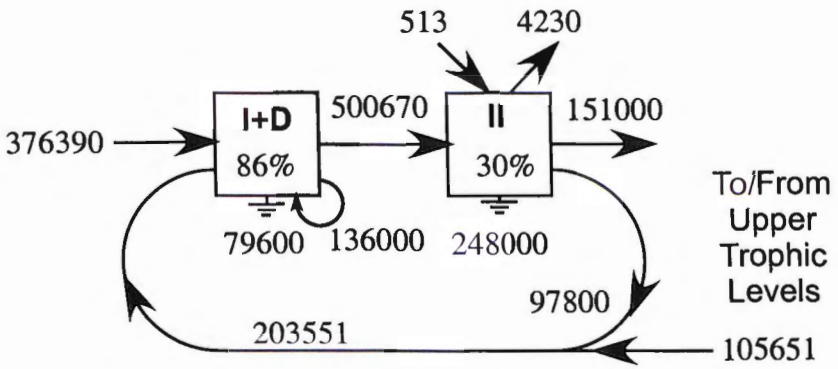


Fig. 6-6. An illustration, for the mid Bay, of how the canonical flows in Figs 6-5a,b can be collapsed into a Lindeman Spine by combining flow due to primary production (I) and detritus (D). The description in the legend for Fig. 6-5a applies to this figure.

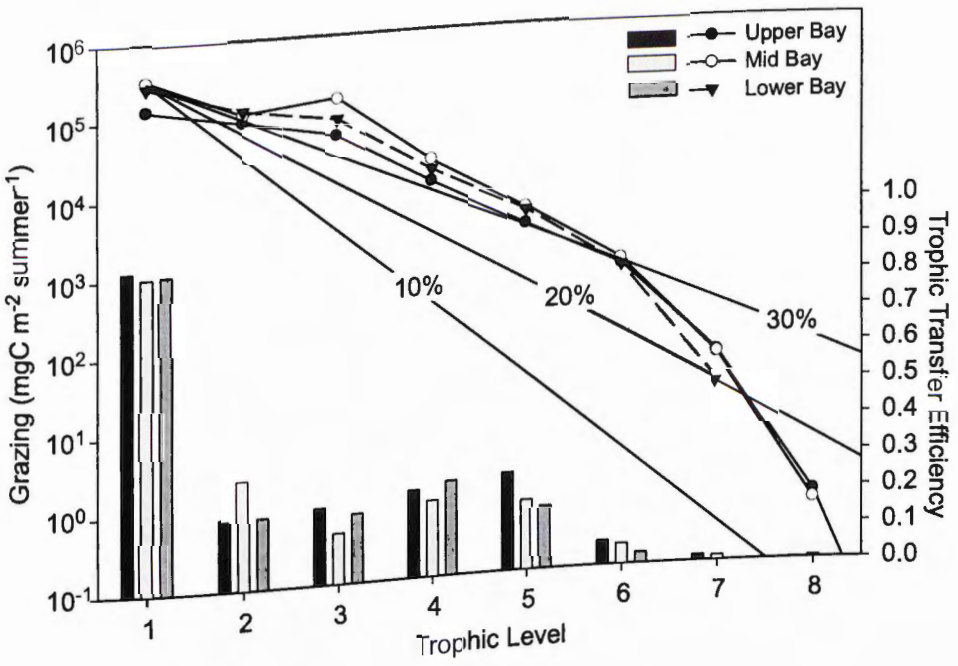
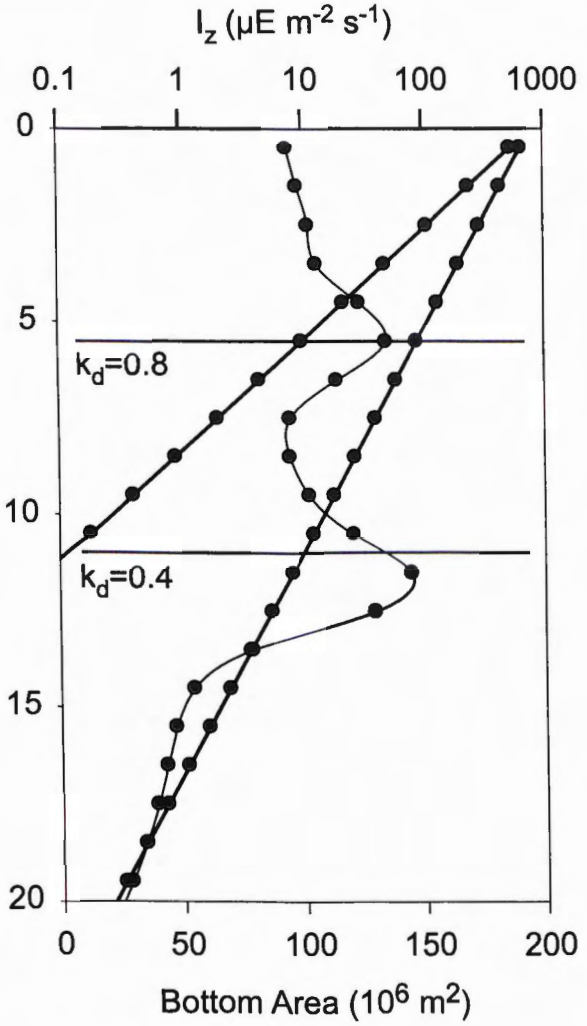


Fig. 6-7. The organic carbon flow to each trophic successive canonical tro-
phic level in the upper, mid and lower Bay food web. Flows are shown up
to trophic level 8, although a very small quantity of flow exceeds this level
for the mid Bay network. Reference lines drawn from the initial input to
TL 1 for the mid Bay at constant efficiencies of 10, 20 and 30% per tro-
phic level reveal the average trophic transfer efficiency (TTE) over *n*
exchanges. Bars show the TTE at each canonical trophic level in each of
the three regions of the Bay.



Fig, 6-8. The bottom area present in 1 m depth increments in the mid Bay region and the the penetration of light at current average light attenuation (k_d=0.8 m^{-1}) as well as at the estimated reduced light attenuation in the restored mid Bay (k_d=0.4 m^{-1}). Horizontal lines indicate the depth of 1% light penetration ($z_{1\%}$) for each light attenuation level.

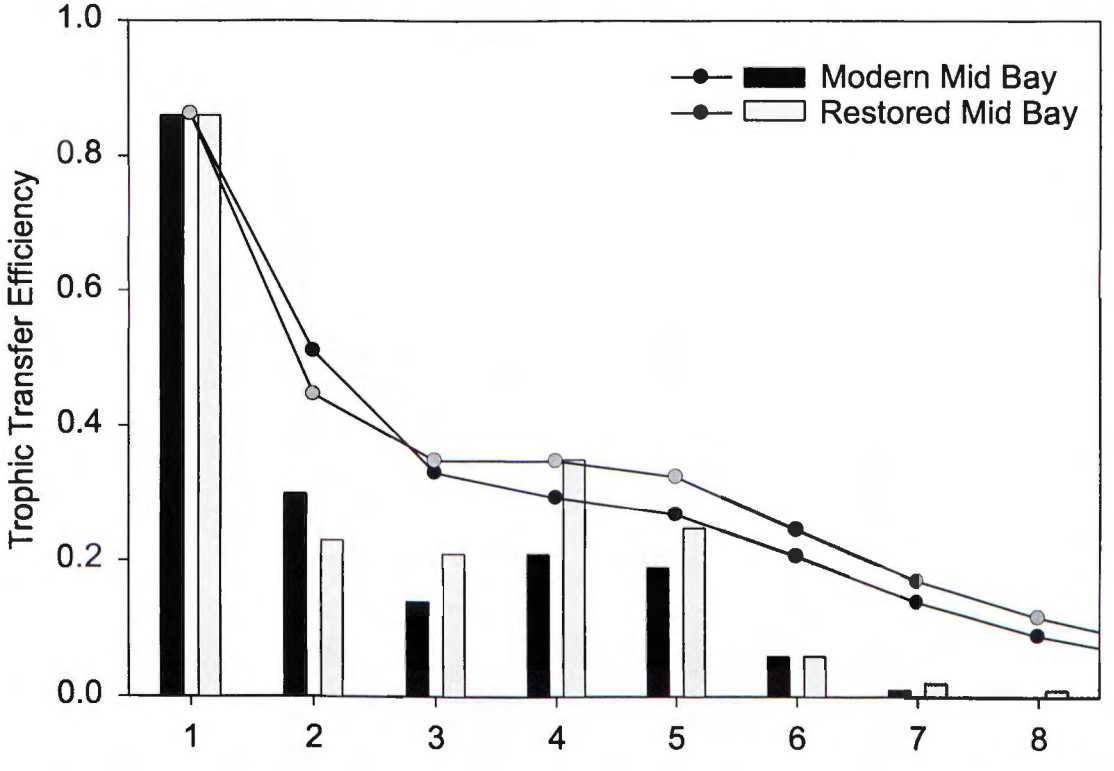


Fig 6-9. Trophic transfer efficiencies for canonical trophic levels computed from the trophic flow networks for the modern mid Bay and the restored Bay (bars). The lines indicate the geometric mean trophic transfer efficiencies for trophic transfers up to the indicated trophic level in the modern mid Bay and the restored mid Bay.

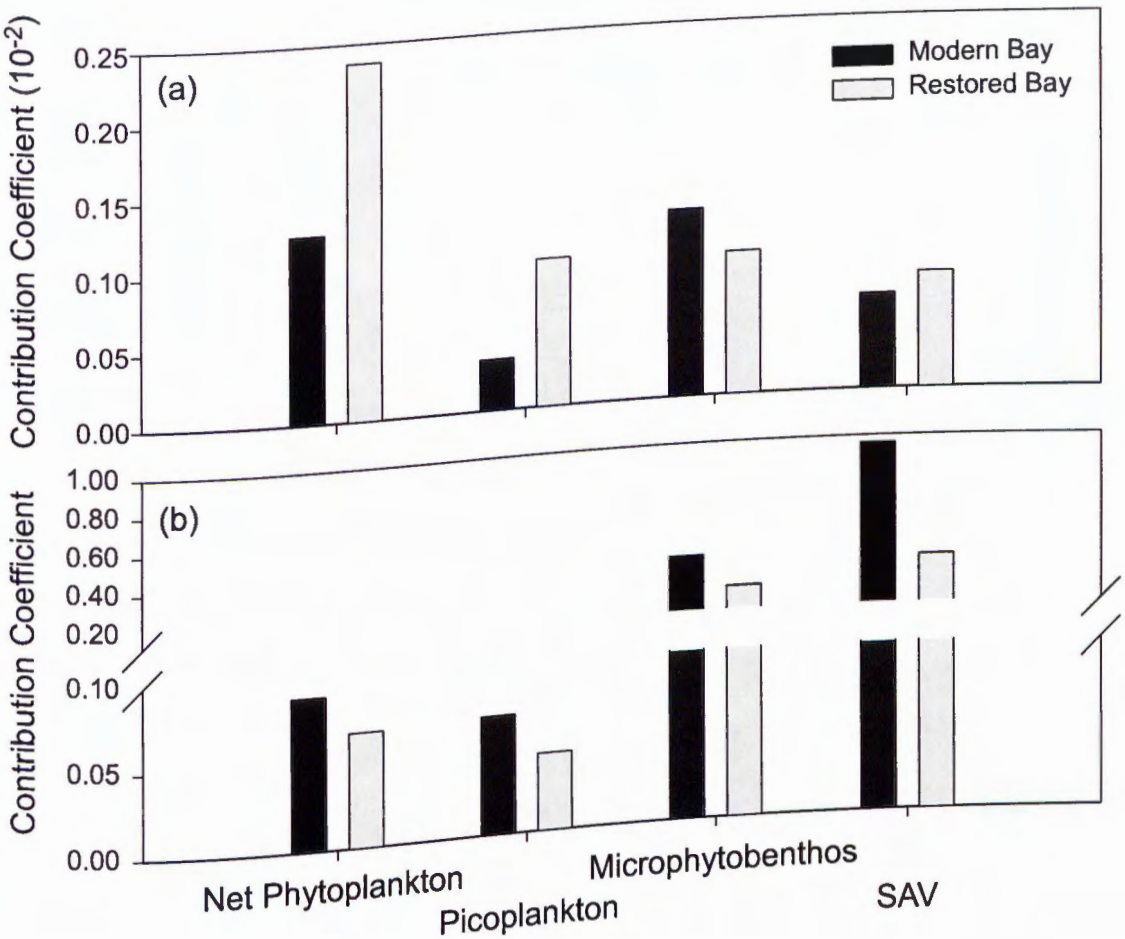


Fig 6-10. Total contribution coefficients, indicating the fraction of net production from the indicated producer eventually reaching (a) striped bass or (b) benthic bacteria over all pathways.

Chapter 6:

VALIDATION OF TROPHIC LEVEL ESTIMATES FOR CHESAPEAKE BAY FOOD WEB USING $^{15}N/^{14}N$.

Abstract

Analysis of the stable nitrogen isotopic composition ($\delta^{15}N$) of Chesapeake Bay biota was used to estimate average trophic level (TL) for 28 taxa or groups of taxa in each of three regions of the Bay during spring, summer and fall. Estimates of TL based on $\delta^{15}N$ (TL_{SI}) were compared to corresponding estimates derived from trophic network analysis (TL_{NA}). Average TL_{SI} for mesozooplankton was found to be higher in the upper Bay compared to elsewhere in the Bay. Although this pattern was also observed for TL_{NA}, the regional differences were smaller. On average for the 28 taxa, TL_{SI} was 0.53±0.10 greater than TL_{NA}. Although analysis of $\delta^{15}N$ provided a useful independent validation of TL_{NA}, natural variability in $\delta^{15}N$ and the large variety of biogeochemical processes potentially affecting $\delta^{15}N$ undermined the effectiveness of $\delta^{15}N$ for this purpose. The smallest differences between TL_{NA} and TL_{SI}, and the narrowest confidence limits for TL_{SI}, were obtained when $\delta^{15}N$ was repeatedly measured. This suggests that repeated measurement of $\delta^{15}N$ would be an effective means of obtaining more certain results.

Introduction

Although the biota that comprise food webs feed on varied diets, the concept of trophic level remains useful, rescued by the introduction of fractional trophic levels (Odum and Heald 1975). Soon after, after a concise numerical procedure was developed to estimate fractional trophic levels from quantitative trophic flow networks (Ulanowicz and Kemp 1979, Ulanowicz 1995). Trophic level estimates prove useful in a number of ways. For example, the concept of trophic level is essential to the fish production computations of Ryther (1969) and Iverson (1990) and estimated trophic level of the harvest is needed if one wishes to estimate the possible harvest. Changes

in the average trophic level of fish targeted by fishing fleets have been cited as evidence for unsustainable fishing at the global scale (Pauly et al. 1998).

Estimates of average trophic level can now be readily obtained as standard output from software packages designed for the analysis of quantitative trophic network models (NETWRK, Ulanowicz 1999, ECOPATH with ECOSIM, Christensen et al. 2000). The data requirements for the specification of such models are substantial, however. Diet composition for each taxa or group of related taxa in the food web must generally be known *a priori*, even if it is possible to later improve or further constrain the estimates through mass balance constraints (i.e. inverse analysis and related methods). Generally, the available diet studies are few, especially if one limits the search to studies conducted in the ecosystem of interest. More likely, diet data come from a potentially similar ecosystem. By obtaining diet information in this way, differences among systems in the trophic levels of species may not be revealed through trophic network models. Even a detailed seasonal study of diet within the ecosystem of interest may not provide all the information that it needed. For example, Hartman and Brandt (1995) reported age-structured and seasonally resolved diets for three piscivorous predators in the mid Chesapeake Bay in the early 1990's. However, the diet of striped bass (*Morone saxatilis*) in the upper Chesapeake Bay was different, at least in the 1930's, including more prey items that were present in low salinity waters (Hollis 1952). The possible seasonal, spatial and interannual differences in diet most likely preclude consistent resolution of diet variations through gut contents analysis. Examining the diets of very small organisms such as the mesozooplankton, microzooplankton, or even protozoa poses an even larger challenge, since gut contents analysis is not feasible. For these animals, carefully constructed grazing experiments can reveal diet preferences (Stoecker and Cupuzzo 1990), but this may differ from the *in situ* diet.

Analysis of the natural abundance of stable isotopes in tissues, particularly $^{15}N/^{14}N$, has become a well known method for examining trophic relationships and sources of organic matter to food webs (Peterson and Fry 1987, e.g. Fry 1988). The suitability of stable isotopes for this purpose depends on two empirically observed

properties. First, the stable isotopic composition of tissues reflects the stable isotopic composition of the diet. Secondly, and as important, is the fact that while the different isotopes function similarly in chemical reactions, reaction rates for the heavier isotope (i.e. ^{15}N) proceed slightly more slowly. The result is a process called isotopic fractionation. Empirically, the ratio $^{15}N/^{14}N$ increases with each trophic transfer due to excretion of ^{15}N depleted nitrogen (Peterson and Fry 1987). Because of the very small differences that are observed, standard notation ("del" notation) is commonly used in which the $^{15}N/^{14}N$ ratio for the sample (R_{sample}) is expressed relative to the same ratio ($R_{standard}$) for a standard according to

$$\delta^{15}N = \left(R_{sample} / R_{standard} - 1\right) \times 1000 \qquad (1)$$

with units ‰, or "per mil." The standard for $\delta^{15}N$ is $^{15}N/^{14}N$ for dinitrogen gas (N_2) in air. The difference between $\delta^{15}N$ for the animal and its diet, $\Delta\left(\delta_{animal} - \delta_{diet}\right)$, varies between 2‰ and 6‰ but has been reported to be less variable than that suggests, with a mean value of about 3.4‰ (Montoya et al. 1990). The application to the estimation of trophic level is relatively straightforward, namely,

$$TL = TL_{ref} + \left(\delta^{15}N_{sample} - \delta^{15}N_{reference}\right) / 3.4 \qquad (2)$$

where the reference organic matter pool may be particulate nitrogen (PN), or perhaps the mesozooplankton. Kline and Pauly (1998) estimated trophic levels using this approach to cross-validate trophic level estimates obtained using network analysis, apparently the first application of stable isotope methods for that purpose. Compared to the high cost of labor intensive grazing experiments and gut contents analysis, stable isotope methods can be applied inexpensively. For this reason, the approach is suitable for examining seasonal and regional differences in trophic relationships (e.g. Montoya et al. 1990). Such differences can also be compared to seasonal or regional differences resolved using trophic network models (Baird and Ulanowicz 1989, Chapter 5), similar to the approach of Kline and Pauly (1998).

In this study, the stable nitrogen isotopic composition of many components of the Chesapeake Bay food web was examined for three distinct regions of the Bay (upper Bay, mid Bay, lower Bay) in each of three seasons (Spring, Summer, Fall)

during fall 1995 to fall 1998. Average trophic level for each food web component was derived from $\delta^{15}N$ and compared to summer trophic level estimates obtained through analysis of trophic flow networks (Chapter 5).

Methods

Samples were collected from R/V Cape Henlopen within 3 general areas (upper Bay, mid Bay, lower Bay) during three week long cruises each year beginning in fall 1995 and concluding in fall 1998 (Fig. 7-1, Table 7-1). During 1996, samples were also collected in an additional area at the southern limit of the upper Bay region, the Gibson Island transect (Fig. 7-1). A total of 274 samples were collected for stable isotope analysis. These organic matter sources that were sampled included surficial sediments, seston (PN), microplankton, mesozooplankton, gelatinous plankton, and fish. Undisturbed surficial sediments were obtained with a Smith-Macintyre grab sampler. A 30 ml sample of the top 2 mm was obtained from the core and immediately frozen. PN was obtained from water samples collected by Niskin bottle from near bottom, pycnocline and surface and combined in equal amounts. The water sample was passed through a 40 μm screen, then filtered onto pre-combusted GF/F filters (450 °C for 5 hr.) until clogged. The filters were wrapped in foil and immediately frozen. The procedures for sampling microzooplankton and mesozooplankton changed over the course of the study and can be described as follows.

Before 1997: Mesozooplankton were obtained via a 5-minute oblique Tucker Trawl tow with a 280 μm net. The trawl captured only larger copepods and fish larvae. The sample was sieved dry, rinsed in deionized water and frozen immediately.

1997-1998: A 40 μm plankton net with a non-filtering cod-end was repeatedly towed vertically through the water column to obtain a concentrated sample of the plankton (>40 μm). The sample was gently passed serially through 200 μm and 40 μm screens. The two larger fractions were concentrated then added to 0.2 μm filtered seawater in a

40 μm mesh-bottomed incubator. The plankton were left for 2 hours to clear their guts. Plankton that did not settle to the bottom after 2 hours were removed with a turkey baster, filtered onto precombusted GF/F filters and frozen.

Ctenophores (*Mnemiopsis leidyi*) and sea nettles (*Chrysaora quinquecirrha* and *Cyanea capillata*) were obtained in Tucker Trawls and mid-water trawls. Samples were sorted by hand, rinsed in deionized water and frozen in acid-washed glass jars. Finfish were obtained frozen as surplus collections from mid water trawl samples.

All samples were dried at 60° for 24 hours or until completely dry. Prior to drying, sediment samples and mesozooplankton not collected on filter pads were partially thawed, then scraped into foil pans. Gelatinous zooplankton were partially thawed and transferred to large aluminum pans for drying. Fish were partially thawed and muscle tissue was separated from organs, skin and bones. Only muscle tissue was reserved for drying. Dried sediments, mesozooplankton (except on filters), gelatinous zooplankton, and fish tissue were ground to a fine powder with a mortar and pestle. Measurement of $\delta^{15}N$ via mass spectrometry was performed by the Stable Isotope Laboratory at the Marine Biological Laboratory, Woods Hole, MA. Analytical replicates for $\delta^{15}N$ were generally within 0.2‰. Measurements of $\delta^{13}C$, obtained from the same samples, were previously described by Hagy and Boynton (1998).

Results and Discussion

Seasonal and regional patterns in $\delta^{15}N$ for seston depend in complex ways on biogeochemical processes. For example, isotope fraction associated with uptake of dissolved inorganic nitrogen (DIN) by phytoplankton averages -4 to -6‰ under N-replete (i.e. DIN not limiting) conditions but proceeds without fractionation when N limits the phytoplankton (Peterson and Fry 1987). Moreover, $\delta^{15}N$ in the remaining DIN pool increases because ^{14}N uptake exceeds ^{15}N uptake (Cifuentes et al. 1988). The dynamic nature of $^{15}N/^{14}N$ for DIN and phytoplankton in Delaware Bay that was observed by Cifuentes et al. (1998), it was anticipated the data collected in this study could not resolve the equivalent dynamics in Chesapeake Bay. Nonetheless, the patterns observed for seston $\delta^{15}N$ in Chesapeake Bay generally followed the patterns

that might be expected. To increase the ability to resolve regional and seasonal patterns, samples from several years were combined (Table 7-2). Values were lowest in the upper Bay during spring (~6‰) and increased both down Bay and from spring to summer. Statistically, $\delta^{15}N$ was lower in spring than in summer and fall and higher in the mid Bay than in the upper and lower Bay (Table 7-2)

Seasonal and regional patterns in $\delta^{15}N$ for mesozooplankton loosely reflected the patterns observed in the particulate nitrogen (PN, Table 7-3). Entering $\delta^{15}N$ for mesozooplankton and PN into eq. (2) and assuming that TL_{ref}=1 (for PN), gave initial estimates of trophic level for mesozooplankton (Table 7-3). TL of mesozooplankton was significantly higher ($p<0.05$) in the upper Bay compared to the other regions, for which TL was statistically equal. TL did not vary significantly among seasons, except for in the upper Bay, where TL was significantly greater in summer than in fall. In generating these estimates it was recognized that PN includes components of the microplankton for which $TL_{ref}>1.0$. In addition, it includes a large detrital PN component for which $\delta^{15}N$ can be either less than or greater than $\delta^{15}N$ for phytoplankton. If the detritus pool was recently plankton-derived, $\delta^{15}N$ may be similar to that of the plankton. Additionally, isotopic fractionation during decomposition can increase $\delta^{15}N$ (Cifuentes et al. 1988). On the other hand, $\delta^{15}N$ for surficial sediment was slightly less (0.9‰ to 1.4‰) than $\delta^{15}N$ for PN throughout the Bay, a pattern also observed in the Delaware estuary by Cifuentes et al. (1988). If the sediment PN pool, with depleted $\delta^{15}N$, was mixed with suspended PN via resuspension this would decrease $\delta^{15}N$ for the detrital component of PN. Variations in $\delta^{15}N$ for detritus that is not consumed, relative to phytoplankton and microplankton that are consumed could affect trophic level estimates based on PN as the reference.

The consequence of uncertainty as to the origin and fate of detritus can be evaluated in terms of uncertainty in the value of TL_{ref} for PN. This was examined using estimates of the relative contribution of phytoplankton, bacteria, microplankton and detritus to PN, as well as estimates of trophic level for each of these components based on network models (Chapter 6). Using this approach, it was estimated that TL_{ref} for PN was 1.11, 1.18 and 1.12 in the upper, mid and lower Bay, respectively.

Relative to assuming that TL_{ref}=1, this increased the estimated TL for mesozooplankton (Table 7-4). The estimated trophic level for mesozooplankton in the upper Bay was higher than was estimated using the network model, but lower in the mid Bay and lower Bay. As was suggested above, however, $\delta^{15}N$ for detritus may have been reduced in the upper Bay due to resuspended sediment and increased in the lower Bay due to the preponderance of plankton derived organic matter in the PN (Canuel and Zimmerman 1999). These effects would tend to reduce the differences between the trophic level estimates derived from network analysis and those obtained here. Although uncertainty in estimates of T_{ref} results in imprecise estimates of TL for mesozooplankton, any estimate is bounded by 2.0 at the lower limit. By increasing consumption of protozoa to the highest extent permitted by mass balance constraints in a trophic network model (Chapter 6), the likely upper limit for the trophic level of mesozooplankton is about 3.0. The estimates based on $\delta^{15}N$ suggest that the average TL for mesozooplankton was towards the upper end of the range in the upper Bay and the lower to middle end of the range in the mid Bay. Differences in the diet composition of the mesozooplankton may have been under-represented in the network models (Chapter 5).

Trophic level estimates for biota other than mesozooplankton were computed using eq. 2 with mesozooplankton and the reference, similar to the approach of Kline and Pauly (1998). This approach takes advantage of the fact that mesozooplankton can be definitively isolated for isotopic analysis. Four different biota, the microzooplankton (40-200 μm size fraction of the plankton), ctenophores, sea nettles and bay anchovy, were collected in most regions of the Bay and in most seasons, enabling trophic levels (±standard error) to be computed on a regional and seasonal basis (Fig. 7-2). Trophic level estimates for the microplankton were lowest in spring. Consistent with observation in the field, this suggests that larger phytoplankton cells (or chains of cells) were retained on the sieve. TL estimates for summer and fall remained less than estimates for mesozooplankton. Considering that estimated trophic levels for ciliates and rotifers based on network analysis were 2.6 and 2.3, respectively (Chapter 6), it seems likely the 40-200 μm size fraction samples included

phytoplankton or detritus at all times of the year. Particles smaller than 40 μm were likely retained on the sieve due to clogging.

Ctenophores have been reported to consume a diet consisting almost exclusively of mesozooplankton, but also including a small quantity of ichthyoplankton (Purcell et al. 2001). As a result, it was expected that their TL would be ~1 integer step greater than mesozooplankton, or possibly slightly higher. This was observed almost exactly in 5 of 8 season/region combinations for which data were available (Table 7-2). Ctenophore trophic level was slightly lower than expected in the upper Bay in spring and the lower Bay in summer. In contrast, ctenophores were more than 2 trophic levels higher than mesozooplankton in the upper Bay fall (Fig. 7-2). Although one cannot rule out the possibility that ctenophores consumed a diet at such a high trophic level, an alternate explanation seems more likely. As have been noted before, isotope fractionation results from preferential excretion of the lighter isotope. Therefore, maintaining a constant $\delta^{15}N$ depends on a dynamic balance between consumption and excretion. Under conditions of starvation, excretion depletes ^{14}N from the animal more rapidly than ^{15}N, while it is not replaced via the diet. Therefore, $\delta^{15}N$ increases. Although this process has not been described for ctenophores, Rosen (1994) demonstrated this process experimentally for the sea nettle *Chrysaora quinquecirrha*. Thus, it was not surprising to observe that *Chrysaora* also exhibited elevated $\delta^{15}N$ on several occasions (Fig. 7-2). Contrary to these more extreme observations, estimates for the mid Bay in summer, where both ctenophores and sea nettles were most abundant, were more consistent with expectation. Ctenophores were slightly more than one trophic level higher than mesozooplankton, consistent with a diet of mesozooplankton plus a small fraction of ichthyoplankton. The estimated trophic level for ctenophores was also in reasonable agreement with estimates based on network analysis. Similarly, the average trophic level of *Chrysaora* was about one level above ctenophores, reflecting their expected diet of ctenophores. The trophic level of *Chrysaora* in the mid Bay was slightly higher than would be suggested by an exclusive diet of ctenophores or mesozooplankton (Fig. 7-2). Although *Chrysaora* is known to consume Bay anchovy eggs and larvae, this

would not increase its $\delta^{15}N$ as compared to an exclusive ctenophore diet because $\delta^{15}N$ for bay anchovy was similar to that of ctenophores (Fig. 7-2). As elsewhere in the Bay, elevated $\delta^{15}N$ for *Chrysaora* simply indicate differences in isotope fraction, due to starvation or other causes. The observed $\delta^{15}N$ for *Chrysaora* was higher than values reported by Montoya et al. (1990). The estimates from both studies were difficult to fully explain in terms of trophic interactions.

Trophic level estimates for bay anchovy were highly conserved throughout the Bay, averaging almost exactly one trophic level higher than mesozooplankton, their principle diet (Klebasco 1991). During summer in the mid Bay, trophic level estimates for bay anchovy were the same as was predicted by network analysis (Fig. 7-2.). The exception, as with ctenophores and sea nettles was the upper Bay in fall. Here, bay anchovy were ~1.5 trophic steps higher than mesozooplankton. The reasons for this are uncertain since there is little evidence that anchovy consume alternate diets, other than small quantities of ciliates.

Average trophic level estimates were computed for 27 taxa or groups of taxa for which samples were obtained an irregular basis (Table 7-5, regularly sampled biota also included). In all cases, trophic level was computed with mesozooplankton as the reference (eq. 2). Average trophic level was found to vary between ~2 and 5.0 and on average was 0.5 trophic steps higher than estimates derived from trophic flow networks (Table 7-5). The suspension feeding polychaetes *Chaetopterus variopedatus* (collected in lower Bay) and *Pectinaria gouldi* (collected in mid Bay) were both very close to TL 2, consistent with the predicted TL. However, *Mulinia lateralis* and *Macoma balthica* (which can also deposit-feed) had a higher trophic level (3.0) than expected (2.1). Since these bivalves were collected in the upper Bay during fall, explanations of inflated TL similar to those for mesozooplankton in the upper Bay may apply here as well. Estimated trophic level for Atlantic menhaden was much greater than the prediction from network analysis, which was based on the assumption that these fish were primarily herbivorous. However, it is known that menhaden consume zooplankton as juveniles and the results obtained here were more consistent with that than with herbivory (Table 7-5). TL estimates for blue crab, spot and

Atlantic croaker, all demersal feeders, were between 3.57 and 3.88 and were consistently a fractional trophic level higher than the 3.2-3.4 estimates obtained from the network analysis (Table 7-5). Average trophic level for weakfish was 3.92, while the average for white perch and striped bass was slightly higher. Estimated TL for these taxa based on $\delta^{15}N$ was nearly a full trophic level higher than the estimates based on network analysis, but was within reasonable statistical uncertainty. Interestingly, the estimated trophic level for *Cyathura*, an isopod that was found in the gills of fish, had a $\delta^{15}N$ suggesting that it had obtained its diet at a very high trophic level. Although *Cyathura* could conceivably have consumed tissues from its host, that would have resulted in higher $\delta^{15}N$ and TL higher than the host, contrary to observation. An alternative possibility is that *Cyathura* was a cleaning symbiont.

Analysis of stable nitrogen isotopic composition in Chesapeake Bay food webs suggested that the average TL for mesozooplankton (TL_{SI}) in the upper Bay was higher than in other regions of the Bay. Although this pattern also appeared in the estimates based on network analysis (TL_{NA}), it was much more pronounced here. Over a large number of taxa, TL_{NA} was 0.53±0.10 (±se) less than TL_{SI}. TL_{SI} was most similar to TL_{NA} when the number of $\delta^{15}N$ observations was large. Stable isotope analysis appeared to provide an interesting independent test of TL_{NA}, but often the likely uncertainty in TL_{SI} was as wide as the plausible range for TL_{NA} unless there is no *a priori* knowledge of diet composition. In addition, in a few instances where TL_{SI} was substantially different from TL_{NA}, complex biogeochemical explanations could sometimes be found, undermining the utility of TL_{SI} as a definitive test of the network model.

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Table 7-1. The date of the sampling cruises during which organic matter samples were collected for stable isotope analysis.

Season (Cruise Id.)	Dates
Fall 1995 (95-4)	10/27-11/3/1995
Spring 1996 (96-1)	4/27-5/7/1996
Summer 1996	7/17-7/26/1996
Fall 1996	10/22-11/1/1996
Spring 1997	4/20-4/24/1997
Summer 1997	7/11-7/15/1997
Fall 1997	10/29-11/5/1997
Spring 1998	4/11-4/19/1998
Summer 1998	8/4-8/12/1998
Fall 1998	10/19-10/23/1998

Table 7-2. Mean (±standard error) $\delta^{15}N$ in for each region/season combination. Letters indicated in parentheses show statistical significance of differences between main effect means. Classes not sharing the same letter statistically different ($p<0.05$).

Region	Spring (a)	Summer (ab)	Fall (b)
Seston			
Upper Bay (a)	6.6 (0.42)	8.0 (0.48)	7.9 (0.79)
Mid Bay (b)	9.6 (0.97)	10.4 (0.31)	10.9 (0.24)
Lower Bay (a)	7.3 (0.56)	8.9 (0.58)	7.9 (1.3)
Mesozooplankton			
Upper Bay (a)	12.0 (0.15)	13.8 (0.66)	12.33 (0.58)
Mid Bay (b)	12.3 (0.73)	13.8 (0.79)	14.2 (0.50)
Lower Bay (a)	11.7 (0.13)	12.5 (0.53)	12.6 (0.24)

Table 7-3. Estimated trophic level (±standard error) for mesozooplankton based on PN as the reference sample.

Region	Spring	Summer	Fall
(A)			
Upper Bay	2.64 (0.14)	2.74 (0.11)	2.20 (0.18)
Mid Bay	1.84 (0.09)	2.02 (0.25)	2.05 (0.15)
Lower Bay	2.29 (0.13)	1.91 (0.50)	2.04 (0.09)

Table 7-4. Estimated reference trophic level for mesozooplankton (used in eq. 2) and the resulting trophic level estimates for mesozooplankton based on $^{15}N/^{14}N$. For comparison, the estimated trophic level for mesozooplankton computing from trophic flow networks (Chapter 6) are also shown. Values are for summer (June-August) only.

Region	TL_{ref}	TL_{SI}	TL_{NA}
Upper Bay	1.11	2.85	2.6
Mid Bay	1.18	2.20	2.5
Lower Bay	1.12	2.03	2.5

Table 7-5. Trophic level estimates, referenced to mesozooplankton, for 27 taxa or groups of taxa, arranged in order of increasing trophic level estimate. Trophic level estimates for the most appropriate node of a trophic network model are presented for comparison. YOY=young of the year age class, 1+ = 1+ age class.

Variable	N	TL_{SI}	SD	TL_{NA}	TL_{NA}-TL_{SI}
Microplankton	16	1.82	0.40		
Chaetopterus variopedatus (SF benthos)	1	1.88		2.1	0.22
Pectinaria gouldi (SF Benthos)	2	1.98	0.02	2.1	0.12
Amphipods (unclassified)	2	2.91	0.00	2.1	-0.81
Mysids (unclassified)	1	2.91		2.1	-0.81
Mulinia lateralis	3	3.00	1.10	2.1	-0.90
White Perch (YOY)	2	3.05	0.67	3.4	0.35
Herrings and Shads	6	3.05	0.42	3.6	0.55
Macoma balthica	2	3.08	0.07	2.1	-0.98
Mnemiopsis leidyi	16	3.55	0.65	3.5	-0.05
Atlantic Croaker (1+)	1	3.55		3.2	-0.35
Atlantic Menhaden	4	3.56	0.73	2.1	-1.46
Blue crab	4	3.57	0.80	3.2	-0.37
Spot	2	3.60	1.14	3.2	-0.40
Bay Anchovy	17	3.69	0.43	3.4	-0.29
Atlantic Croaker	1	3.85		3.2	-0.65
Atlantic Croaker (YOY)	1	3.88		3.2	-0.68
Weakfish (YOY)	7	3.92	0.74	3.9	-0.03
Cyathura spp. (parasitic isopod)	1	4.14			
Polychaetes (unclassified)	2	4.16	0.15	2.5	-1.66
White Perch	1	4.29		3.4	-0.89
Striped Bass (YOY)	3	4.35	0.49	3.6	-0.75
Striped Bass (1+)	3	4.46	0.97	3.6	-0.86
White Perch (1+)	1	4.46		3.4	-1.06
Striped Anchovy (*Anchoa hepsetus*)	1	4.52			
Cyanea capillata (nettle)	1	4.88		4.4	-0.48
Chrysaora quinquecirrha (nettle)	8	5.02	0.81	4.4	-0.62

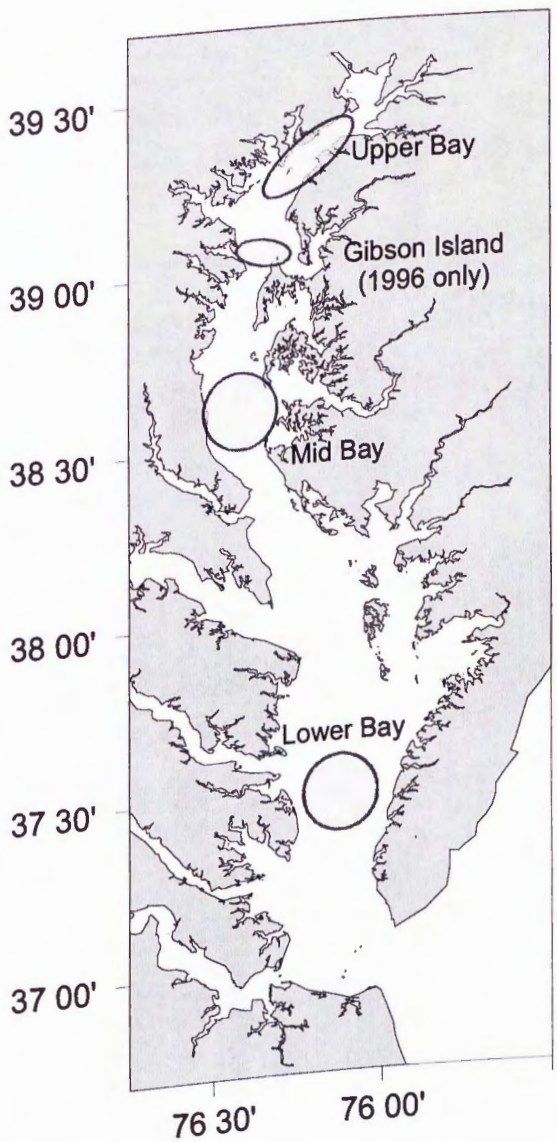

Fig. 7-1. The three general regions of the Chesapeake Bay within which collections of organisms and organic matter were completed for stable isotope analysis.

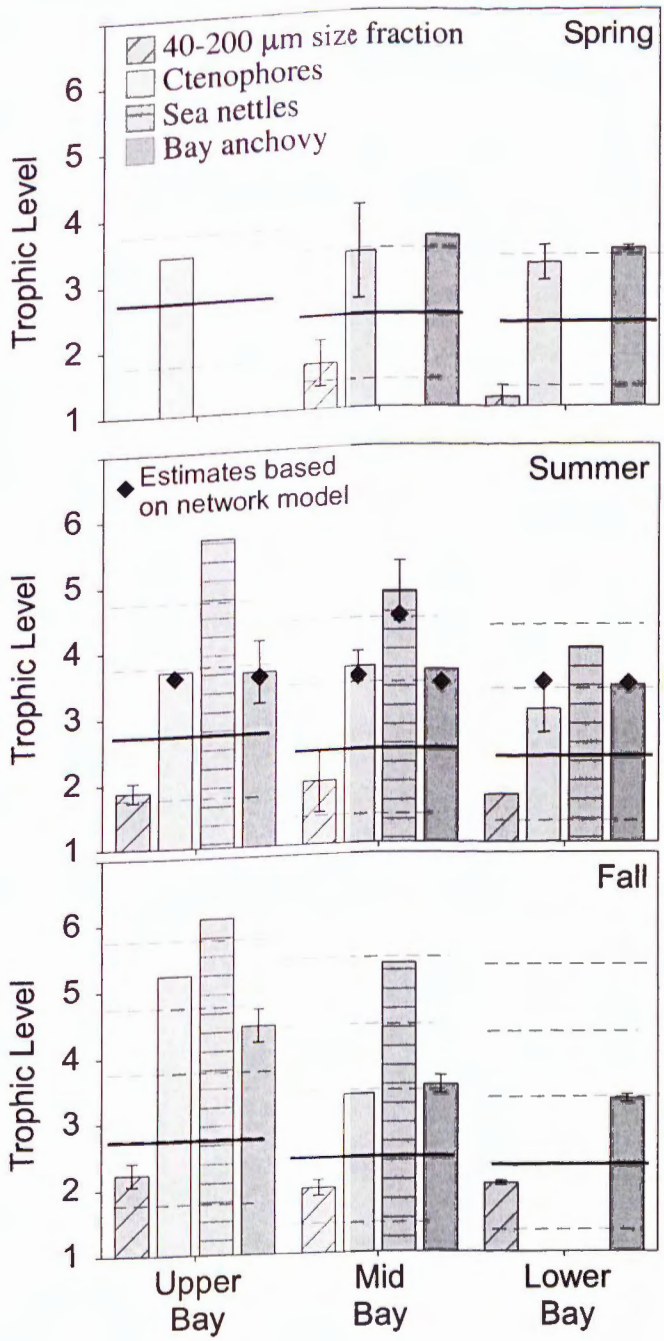

Fig. 7-2. Average (±standard error) trophic level (TL) estimates for the 40-200 µm plankton size fraction, ctenophores (*Mnemiopsis leidyi*) , sea nettles (*Chrysaora quinquecirrha*), and bay anchovy (*Anchoa mitchilli*) during spring, summer and fall. Heavy references lines indicate the TL estimate for mesozooplankton, which was used as a reference (eq. 2). Dotted lines indicate integer trophic steps from the TL of mesozooplankton. Summer TL estimates based on network analysis were obtained from Chapter 6.

Appendix:

PARAMETERIZING THE SUMMER TROPHIC FLOW NETWORKS FOR CHESAPEAKE BAY

This appendix provides supporting methodological details and discussion relating to the estimation of the parameters of the trophic flow networks presented in Chapter 6. The appendix is organized into sections based on sub-sections of the trophic flow networks (e.g. primary production, zooplankton, benthos, nekton).

Organic Storage, Primary Production and Bacteria

The major sources of organic matter for Chesapeake Bay food webs include external inputs of particulate and dissolved organic carbon from rivers and phytoplankton production. Kemp et al. (1997) estimated that these sources account for 98.7% of their 3.96 10^{12} gC estimate of the annual organic matter supply, with 92% of the total coming from phytoplankton production. The remainder was estimated to come from submersed and emergent vascular plants (1.3%) and atmospheric inputs (<1%). For this study, microphytobenthos was also considered as a possible source of organic matter, which increases the total input estimate slightly. Total phytoplankton production was divided into net phytoplankton and autotrophic picoplankton. Because all calculations were made to pertain only to summer, net changes in organic matter storage is also possible. A net decrease in organic matter

storage (e.g. in sediments) amounts to a detritus subsidy of the summer food web by the spring food web.

POC and DOC Storage and Physical Transport

Kemp et al. (1997) describe an annual organic carbon budget for Chesapeake Bay. Organic matter inputs come from the Susquehanna River, other tributary rivers, below fall-line sources, and atmospheric deposits. Because the present study was limited to summer, new estimates were made using these estimates as a general guide.

Summer average total organic carbon loads from the Susquehanna River at Conowingo Dam were obtained from the USGS River Input Monitoring Program (Langland et al. 2001) and apportioned into particulate and dissolved fractions according to the ratio of summer average particulate organic carbon (POC) and dissolved organic carbon (DOC) at the Chesapeake Bay Water Quality Monitoring Program station located adjacent to the Susquehanna River mouth (station CB1.1). From 1992 to 1995, POC and DOC at this station averaged (±sd) 2.8±0.42 and 0.95±0.23 mg l^{-1}, respectively, giving an ~3:1 ratio. The summer average loading of TOC to the upper Bay from the Susquehanna River during 1985-1999 was 165±49 tons d^{-1} (tons=10^6 g). Therefore, POC and DOC inputs were estimated to be 41 and 124 tons d^{-1}, respectively. The estimated summer TOC input rate is 40% of the rate reported by Kemp et al. (1997), reflecting TOC input from the Susquehanna River below the annual average.

Transport of organic carbon between the regions and between the lower Bay and the coastal ocean is difficult to calculate reliably, especially for particulates for

which transport depends not only on patterns of water transport, but also on sinking, deposition to sediments, and resuspension. In part, these dynamics explain the strong tendancy for estuaries to retain particles, most notably the upper Bay, within which it has been suggested that nearly all particulates entering from the Susquehanna river are retained (e.g. Schubel and Carter 1977, Hobbs et al. 1992). Recent studies also show that in the upper Chesapeake Bay this retention mechanism can extend to biological particles such as zooplankton (Roman et al. 2001) and fish eggs and larvae (North 2001). It was assumed here that throughout the tidal Chesapeake Bay system, all seaward POC transport during summer was balanced by an equal landward POC transport. This includes transport between the regions and between the mainstem Chesapeake Bay and the tidal trbutaries.

DOC can be assumed to remain relatively well mixed within the mixed layers of the water column. Therefore, the DOC transport was estimated as the product of average advection rates between the regions, estimated using a box model (Chapter 1), and average DOC concentrations in the advected water. DOC export from major tributaries was estimated as the product of surface water DOC concentration and the net outflow of water. For the upper Bay, summer advection from the upper Bay into the mid Bay averaged 1127 $m^3 s^{-1}$ during 1986-1998. Landward advection from the mid Bay accounted for 593 $m^3 s^{-1}$, while freshwater inputs accounted for the remainder, 98% of which came from the Susquehanna River. The outflowing water had a summer average DOC concentration of 2.84 mg l^{-1}, while the landward advecting water had average concentration of 2.57 mg l^{-1}. Therefore, the net DOC transport to the mid Bay amounts to 135 tons d^{-1}.

The average surface layer advection from the mid Bay to the lower Bay during summer was estimated to be 4661 $m^3 s^{-1}$, while the landward advection in the bottom layer was 3846 $m^3 s^{-1}$. Net advection from the upper Bay plus the Potomac River discharge (above and below fall line, Chapter 1) account for 91% of the difference, the remainder coming from smaller tributaries. The seaward and landward flowing water had average DOC concentrations of 2.88 mg l^{-1} and 3.06 mg l^{-1}, respectively, giving a net DOC transport to the lower Bay of 199 t d^{-1}. Freshwater discharge from the Potomac River averaged 207 $m^3 s^{-1}$ in summer, while the DOC concentration in outflowing surface waters in summer averaged 2.77±0.34 mg l^{-1}. Therefore the net advective output from the Potomac River estuary was 49.5 tons d^{-1}. Combined with the DOC exported from the upper Bay, this accounted for 93% of the export. The remaining external DOC sources were not estimated and may be smaller or greater than the remaining 7%.

Advection from the lower Bay to the coastal ocean was estimated to average 10152 $m^3 s^{-1}$ during summer. Landward advection was 9058 $m^3 s^{-1}$ and the net advection from the mid Bay was 815 $m^3 s^{-1}$, accounting for 97% of the seaward flow. The combined discharge of the James and Appomattox Rivers was 170 $m^3 s^{-1}$, 60% of the remainder. The average DOC concentration in the waters advecting into the coastal ocean was 2.2 mg l^{-1}, while landward flowing water had a DOC concentration of 1.77 mg l^{-1}, giving a net DOC export of 586 tons d^{-1}. This summer rate is 25% less than the annual average carbon export rate which can be computed from Table 5 in Kemp et al. (1997). Since summer export is probably lower than the annual average, this is taken to indicate reasonable agreement between these two studies. The average

DOC concentration in the seaward flowing waters of the James River during summer was 3.26±0.38 mg l^{-1}, giving an average DOC export of 48 tons d^{-1}. Combined with the net seaward transport from the mid Bay, the total net inputs amount to 247 tons d^{-1}, only 42% of the net export. This implies that the lower Bay ecosystem was either a substantial net source DOC during summer, that a significant source has been omitted, or that the export has been significantly overestimated.

The storage of POC and DOC in the three regions was computed from the Chesapeake Bay Monitoring Program water quality data at a series of 20 stations located down the axis of Chesapeake Bay (Table A-1). Phytoplankton biomass accounted for 30%, 38%, and 30% of POC in the upper, mid and lower Bay respectively and was subtracted from the POC to obtain estimates of detrital POC storage (Table A-2). Bacterial biomass was also a significant component of the suspended POC (Table A-6), but could not anambiguously be subtracted from the POC because the GF/F filters used to measure POC cannot be expected to retain all free-living bacteria. Therefore, 50% of free-living bacterial biomass was subtracted from POC while the remainder was subtracted from DOC, a miniscule adjustment to the DOC pool (Table A-1). Regional differences in detrital POC and DOC storage mostly reflect differences in mean depth.

Phytoplankton

Phytoplankton production (PP) in Chesapeake Bay has been studied in extraordinary detail, with at least two studies resolving spatial, seasonal and interannual variability (Kemp et al. 1997, Smith 2000, Harding et al. 2001) using a

large number of observations, each of which was derived from carefully executed field assays. Seasonal/regional estimates of primary production rates determined using ^{14}C-uptake vs. O_2-evolution methods (Kemp et al. 1997, Harding et al. 2001) do not diverge exceedingly, providing some confidence that large errors in specifying the average PP can be avoided. However, methodological concerns persist. In particular, ^{14}C-based methods may underestimate gross PP due *inter alia* to excretion of photosynthate as DOC and phytoplanktonic respiration. Correction for excretion is complicated by the potential for DOC to reenter the particulate phase through bacterial uptake. In applying ^{14}C-uptake assays, shorter incubations lead to estimates closer to gross PP, while longer incubations appproximate net PP. Harding et al. (2001) estimated gross PP using a series of 4-6 hr incubations and net PP using a single 24-hour incubation, finding that gross ^{14}C-PP was ~23% higher than net ^{14}C-PP. Using concurrent estimates of net and gross PP measured as O_2-evolution (e.g. Smith 2000), Harding et al. concluded that the photosynthetic quotient (=O_2 produced/CO_2 fixed) was as high as 1.48 for gross PP, higher than the estimate of Stokes (1996), suggesting that the gross PP estimates of Kemp et al. (1997) should be revised downward. Due to the ambiguity inherent in using ^{14}C-uptake assays to estimate gross PP, it was assumed here that the estimate of Stokes (1996) for PQ (=1.2) was correct. Therefore, estimates of gross PP were derived from the summer average net ^{14}C-PP values of Harding et al. (2001) by converting to gross ^{14}C-PP (x 1.229), then applying the further correction implied by the discrepancy in PQ estimates (1.48/1.2=1.233). Thus, gross PP=(1.233)(1.229)(net ^{14}C-PP). The resulting estimates of gross PP should be comparable to the summer gross O_2-PP estimates computed from data in Kemp et al.

(1997). While there was no obvious bias, it was found that differences among the regions persisted, which was interpreted here as natural variability resulting from different years being included in the two studies. The final estimates of gross PP (hereafter GPP) adopted for this study were those in column (B) of Table A-2. Based on these estimates, phytoplankton GPP/B was estimated to be 0.77, 0.84 and 0.86 d^{-1} for the upper, mid and lower Bay, respectively. Net ^{14}C-PP per unit biomass provided an estimate of regional average phytoplankton growth rates, which were 0.51, 0.56. 0.57 d^{-1} for the same regions.

The fraction of GPP that contributed to phytoplankton growth (i.e. POC production) is reduced by extracellular release of photosynthate as DOC and by algal respiration. Algal respiration is temperature and size dependent and may depend on other factors as well, such as irradiance and taxonomic differences (Tang and Peters 1995). Algal respiration estimates were obtained from the temperature-dependent allometric relationship in Table III of Tang and Peters (1995) and converted to a daily rate by multiplying by a 14-hour daily photoperiod and assuming algal respiration is related to production, with minimal maintenance respiration at night. Thus, specific respiration for microalgae at summer surface water temperatures in Chesapeake Bay (27° C) was estimated to be 0.20 to 0.25 d^{-1}, depending on cell size (see below). Baines and Pace (1991) reviewed estimates of extracellular release (ER) of DOC by phytoplankton from 16 studies providing a total of 225 observations. Importantly, they compared ER to particulate primary production, not GPP. They concluded that ER accounted for 12% of particulate production. In marine systems, this fraction was independent of the primary production rate and of the phytoplankton biomass (Baines

and Pace 1991). Malone et al. (1991) arrived at a similar estimate (15%) for Chesapeake Bay. Expressing particulate production (PP) as $PP=GPP-R-ER$ and substituting $0.12PP$ for ER, it can be shown that $ER=(0.12/1.12)(GPP-R)=10.7(GPP-R)$. Assuming a specific respiration equal to 0.2 d^{-1}, extracellular excretion amounts to ~7% of GPP in all the regions of the Bay. The resulting estimate of phytoplankton growth (i.e. particulate production) is similar to net ^{14}C-PP (Table A-1, Table A-2).

The relative fraction of production contributed by picoplankton (<3 μm equivalent spherical diameter) varies in Chesapeake Bay from <2% from February to May and increases to a summer maximum. Malone et al. (1991) reported that picoplankton production accounted for a maximum of 20% of total production in summer, while Smith (2000) and Smith and Kemp (2001) estimated that this figure may be as high as 45%. The difference may be methodological, since Smith (2000) used a 3 μm filter while Malone et al. (1991) used a 1 μm filter. Smith (2000) also noted that picoplankton accounted for a smaller fraction of phytoplankton biomass and production at shallower stations compared to those in the central channel of the estuary. Thus, the fraction of total production contributed by picoplankton adopted for this study was toward the lower end of estimates (20%), reflecting the large area of shallower waters in the Chesapeake Bay. The fraction of biomass contributed by picoplankton during summer was assumed to be 15% of the total, based on picoplankton vs. total chlorophyll-a concentrations reported by Malone et al. (1991). Specific respiration (R) for picoplankton was assumed to be 0.4 d^{-1} due to smaller cell size (Tang and Peters 1995). Extracellular release of DOC (ER) was estimated using

the procedure described above, although this resulted in slightly lower estimates of ER for picoplankton as compared to GPP because of the higher estimate of R. All rates estimated for net plankton and autotrophic picoplankton are summarized in Table A-3.

Microphytobenthos

The microphytobenthos are the microscopic algae and cyanobacteria that exist on and within the sediments. Although not as well-studied as phytoplankton, recent reviews by MacIntyre et al. (1996) and Miller et al. (1996) provide a perspective on research to date, as well as part of the basis for estimating the production and fate of the microphytobenthos in the mainstem of Chesapeake Bay during summer. In most cases, biomass (chlorophyll-a) and light availability were the most important factors affecting benthic primary production (MacIntyre et al. 1996). Unfortunately, very few measurements have been made in Chesapeake Bay, while Rizzo and Wetzel (1985), who examined the microphytobenthos in the lower Chesapeake Bay, and Macintyre et al. (1996) both emphasized that due to small-scale temporal and spatial variability, a large number of measurements are needed to characterize biomass with precision. Therefore, for this study, emphasis was placed on estimating the available light field and the distribution of shallow water sediments. The daytime average light-saturated gross production rate (Pmax) during summer was reported to be ~80 mg C m^{-2} h^{-1} (Rizzo and Wetzel 1985), which was converted to a daily integrated rate of 1120 mg m^{-2} d^{-1} by assuming that this average rate was sustained over an average photoperiod of 14 hours. Values of 1.4, 0.8 and 0.6 m^{-1} were adopted for the summer light attenuation coefficient (k_d) in the upper, middle and lower Bay, respectively (Harding

et al. 2001), although it has been shown that nearshore light attenuation in Chesapeake Bay can be very different from open water (Boynton et al. 1999). Daytime average incident PAR during summer was assumed to be 800 $\mu E\ m^{-2}\ d^{-1}$ and P_{max} was adjusted for light limitation using the hyperbolic tangent P-I function of Jassby and Platt (1976). The light saturation parameter was assumed to be 100 $\mu E\ m^{-2}\ s^{-1}$, which is at the low end of the range suggested by Macintyre et al. (1996) but is consistent with the results presented by Kemp et al. (1999). Thus, daily production by microphytobenthos in each region was computed as $\sum_z A_z P_{\max} TANH(I_z/E_k)$ where A_z is the sediment area within 1m depth intervals and $I_z = I_0 e^{-k_d z}$. This model assumes that Pmax does not vary with depth.

Average production for each region was computed by dividing the integral production by the total surface area of the region, which includes a large area of aphotic sediments. Thus, the estimated average production rate for each region is much lower than the production rate for euphotic sediments. Regional mean gross production by microphytobenthos during summer was estimated to be 234, 212, and 234 $mgC\ m^{-2}\ d^{-1}$ in the upper, middle and lower Bay respectively. This amount of production amounts only 6-19% of gross phytoplankton production, indicating that the microphytobenthos are an important carbon source. As indicated by Kemp et al. (1999), the benthic microalgae may be an even more important source of carbon for shallow water habitats (e.g. <4m) where benthic production is greater and phytoplankton production possibly lower.

The biomass of benthic microalgae is very difficult to quantify directly, for reasons outlined by Macintyre et al. (1996). Therefore, the biomass of benthic microalgae was inferred from the estimate of their respiration, by assuming a mass-specific respiration rate of 0.2 d^{-1}. Respiration and extracellular DOC release were assumed to account for 25% and 7% of gross production, respectively, consistent with the rates estimated for net phytoplankton (Table A-3). Thus, the biomass of benthic microalgae was estimated to average 265-293 mg C m^{-2} (Table A-4). As with production, the biomass of benthic microalgae is higher if one considers only shallow waters. According to this computation, the average biomass in sediments 0-4 m deep, converted to chl-a (C:chl-a=50) averaged 14, 23 and 26 mg chl-a m^{-2} in the upper, middle and lower Bay, respectively. The lower Bay estimate is consistent with the 20 mg m^{-2} estimate of Rizzo and Wetzel (1985) for a shallow site in the lower Chesapeake Bay. Many estimates for the biomass of microphytobenthos are much higher (MacIntyre et al. 1996). However, this was not considered cause for revision. Many of the estimates were for intertidal mudflats which can achieve much higher biomass and production due to high light levels when exposed at low tide.

Vascular Plants

Submersed aquatic vegetation (SAV) is believed to have been much more extensive in Chesapeake Bay in the past than at present. Based on the 1995-1996 average, approximately 9600 ha in the mainstem Bay were vegetated, accounting for ~5% of total surface area in the upper Bay, and 1.5% of total surface area in the middle and lower Bay (Table A-5, Orth et al. 1997). Since the potental SAV habitat is

probably much less than the entire bottom, this overstates the possible extent of degradation, but this small fraction illustrates the limited contribution of SAV to total primary production in Chesapeake Bay. That said, SAV communities are among the most productive plant communities in the world (Duarte and Chiscano 1999), justifying some further consideration.

The SAV communities in mainstem Chesapeake Bay include a mixed assemblage of freshwater and low salinity species (e.g. *Vallisneria americana*, *Myriophyllum spicatum*) in the upper Bay. The mid Bay community included *Ruppia maritima* and *Zostera marina*, but for this study was assumed to be dominated by Z. *marina* since most of mid Bay SAV was at the southern extreme of the region (Orth et al. 1997). The lower Bay community was clearly dominated by *Zostera marina*. For the upper Bay, the biomass in vegetated areas was estimated to average 120 g dry wt. m^{-2}, of which 20% is below-ground biomass (Kemp et al. 1984). For the lower Bay, the biomass density in vegetated areas was estimated to average 300 g dry wt. m^{-2}, of which 33% is below-ground biomass. This biomass estimate is at the upper end of estimates for Z. *marina* communities in Chesapeake Bay reported by Wetzel and Penhale (1983), well within the range reported by Orth and Moore (1986) and at the low end for Z. *marina* wordwide (Duarte and Chiscano 1999). The carbon content of SAV was assumed to be 45% of dry weight.

Kemp et al. (1986) estimated a maximum summer SAV production rate of 1.3 g O_2 m^{-2} d^{-1} for upper Bay SAV communities. This was converted to carbon units assuming PQ=1.2 to obtain a rate of 406 mgC m^{-2} d^{-1}. An estimate of production for the middle and lower Bay was derived from Fig. 1 in Duarte and Chiscano (1999) by

assuming that *Z. marina* beds in Chesapeake Bay were slightly less productive than most (i.e. the mode). Thus, above and belowground production was estimated to total 2.8 g dry wt. m^{-2} d^{-1}, or 1260 mgC m^{-2} d^{-1}. The turnover rate amounts to ~0.01 d^{-1}, consistent with rates reviewed by Cebrian (1999). Although this production rate is comparable to that of phytoplankton, the contribution to total primary production is minimal since SAV communities account for only a small fraction of the total area of each region (Table A-5).

Planktonic Bacteria

The bacterioplankton and protozoa are an important part of the food web, providing a trophic pathway between dissolved organic carbon (DOC) and metazoans as well as dissipating considerable quantities of energy from the ecosystem. Bacterial biomass is commonly estimated using acridine orange direct counts (AODC), which provides an estimate of bacterial abundance. Ducklow and Shiah (1993) and Shiah and Ducklow (1994) estimated bacterial abundance in surface and bottom waters at a series of stations along the axis of Chesapeake Bay and reported averages for the upper, middle and lower Bay. Observations were collected thorughout the year during 1990 and 1991. Ducklow and Shiah (1993) converted bacterial counts to carbon biomass using the factor 2 x 10^{-14} gC $cell^{-1}$ and this was adopted here as well. An assay utilizing a fluorogenic tetrazolium dye (CTC) has been used to show that much of the bacterial community in Chesapeake Bay is not active, a result which has been repeatedly observed elsewhere as well (Smith 1998). The largest fraction of CTC-active bacteria (27%) was found in summer, while in other seasons an even larger

fraction was inactive (Smith 1998). These results indicate that metabolic rates for the bacterioplankton as a whole should not be based on cell-specific rates. This suggestion was heeded, as rates were based on direct measurements. However, estimates of bacterial biomass utilized for this study were not adjusted to reflect only CTC-active cells. CTC-inactive cells were considered living biomass (rather than detritus) because at least one study has demonstrated that these cells can become CTC-active under appropriate environmental conditions (Choi et al. 1999).

Bacterial production is commonly quantified by measuring uptake of tritiated (^{3}H) thymidine (TdR) or leucine during short incubations. Rates based on TdR obtained from Shiah and Ducklow (1994) and Ducklow and Shiah (1993) were utilized for this study. TdR assays were performed at the same locations and times that AODCs for bacterial abundance were performed. For this study, a factor of 2 x 10^{18} cells produced per mole of thymidine incorporation (Ducklow and Shiah 1993), combined with the above biomass per cell, was used to convert TdR to carbon production rates. Hourly rates were extrapolated to daily rates by assuming constant bacterial production.

Summer bacterial biomass was much higher in the mid Bay (2710 mgC m^{-2}) than in the other regions of the Bay, despite the fact that bacterial abundance was reduced in bottom waters in the mid Bay, but not elsewhere (Table A-6, Shiah and Ducklow 1994). Similar measurements reported by Duckow and Shiah (1993) for the 1980's indicated slightly lower, but still high bacterial biomass (2059 mgC m^{-2}). Summer average bacterial production in the mid Bay was 1633 mgC m^{-2} d^{-1}, giving an average turnover time of 1.25 d. Because many cells are inactive (e.g. Smith 1998),

turnover times for actively growing cells was likely much higher. Bacterial biomass in the upper Bay averaged 709 mgC m^{-2}, while production was 390 mgC m^{-2} d^{-1}, giving an average turnover time of 1.8 d, somewhat slower than in the mid Bay. Bacterial biomass and production in the lower Bay was 924 mgC m^{-2} and 557 mgC m^{-2} d^{-1}, indicating that biomass turned over every 1.7 d (Table A-6). The spatial pattern of bacterial biomass and production mirrored that of phytoplankton production, perhaps reflecting the coupling between plankton production and respiration (e.g. Smith 2000).

Bacterial consumption and respiration was estimated via an assumed bacterial growth efficiency (GE). del Giorgio and Cole (1998) found in a review that this value increased with bacterial production rates from a minimum value toward an asymptotic value of ~0.5 when bacterial production reached 5 μgC l^{-1} h^{-1} according to $GE = \frac{0.037 + 0.65P}{1.8 + P}$. Using surface water bacterial production rates in this equation, GE for Chesapeake Bay during summer was to be 0.43, 0.52, and 0.39 in the upper, mid and lower Bay, respectively. These rates are slightly higher than the average (0.30) estimated for the York River, VA on a summer cruise (Raymond and Bauer 2000), but were within the range of rates observed (8-56%). Smith (2000) estimated that growth efficiency was 24-40% during summer, somewhat lower than suggested here and indicating that a downward revision of the above estimates would be reasonable. Bacterial consumption and respiration was derived from estimated production using these growth efficiencies (Table A-6). The same growth efficiencies were used for both particle-attached and free-living bacteria.

The Plankton Community

The plankton community has been conceived to consist of 5 living components: phytoplankton, bacteria (free and attached), ciliates, heterotrophic microflagellates, rotifers, meroplankton, mesozooplankton, ctenophores (principally *Mnemiopsis leidyi*) and the sea nettle, *Chrysaora quinquecirrha*. The biomass and bioenergetics of phytoplankton and bacteria in Chesapeake Bay have already been described. The remaining components, consisting of the heterotrophic eukaryotic protozoa and metazoans, encompass an approximate size range of 2 μm up to a meter or more in length (*Chrysaora*). The literature describing mixotrophy in Chesapeake Bay was considered; however, it was decided that the biology and particularly the quantitative importance of this process was too poorly known to consider in this study. Heterotrophic microflagellates are typically 2-10 μm. The ciliates include small oligotrichs, scuticociliates, the larger tintinnids. The microzooplankton, ~20-200 μm, include a community of micrometazoa such as rotifers, copepod nauplii, meroplankton and smaller copepodids. Of these, the rotifers and meroplankton were considered separately, while the nauplii and copepodids were evaluated as a component of the mesozooplankton via a stage-structured analysis. Including nauplii, copepodids and adult copepods in a single node was necessary to avoid an error in network analysis procedures for estimating trophic levels that would be caused by improperly representing non-trophic mass-transfers among nodes as predation.

The Chesapeake Bay Monitoring Program conducted monthly surveys of microzooplankton abundance at a series of stations down the axis of Chesapeake Bay since 1984 in Maryland and since 1993 in Virginia. The Maryland and Virginia

components of the program used different sampling protocols, affecting the suitability of the data for use here. Whereas the Virginia monitoring program enumerated all the organisms that passed through a 202 μm mesh by settling the preserved whole water sample, the Maryland monitoring program enumerated all the organisms that passed through a 202 μm mesh but were retained on a 44 μm mesh (EPA 2000). The latter approach is not adequate for sampling the protozooplankton because smaller and relatively fragile organisms are either destroyed or will pass through the larger mesh size utilized (Dolan 1991a, Gifford and Caron 2000). Therefore, the Maryland Chesapeake Bay Monitoring Program data were used only to quantify abundances of metazooplankton, while the Virginia data were also used for estimating ciliate abundance. Data from one station in each region of the Bay were analyzed to estimate summer average abundances, which were converted to biomass using the most taxon-specific factors available. Above- and below-pycnocline averages in each region were combined using appropriate volumes to compute integrated water column biomass. Average abundances for the other groups were obtained from literature values. All biomasses and estimated rates for the zooplankton community are summarized in Table A-7.

Heterotrophic Flagellates

The above- and below-pycnocline abundance of heterotrophic flagellates (H-flag) in the mid Bay was estimated to average 4.5 and 0.8 10^9 m^{-3}, respectively, during summer based on monthly data reported by Dolan and Coats (1990). Using appropriate mixed layer volumes, depth-integrated H-flag abundance was 43 10^9 m^{-2}.

Based on the assumption that these organisms have an equivalent spherical diameter of 2-10 μm, the biovolume per individual was estimated to be 4-104 μm^3, which was converted to carbon using the factor 100 fgC μm^3 reported by Børsheim and Bratbak (1987). A mid-range diameter of 5-6 μm gave a biomass estimate of 3.5 pg C $cell^{-1}$. Thus, the summer biomass of H-flag was estimated to be 149 mgC m^{-2} (Table A-7).

Fenchel (1982) found that H-flag growth increased with bacterial abundance, reaching maximal rates of 0.15-0.25 h^{-1} at saturating at abundances of 50-100 10^9 l^{-1}. Thus, the highest bacterial abundances in Chesapeake Bay are sub-saturating, suggesting sub-maximal growth rates for H-flag. Moreover, Dolan and Coats (1990) reported that in natural assemblages H-flag was related to bacterial production, rather than bacterial abundance. For this study, it was assumed that *in situ* growth rates were 0.08 h^{-1}, less than the maximal rates. This is equivalent to a doubling time of ~9 h or a daily specific production of 2.8 d^{-1}. Consumption, respiration, and egesta (Table A-7) were computed using estimates of gross and net growth efficiency of 0.35 and 0.60 (Fenchel 1982).

No direct estimates of H-flag abundances were available for the upper and lower Bay. However, Dolan and Coats (1990) reported that H-flag abundance generally correlates with bacterial production. The present estimates of H-flag consumption in the mid Bay accounts for 73% of estimated bacterial production, suggesting that H-flag are the major bactivores. H-flag consumption for the upper and lower Bay was computed by assuming that the same fraction of bacterial production was consumed. H-flag biomass and corresponding bioenergetic rates were computed using the same gross and net growth efficiencies (Table A-7). In all three regions of

the Bay, H-flag biomass was equal to ~5% of bacterial biomass, at the low end of the range reported by Linley et al. (1983) for coastal waters.

Ciliates

The above- and below-pycnocline biomass of ciliates in the mid Bay was estimated to average 14 and 8 mgC m^{-3}, respectively, during summer based on monthly data reported by Dolan and Coats (1990). Using appropriate mixed layer volumes, depth-integrated ciliate abundance was 147 mg C m^{-2}. Ciliate abundance in the upper Bay is poorly known compared to elsewhere in the Bay and has been assumed here to be equal to that of the mid-Bay. For the lower Bay, the Chesapeake Bay Monitoring Program data give a summer average biomass of 13 mg C m^{-2} or 87 mgC m^{-2}, of which equal fractions of the biomass were contributed by tintinnids and oligotrichs (Table A-7).

Dolan (1991b) estimated summer growth rates of ciliates in mesohaline Chesapeake Bay to be ~0.09 h^{-1}, from which a daily production rate of 3.1 d^{-1} can be derived. Verity (1985) reported the food and temperature dependence of tintinnid growth, suggesting maximal growth rates of 2.9 d^{-1} at 25°C. Verity (1991) gave slightly lower rates (0.8 to 2.3 d^{-1} depending on diet) for experiments conducted at 20°C. For this study a growth estimate of 2.5 d^{-1} was utilized for ciliates throughout Chesapeake Bay, reflecting the high water temperature in Chesapeake Bay during summer. Gross growth efficiencies for both tintinnid and oligotrich ciliates have been estimated to be ~50% (Verity 1985, 1991). Verity (1985) estimated the carbon assimilation efficiency for tintinnids to be 63% and this value was applied to all

ciliates. Consumption, respiration and excretion plus egestion was computed from production using these values (Table A-7).

The diet composition of ciliates depends critically on the type of ciliates involved and is therefore difficult to resolve quantitatively with the data available. Dolan (1991a) identified three guilds of ciliates. Microphagous ciliates consume picoplankton sized prey, including bacteria, and are mostly small oligotrichs and scuticociliates. Macrophages consume larger cells and mostly consist of tintinnids and large oligotrichs. The third guild, predatory ciliates, consumes other ciliates and usually contributes a small fraction (3.5%) of total ciliate biomass (Dolan 1991a). Macrophages are usually present only in the surface layer, while microphages are present throughout the water column. Microphages dominate the bottom layer assemblage and can thrive in anoxic conditions by consuming bacteria in the absence of predation by copepods (Dolan 1991b). By comparing clearance rates for a number of bactivores, Dolan (1991a) estimated that ciliates account for ~15% of total bacteriovory. Assuming that all bacterial production is grazed, consumption of bacteria by ciliates is 59, 244 and 84 mgC m^{-2} d^{-1} in the upper, mid and lower Bay respectively. For the mid and lower Bay, this is 33% and 39% of ciliate consumption, respectively, while for the upper Bay, this amounts to only 18% of ciliate consumption. One may speculate that total consumption of bacteria by ciliates exceeds bacterial production in the upper Bay due to allochthonous inputs of bacterial cells. Therefore, it has been assumed here that ciliate consumption of bacteria also accounts for 33% of ciliate consumption in the upper Bay. The Chesapeake Bay Monitoring program data showed that the biomass of oligotrichs and tintinnids was

similar in the lower Bay during summer. Assuming that oligotrichs were microphages and consumed a mixture of bacteria and picoplankton, while the tintinnids were macrophages and did not consume bacteria, the bacteria may be expected to account for about 25% (0-50%) of the ciliate diet, in the same general range as the estimate above.

Rotifers

Rotifers, an important component of freshwater plankton (e.g. Gaedke and Straile 1994), were found by the Chesapeake Bay Monitoring Program to be present during summer in the upper and mid Bay, but not in higher salinity areas. Water-column integrated rotifer biomass was computed to be 14 and 25 mgC m^{-2} in the upper and mid Bay, respectively (Table A-7). Adundances were up to ~100 l^{-1} in surface waters and much lower in mid Bay bottom waters. Two recent studies examined the ecology of the rotifer genus *Synchaeta*, the biomass dominant in Chesapeake Bay, during early spring and late fall (Heinbokel et al. 1988, Dolan and Gallegos 1991). These studies found rotifer abundance to be higher than estimated here for summer, often by 10-fold or more. Loftus et. al. (1972) measured rotifer abundances in summer phytoplankton blooms in the mid Bay during 1971 and also found much higher abundances than were found here. Based on the descriptions of rotifer ecology (e.g. Stemberger and Gilbert 1985), it is speculated that the high abundances that were observed occurred under conditions of higher phytoplankton abundance than is characteristic of Chesapeake Bay during summer. Morover grazing pressure on rotifers may have been reduced (i.e. lower mesozooplankton abundance). As there is

no reason to believe that the sampling protocol employed by the Monitoring Program was not sufficient to accurately sample rotifers, the abundances computed from Monitoring Program data were utilized without modification (Table A-7).

Specific growth rates for two species of rotifers of the genus *Synchaeta* growing at 19°C were 0-0.8 and 0-0.2 d^{-1} and depended on food concentration (Stemberger and Gilbert 1985). The same study estimated food concentrations at half-saturation for these species to be 0.29 and 1.04 $\mu g\ ml^{-1}$ algal dry weight, which is approximately equal to 3 and 10 $\mu g\ l^{-1}$ chl-a. Thus, growth rates may be ~50% of maximal rates. Egg development times decrease 30% as temperature increases from 19-25°C, suggesting similarly higher growth rates at summer temperatures in Chesapeake Bay. A rate of 0.3 d^{-1} was adopted here based on the temperature-corrected average of these two species growing at half-maximal rates. In the absence of specific data to indicate otherwise, net growth efficiency and assimilation efficiency were assumed to be 0.5 and 0.6, respectively, similar to rates adopted for ciliates (Table A-7).

The diet of rotifers depends to some extent on taxonomic differences in feeding mode. The genus *Synchaeta* accounted for 81% and 91% of rotifer biomass in the upper and mid Bay. It employs a rapid sucking action to capture particles and is only effective at ingesting larger algal cells. Therefore, it's diet has been assumed to consist entirely of net plankton. The genus *Brachionus*, which contributes the remaining portion of the biomass, uses ciliary currents to entrain food particles and can ingest a wider variety of particle sizes (Bogdan and Gilbert 1982, 1984, cited in

Stemburger and Gilbert 1985). Its diet was assumed to consist of a mixture of heterotrophic flagellates and autotrophic picoplankton.

Meroplankton

The meroplankton consist of the plankton dwelling larval forms of benthic animals. The Chesapeake Bay Monitoring Program enumerated the meroplankton in the 44-202 μm size-fraction as well as in the >202 μm size fraction. Average summer abundance in both size fractions was greatest in the lower Bay (13 l^{-1}) and least in the upper Bay (7 l^{-1}). Integrated biomass followed the same pattern with biomass approximately 3, 19, and 31 mgC m^{-2} in the upper, mid and lower Bay, respectively (Table A-7). In the absence of more information on these organisms, the specific growth rate for these organisms was assumed to be 0.5 d^{-1}, with assimilation and net growth efficiencies equal to 0.6 and 0.5, respectively. The diets of the organisms is uncertain and their sizes are likely to be variable. It has been assumed that the diet consists of larger phytoplankton cells and microplankton, including ciliates and rotifers.

Mesozooplankton

The biomass and abundance of mesozooplankton was estimated from Chesapeake Bay Monitoring Program data, which utilized both 44 μm (Microzooplankton Monitoring Component) and 202 μm nets (Mesozooplankton Monitoring Component). Data from one station centrally located in each region of the Bay was utilized to compute average abundances of the organisms in this size class.

For the 44 μm fraction, above and below pycnocline abundances were combined in an average weighted by the respective mixed layer volumes in each region. The 202 μm data samples were composited for the entire water column based on oblique tows.

The 44-202 μm fraction sampled the abundance of copepod nauplii which are considered here to be mesozooplankton since production by nauplii contributed to mesozooplankton biomass without trophic transfer. Mean summer abundance of nauplii in the surface layer was estimated to be 84, 108 and 131 l^{-1} in the upper, mid and lower Bay, respectively. Integrated biomass of nauplii, which utilized the bottom layer abundances as well was 31, 83 and 107 mgC m^{-2} (Table A-8).

Abundances in the 202 μm size fraction consistent mainly of calanoid copepods with a small additional contribution by cladocerans. In the upper Bay, three taxa, *Acartia tonsa* (63%), *Eurytemora affinis* (20%) and *Bosmina longirostris* (4%) dominated the summer assemblage. In the mid Bay, *Acartia tonsa* accounted for 94% of total abundance. In the lower Bay, *Acartia tonsa* and *A. hudsonica* combined to account for 51% of abundance, with much of the remainder contributed by cladocerans of the genus *Evadne* and *Podon*. Because of the relatively larger size of *Acartia* spp., however, *Acartia* accounted for 85% of mesozooplankton biomass in the lower Bay. In mid Bay, *Acartia* accounted for 98% of biomass, while *Acartia* and *Eurytemora* combined to account for 95% of biomass in the upper Bay. The biomass of *Eurytemora* in the upper Bay may be underestimated by these data because recent research has shown that abundance is often much greater near the bottom in the vicinity of the estuarine turbidity maximum than in the water column as a whole

(Roman et al. 2001). However, because it is not clear at present how to properly adjust abundance to account for this, no adjustment was made.

Total mesozooplankton biomass in the >202 μm size fraction was estimated to be 57, 43 and 105 mgC m^{-3} in the three regions of the Bay, which when integrated over mean depth amounts to 251, 443 and 966 mgC m^{-2} (Table A-8). Because substantial dominance of biomass by *Acartia* spp., energetic rates and diet information for this taxa were applied to the entire mesozooplankton biomass. The abundance of copepod nauplii has already been considered based on the 44-202 μm size fraction. To examine the production of *Acartia*, the >202 μm data were used to examine the relative abundance of copepodites and adults, which have substantially different patterns of production (Heinle 1966, Kimmerer 1987, White and Roman 1992). Heinle (1966) estimated stage durations, mean weight at each stage, stage-specific mortality, and total production of *Acartia tonsa* in Patuxent River, MD. White and Roman (1992) estimated egg production rates for *Acartia* in mesohaline Chesapeake Bay. The stage-structured modeling approach suggested by Kimmerer (1987) was used to reconcile abundance estimates for nauplii, copepodites and adults and compute specific production rates. This computation suggested that the estimated rates and abundances were essentially compatible, except for the abundance of copepodids, which was improbably low considering the abundance of nauplii and adults. One hypothesis is that given the mesh size used (202 μm), the smaller copepodite stages were undersampled. Including these stages would likely increase copepodite numbers and biomass ~2-fold. An alternative hypothesis, however, is mortality rates for copepodids was higher than suggested by Heinle (1966), due to predation or

starvation. These two possibilities cannot be resolved here. Based on the stage durations and weight at stage obtained from Heinle (1966), specific production of nauplii was estimated to be ~1 d^{-1}, while that of copepodites was ~0.5 d^{-1}. Production by adult copepods was assumed to consist solely of egg production, for which a summer average carbon-specific rate of 0.14 d^{-1} was determined for the mid Bay from White and Roman (1992, avg. 1.37 μgC female d^{-1}, ~5 μgC $female^{-1}$, ♂:♀=0.5). Overall population P/B for the mid Bay was ~0.5 d^{-1}, which was consistent with food-replete specific growth rates estimated by Berggreen et al. (1988). This rate was therefore applied to the combined biomass of nauplii plus mesozooplankton in the mid Bay (Table A-8).

Adult copepod abundance in the lower Bay was much higher than in the mid Bay, perhaps due to reduced predation pressure. While the abundance of nauplii was also slightly higher than in the mid Bay, the ratio of nauplii abundance to adult abundance was 6.0, ~41% of the mid Bay value. This implies that *Acartia* egg production in the lower Bay was lower than in the mid Bay, perhaps due to food limitation (White and Roman 1992, Kiørboe et. al. 1985, Kiørboe and Nielsen 1994). Berggreen et al. (1988) showed that under food limited conditions, mortality rates, stage duration and weight at stage change for copepodids, but not nauplii. Accordingly, egg production is an index for overall population growth (Berggreen et al. 1988). Thus, it was assumed that production by copepods in the lower Bay was ~50% of mid Bay rates, or 0.25 d^{-1}. The ratio of nauplii abundance to adult abundance in the upper Bay was between the respective values for the mid and lower Bay.

Accordingly, production in the upper Bay was assumed to be 0.37 d^{-1}, an intermediate value (Table A-8).

The bioenergetics of *Acartia tonsa* were examined in considerable detail by Kørboe et al. (1985), who showed that assimilation efficiency and net growth efficiency changed with food concentration. At high food concentrations, both assimilation and net growth efficiencies were reduced. In all regions of Chesapeake Bay, estimated concentrations of phytoplankton and ciliate carbon are sufficient to ensure that the lower efficiencies are applicable. Accordingly, carbon assimilation efficiency has been assumed to be 0.55, while net growth efficiency is 0.75 (Kørboe et al. 1985). Identical efficiencies were assumed for nauplii, copepodites and adults (Table A-8).

Gelatinous Zooplankton

There are 5 major taxa of gelatinous zooplankton in Chesapeake Bay. These include the scyphomedusae *Chrysaora quinquicirrha* and *Cyanea capillata*, the ctenophores *Mnemiopsis leidyi* and *Beroe ovata* and the hydromedusan *Nemopsis bachei*. *Nemopsis* is the most important gelatinous predator in late spring, but abundance declines into summer, while other species become more abundant (Purcell and Nemazie 1992). Sampling difficulties also impede quantification of *Nemosis* abundance when large quantities of *Mnemiopsis* are present (J. Purcell, personal communication). *Cyanea* and *Beroe*, although not rare, are present in insignificant numbers during summer relative to the other species. *Beroe* was present in <4% of samples collected during summer in the mid-Bay by the Chesapeake Bay Monitoring

Program (CBMP, unpublished data). *Beroe* abundances are typically highest in the high salinity waters of the lower Chesapeake Bay during fall (Purcell et al. 2001). *Cyanea* typically disappears from Chesapeake Bay by May. Thus, the gelatinous zooplankton community, as represented in the trophic network models for summer, includes only *Mnemiopsis leidyi* and *Chrysaora quinquecirrha*.

Abundance of *Mnemiopsis* and *Chrysaora* was estimated using data from the Chesapeake Bay LMER (TIES) program and from the Chesapeake Bay Monitoring Program (CBMP). Data from TIES included ~50 stations throughout the Bay sampled once per summer using two 2-minute Tucker Trawl tows per station, each with a 1 m^2 net opening and a swept volume of ~115 m^3. Data were obtained for the summer cruises in 1995, 96, 97 and 2000. Data from the CBMP included 4 stations sampled three times per summer in each year from 1984-1998. One station (CB2.2) was in the upper Bay, while three stations (CB3.3C, CB4.3C, CB5.2) were in the mid-Bay. Oblique tows with bongo nets were used, filtering ~15 m^3 tow^{-1}.

Biovolumes of *Mnemiopsis* varied regionally within the Bay and interannually (Table A-9). *Mnemiopsis* biovolume was minimal within the upper Bay, highest in the mid-Bay, and slightly lower in the lower Bay. Interannual variations were likely related to temperature and freshwater inputs, which affect reproduction of both *Mnemiopsis* and *Chrysaora* (Purcell et al. 1999). The estimated summer average biomass for *Mnemiopsis leidyi* in the mid-Bay region is 132 mgC m^{-2}, based on the converion 1 ml = 1.012 mg WW = 0.485 mgC (Nemazie 1991). *Mnemiopsis* biomass for the upper Bay and lower Bay is estimated to be 18 and 115 gC m^{-2}, respectively.

Abundance estimates for *Chrysaora quinquecirrha* were obtained only from the TIES data (J. E. Purcell, unpublished data) because the Chesapeake Bay Monitoring Program sampling technique did not sweep a sufficient volume to obtain an estimate of *Chrysaora* abundance. Unfortunately, at average abundance levels, even the much higher swept volume of the TIES tucker trawls was marginally sufficient for sampling *Chrysaora* abundance except when abundance was high. For example, the high abundances observed in the mid-Bay in 1995 were 0.03 m^{-3}, or 3.5 tow^{-1} at 115 m^3 tow^{-1}. At the much lower average abundance in the south Bay in 1995 (ie. 0.001 m^{-3}), one expects to catch a single medusa once every 10 tows. At such a low expected catch, these tows provide an uncertain estimate of *Chrysaora* abundance at best.

As with *Mnemiopsis*, summer *Chrysaora* abundance varied regionally and interannually (Table A-10). The highest abundances were always in the mid-Bay region; abundance was usually negligable outside the mid-Bay. Increased abundance occurred in years with low freshwater input (e.g. 1995, 1997). In the mid-Bay, biomass averaged ~6.3 $mgCm^{-2}$ in the mid-Bay, computed using 1 ml biovolume = 1.75 mgC (Purcell 1992; Purcell, J. E., personal communication).

Procedures for estimating consumption and growth of gelatinous zooplankton are described below. Egestion was estimated from the carbon balance equation and the other estimates. The best estimates of the growth dynamics of *Mnemiopsis* are based on laboratory experiments reported by Reeve et al. (1989) for *Mnemiopsis mccradyi*. References to this study by Purcell et al. (2001) and others imply that experts in the field believe it reasonable to also apply these growth dynamics to

Mnemiopsis leidyi. Specific growth for *Mnemiopsis* increases with prey density and decreases with size of the ctenophore. Assuming zooplankton concentrations of ~20 l^{-1}, specific growth for small (15mm) *Mnemiopsis* is ~0.4 d^{-1}, while specific growth for larger individuals (50mm) is ~0.2 d^{-1}. At higher prey density, specific growth of larger ctenophores was only slightly higher (0.3 d^{-1}), while growth for smaller individuals was much greater, 0.8 d^{-1} (Reeve et al. 1989). At lower prey density ~10 l^{-1}, consistent with average abundance in middle Chesapeake Bay during summer, specific growth declined significantly to ~0.1 d^{-1}. *Mnemiopsis* could not grow at zooplankton abundances lower than 8 l^{-1} (Kremer and Reeve 1989). At the lower specific growth rate (0.1 d^{-1}) average *Mnemiopsis* growth in the mid-Bay is 13 mgC m^{-2} d^{-1}, while at the higher, food-replete rate, growth is 38 mgC m^{-2} d^{-1} (B=126 mgC m^{-2}). The food-replete growth estimate is approximately the same as the estimated consumption (see below), which implies an improbably high gross growth efficiency (GGE) near 100%. The lower growth estimate (0.1 d^{-1}) and the estimated consumption gives GGE=31%, only slighly lower than the 40% estimated by Reeve et al. (1989). Assuming GGE=40% and consumption=42 mgC m^{-2} (see below) implies an intermediate rate of growth rate of 17 mgC m^{-2} d^{-1} and specific growth rate of 0.13 d^{-1}, the estimate adopted for the mesohaline Bay. Ctenophore production for the upper and lower Bay was computed using the same specific growth rate.

Clearance rates of *Mnemiopsis* depend on predator size, water temperature, and prey type, but do not depend not significantly on prey density. Therefore, *Mnemiopsis* feeding does not saturate at high prey densities (Purcell et al. 2001). For a moderate-sized individual (biovolume = 14 ml) feeding on *Acartia tonsa*, clearance

rates in the field are ~50 l d^{-1}, a volume-specific clearance rate of 3.57 l ml^{-1} d^{-1}. Assuming a summer copepod density of 15 l^{-1}, a copepod carbon content of 3 μgC ind^{-1} and summer average *Mnemiopsis* biovolume of 264 ml m^{-2} in the mesohaline Bay, the consumption rate is estimated to be 42 mgC m^{-2} d^{-1}. Specific consumption is therefore 0.33 (g g^{-1}) d^{-1}. Consumption by ctenophores in the upper and lower Bay was computed assuming the same specific consumption rate (Table A-7).

Respiration rates for *Mnemiopsis* increase linearly with size (Kremer and Reeve 1989). Specific respiration (R_s, d^{-1}) increases hyperbolically with prey abundance (i.e. with ingestion) according to the function

$$R_s = R_b + R_{\max}\left(\frac{P}{K_s + P}\right)$$

where R_b=0.04, R_{max}=0.11, K_s=30 l^{-1} and P=prey abundance (l^{-1}) (Kremer and Reeve 1989). Thus, at P=15 l^{-1}, R_s=0.08 d^{-1}. The mid-summer *Mnemiopsis* population respiration rate is therefore $R=R_sB=0.08(126\ mgCm^{-2})=10$ mgC m^{-2}. Ctenophore respiration in the upper and lower Bay was computed assuming the same specific respiration rate. Excretion of DOC is estimated to be 50% of respiration (Kremer and Reeve 1989).

Egestion was calculated by difference, giving a mid-Bay estimate of 11 mgC m^{-2}. At 26% of consumption this implies an assimilation efficiency (AE) of 74%. Gross growth efficiency is 40%, while net growth efficiency is 51%. The estimated efficiencies depend on the average size of the ctenophore and prey (copepod) density, which were assumed to be 14 ml ind^{-1} and 15 l^{-1}, respectively. Consumption by ctenophores increases proportionately with prey density since clearance rate is

constant. Specific growth increases rapidly with prey density for small individuals, but only slowly for large individuals. Respiration rates increase toward an asymptote. Thus, in an alternative scenario where prey (copepod) density is 100 l^{-1}, specific growth is 0.5 d^{-1}, specific respiration 0.15 d^{-1}, and specific consumption 2.22 d^{-1}, GGE decreases to 23%, driven significantly by AE decreasing to 31% (Kremer and Reeve 1989). Such high prey abundances are not uncommon in Chesapeake Bay, but exceed the average significantly. This computation illustrates that under these conditions, *Mnemiopsis* grows rapidly and also shunts large amounts of zooplankton production to detritus. As previously noted, below average prey abundance results in mortality of *Mnemiopsis* due to starvation.

The bioenergetics of *Chrysaora quinquecirrha* are not as well-studied as that of *Mnemiopsis*. Some investigators have assumed that growth dynamics of *Chrysaora* are similar to that of *Mnemiopsis* (e.g. Baird and Ulanowicz 1989); however, published sources indicate that this is not appropriate, especially for the mainstem Chesapeake Bay where individual medusae tend to be large. Such large individuals (e.g. 80 mm bell diameter) have very low specific growth (~0.02 d^{-1}; Larson 1986) which contrasts with higher specific growth rates for *Mnemiopsis*. Such low growth rates can be reconciled with the apparently high abundance of medusae in two ways. First, high abundances of smaller individuals occurs in the tributaries, and these areas may serve as a source for larger individuals in the mainstem of the Bay. Secondly, because medusae have no significant predators in Chesapeake Bay, even slow growth rates can lead to significant biomass accumulation over time.

Consumption by medusae is the only well-studied aspect of *Chrysaora* bioenergetics. Like *Mnemiopsis*, diet composition and consumption rates for medusae depend on abundances of suiTable A-prey items. Clearance rates vary significanctly according to prey type, with clearance of *Mnemiopsis* being by far the highest. For a large individual (80 mm diam.), *Mnemiopsis* clearance is estimated to be ~2 m^3 d^{-1} (Purcell and Cowan 1995). At an average mesohaline Bay ctenophore density of 3 m^{-3} (6.7 mgC ind^{-1}) ctenophore ingestion by a single medusa is estimated to be ~40 mgC d^{-1}. At the average medusa density this amounts to 3.5 mgC m^{-2} d^{-1}. The high clearance rate for ctenophores makes *Mnemiopsis* the largest diet component (90%) at ctenophore abundances typical of Chesapeake Bay. However, ctenophores are often nearly eliminated from waters where *Chrysaora* is present in significant abundance, making other diet components more significant at those times. In a scenario where *Mnemiopsis* is absent or nearly so, copepods, anchovy eggs and anchovy larvae are estimated to account for 46%, 42% and 12% of the much smaller diet, respectively.

Volume-specific clearance rates for medusae feeding on copepods is much less than for ctenophores and depends on medusa size, water temperature and prey density (Purcell 1992). An 80 mm medusa (biovolume=41 ml) at 27°C is estimated to clear copepods at density=15 l^{-1} at a rate of 48 l d^{-1}, comparable to an average ctenophore (biovolume=14 ml). At this clearance rate, daily copepod consumption is 720 d^{-1}, or 2.2 mgC d^{-1}. At the average abundance of medusae, this is 0.2 mgC$m^{-2}d^{-1}$, or ~5% of the diet (Fig 2).

Clearance rates for *Chrysaora* feeding on bay anchovy eggs and larvae, the most abundant fish eggs and larvae in the mid-Bay during summer, were estimated by

Purcell et al. (1994) (see also Houde et al. 1994). For an 80 mm diam. medusa, clearance rates for eggs and larvae are approximately 2.5 and 1.5 m^3 d^{-1}, respectively. These estimates are less certain than estimates for other diet components, particularly in the case of larvae. At average summer prey abundances, ingestion of eggs and larvae is estimated to be 250 and 75 $predator^{-1}$ day^{-1}, or 1.9 and 0.6 mgC d^{-1}. For the population, this is 0.17 and 0.05 mgC m^{-2} d^{-1}, a combined 5.5% of the diet. Note that although copepods are 150 times more abundant than bay anchovy eggs, consumption of eggs by *Chrysaora* is the similar due to the much higher clearance rate for fish eggs and larvae.

Total consumption by the average *Chrysaora* population in the mid-Bay is 3.94 mgCm^{-2} d^{-1}, a specific consumption rate of 0.85 d^{-1} (Table A-7). Assuming 2% growth per day, gross growth efficiency is 2.4% and assimilation efficiency (AE) is 10%. If *Mnemiopsis* were absent, however, specific consumption declines to 0.09 d^{-1}, barely exceeding respiratory demands. To allow for a realistic AE, growth under these conditions must be zero or negative. The ability of *Chrysaora* to survive while losing weight during starvation has been demonstrated in the laboratory and can also be justified by an observed decline in abundance of larger medusae in late summer (J. E. Purcell and R. Rosen, unpublished data).

The estimated consumption of *Mnemiopsis* by *Chrysaora* in the mid-Bay is only 22% of estimated production by *Mnemiopsis*. For *Chrysaora* to consume all *Mnemiopsis* production would require increasing the biomass of medusae by 4 times. Although this abundance (~16 ml m^{-2}) has been observed and is not implausible, it is not consistent with the observed average abundances in the mid-Bay. It seems likely

that food limitation of *Mnemiopsis* may be a factor at times. However, correlative evidence suggests that *Chrysaora* can frequently control ctenophore abundances in the mid-Bay. The diets of *Mnemiopsis* and *Chrysaora* are reasonably well studied. Diet composition varies substantially according to available prey, indicating that these predators are not highly selective (Purcell et al. 2001). However, the gelatinous zooplankton are clearly predators, capturing certain types of prey according to their physiological capabilities rather than filtering any type of biological particle from the water (Purcell 1997). Copepods, copepod nauplii, barnacle nauplii, and bivalve veligers comprise 95-93% of the diet of adult *Mnemiopsis*. Other prey items include a variety of larvae plus ichthyoplankton (Purcell et al. 2001), although Purcell et al (1994) found in a study in Chesapeake Bay that *Mnemiopsis* consumption of bay anchovy eggs was negligable. Although *Mnemiopsis* larvae have been shown to consume phytoplankton and ciliates (Purcell et al. 2001), detritus and attached bacteria and phytoplankton cells are not components of the adult ctenophore diet.

The diet of *Chrysaora* includes *Mnemiopsis*, adult copepods and fish eggs and larvae (Purcell 1992; Purcell et al. 1994; Purcell and Cowan 1995). Copepod nauplii are not as readily captured by *Chrysaora* as are copepodites and adults, and are therefore not a significant part of the diet.

The Benthic Community

The benthos has been characterized as including two types of primary producers (submerged vascular plants and microphytobenthos), sediment-associated bacteria, meiofauna, deposit-feeding macrobenthos, suspension-feeding macrobenthos

and reef-dwelling suspension feeders (principally the oyster *Crassostrea virginica*). Other organisms are clearly present, and may include motile and sessile epifauna (e.g. Sagasti et al. 2000). Some of these organisms may be included in the Chesapeake Bay Benthic Monitoring data, however, adequate representation, particularly of motile species, is not assured. Thus, the role of these animals was neglected in this analysis. Demersal fishes and blue crabs, which are associated with the benthos, were considered separately as part of the fish community. The benthos also includes a stored pool of organic carbon. This is conceived here to be a single pool, although it may include a combination of particulate carbon and dissolved organic carbon confined in sediment pore waters.

Sediment Particulate Organic Carbon and Bacteria

The size of the stored organic pool is not easily quantified or characterized, particularly as the boundary between the stored but available carbon and the permanently buried pool is somewhat arbitrary. The distinction is certainly time-scale dependent as episodic erosion of sediments can return buried carbon to the active pool. Fortunately, the indended analyses were not expected to depend on this value; it was estimated mainly for completeness. It was assumed here that the active pool extends to 5 cm depth, that the sediments contain 80% water, and that the density of dry sediment is 1.1 g cm^{-3}. Accordingly, the active pool of dry sediment is 1.1 (10^4) g m^{-2}. The average carbon content of sediments is approximately 31.5, 18.4, and 7 mgC (g dry sediment)$^{-1}$ in the upper, mid and lower Bay (Kemp et al. 1997). Therefore, the active sediment organic carbon pool is these regions is 346500, 202400, and 77000

mgC m^{-2} (Table A-11). The biomass of meiofauna and sediment bacteria, which is methodologically included in these figures, accounts for <1% of biomass.

Metabolic rates due to sediment bacteria in Chesapeake Bay have been estimated by Cowan and Boynton (1996) and Marvin-DiPasquale and Capone (1998). Cowan and Boynton (1996) described rates of sediment oxygen consumption (SOC) while Marvin-DiPasquale and Capone (1998) measured rates of benthic sulfate reduction (SR). Kemp et al. (1997) assumed that half of SOC was due to SR, and therefore estimate total sediment metabolism SR+0.5(SOC). Furthermore, they assumed that due to substrate limitation, sediment metabolism was reduced by half in shallower waters as compared to the deeper channel regions were the benthic rates were measured more often. This same approach was adopted here. Rates might have been obtained directly from Kemp et al. (1997), except that summer rates were required, while they provided annual estimates. Macrobenthic respiration is theoretically not excluded from the benthic flux measurements. However, it was assumed here that the macrobenthos were patchily distributed and not adequately reflected in the small cores utilized used to measure sediment fluxes. This is known to not be strictly true as macrobenthos, especially smaller animals, were sometimes if not often retained in cores (W. R. Boynton, pers. comm.). The production of bacteria was estimated from benthic respiration assuming bacterial growth efficiency = 0.30. Biomass was estimated from production assuming P/B=1.13 d^{-1} (Table A-12).

Meiobenthos

The benthic meiofauna are commonly defined operationally as those animals retained on an ~50 μm sieve but passing through the 500 μm sieve typically used to retain the macrobenthos. The meiobenthos are often divided into two main groups, harpacticoid copepods and nematodes, which usually constitute a major fraction of the biomass (Fenchel 1978). Other important biota include benthic foraminiferans, ostracods and juvenile polychaetes (Sundbäck et al. 1996). Production of meibenthos has been related to production of microphytobenthos (Montagna et al. 1995), especially in intertidal and lotic environments where the meiobenthos have been studied most extensively. The biomass of meiobenthos has also been estimated via empirically determined ratios between the biomass of meiofauna and that of deposit feeding macrobenthos. It has been suggested that the biomass of meiobenthos amounts to 3-13% of the biomass of deposit feeders (Ulanowicz and Baird 1986 and references cited therein), however, the ratio can be even more variable than that (Flach et al. 1999). Thus, it was assumed here that meiofaunal biomass in Chesapeake Bay was comparable biomass in other mesotrophic to eutrophic temperate estuaries, without consideration of the macrobenthic biomass in Chesapeake Bay. Smol et al. (1994) examined the summer biomass of meiobenthos in the Oosterschelde estuary during summer and observed a total biomass equal to 400-4200 mgC m^{-2}. Further, they noted that higher numbers were associated with higher silt content of sediments. However, the highest biomass was found only on intertidal flats, which are not present in Chesapeake Bay. Sundbäck et al. (1996) examined the meiobenthos at sandy sites in the Skagerrak (Swedish west coast), observing summer biomass at 4 m depth to be

~700 mgC m^{-2}, consistent with the lower numbers suggested by Smol et al. (1994). Sundbäck et al. (1996) also estimated the benthic microalgae at their sites to have a summer biomass of ~1000 mgC m^{-2}, which suggests a similarity between these sites and shallow Chesapeake Bay sites. Accordingly, the meiobenthic biomass in the upper and lower Bay, and at above-pycnocline sites in the mid Bay was assumed to be 700 mgC m^{-2} (Table A-12). Below the pycnocline in the mid Bay, meiobenthic biomass was assumed to be greatly reduced due to the effect of anoxia. A figure of 70 mgC m^{-2} was adopted by assuming that only hypoxia tolerant foraminiferans were present in these areas (Sundbäck et al. 1996, see also Karlsen et al. 2000), and biomass was computed as a weighted mean of above- and below-pycnocline biomass (Table A-12).

Production of meiobenthos was computed using the allometric relation of Banse and Mosher (1980), which is $P/B = 0.65 M_s^{-0.37}$, where M_s is the mass equivalent in kcal (1 g AFDW = 5.5 kcal). They also noted that production for meiofauna may be 3-5 times lower. Ash-free dry weights for typical meiobenthos are: nematodes (0.15-0.59 µg), foraminifera (0.5 µg), harpacticoids (1.2 µg), ostracods (7.5 µg) (Widbom 1984). Thus, these organisms are in the size range of 10^{-7} to 10^{-5} g AFDW, with most being at the smaller end of this range. Thus, appropriate P/B for meiofauna may be 0.01 to 0.07 d^{-1}. Accounting for the dominance of the smaller animals and high summer temperatures, a value of 0.07 d^{-1} was adopted for Chesapeake Bay, similar to the value of 0.1 d^{-1} suggested by Gerlach (1971). Consumption and respiration were computed by setting assimilation efficiency and net growth efficiency to 50%, which is appropriate for a class of aquatic animals

consuming a mixture of algae and detritus (Schroeder 1981). This computation gives an estimated meiobenthic respiration for the upper Bay that is a greater, possibly implausibly greater, fraction of total sediment metabolism than was observed for the other regions of the Bay. The is partly due to the high rates of sulfate reduction which were only found outside the upper Bay. Alternatively, meiobenthic biomass and production may in fact be lower in the upper Bay than suggested here. The diet composition of meiofauna mainly includes benthic algae and sediment bacteria (Sundbäck et al. 1996), but may also include other meiofauna (Table A-12).

Macrobenthos

The macrobenthos are operationally defined as those benthic animals which are retained on a 500 μm seive. The biomass of macrobenthos was estimated from the Chesapeake Bay Monitoring Program, which has quantified the biomass and abundance of the macrobenthos at many sites in Chesapeake Bay on a seasonal basis since 1984. A detailed analysis of macrobenthic biomass and production in Chesapeake Bay was presented in Chapter 4. For this study, the macrobenthos were divided into two feeding guilds, suspension feeders and deposit feeders. Biomass estimates for each region of the Bay for each of these guilds was obtained directly from Chapter 4. Average production/biomass for each region was used for both guilds, except for in the upper Bay, where P/B for deposit feeders was not assumed to be equal to average for the macrobenthos in the region, due to the dominence of slower growing *Rangia*. Rather, a P/B typical of other deposit feeding communities ($0.014\ d^{-1}$) was assumed (Table A-12). Respiration, consumption and egestion were

generated by assuming that net growth efficiency was 0.4 and assimilation efficiency was 0.5, intermediate values within the range considered in Chapter 4 (Table A-12). The diet of the suspension-feeding macrobenthos was assumed to consist primarily of a mixture of particulate organic carbon and net phytoplankton cells.

The macrobenthos is grazed heavily by demersal-feeding fish and crabs. However, harvest by fisheries can also be a significant fate of production. Other than oysters and blue crabs, which are considered separately, the soft-shell clam, *Mya arenaria*, is the only macrobenthic species supporting a significant fishery in Chesapeake Bay (NOAA landings data). Maryland landings reached a peak of ~3500 tons y^{-1} in the 1960s but declined significantly in 1972 and later. The average Maryland landing during 1985-1999 was 634 tons y^{-1}. The catalyst for this change was most likely hurricane Agnes, in June 1972. Landings of *Mya* occur throughout the Chesapeake Bay region and it is likely that a large fraction came from outside of the mainstem Bay. In addition, it is also likely that some of the harvest resulted from production that occurred outside of summer. However, for the purpose of marking a conservative estimate, it was assumed here that all of the landings resulted from summer production in the mesohaline portion of the mainstem Bay (area=2,338 km^2). Accordingly, the production is equal to 0.27 g wet weight m^{-2}, or 0.29 mgC m^{-2} d^{-1} (assuming AFDW=0.2 wet weight, 500 mgC=1g AFDW, summer=92 d). This is equal to 5.3% of the summer suspension feeder production in mesohaline Chesapeake Bay. Considering the extremely generous assumptions, it can safely be concluded that the estimated production of suspension feeders is consistent with the fisheries

landings. Furthermore, the landings do not consitute a significant removal of suspension-feeding production from the system and can be ignored.

Oyster

The biomass and production of the oyster (*Crassostrea virginica*) has been considered separately from the macrobenthos because these animals are known to occupy discrete reef areas and were not sampled by the Chesapeake Bay Benthic Monitoring Program. A separate analysis also permits direct evaluation of the trophic role of this historically important species, which was an important goal of this analysis.

It is well known that the abundance of oysters in Chesapeake Bay and its tributaries has decreased enormously since the early part of the century (Newell 1988, Rothschild et al. 1994). Newell (1988) estimated that by 1988 total biomass had decreased by >99% from pre-1900 levels. An examination of commercial landings statistics shows that oyster landings in both Maryland and Virginia declined in weight and value from most important prior during 1950-1985 to relative obscurity after 1985.

The oyster population that remains at present has been severely affected by diseases (MSX, Dermo) that arrest growth before market size is reached, leading to substantial mortality. Commercal oyster harvest appears to be concentrated into areas where salinity is low enough to reduce disease prevalence, but not low enough to kill the oysters. This makes these populations vulnerable to mortality due to low salinity following flood events (Tarnowski et al. 1994). Appropriate habitats are often short

reaches of the tidal tributaries, which is where repletion efforts have been concentrated (Jordan et. al. 1994). The lower reaches of the same tributaries (e.g. Choptank R., Chester R.) have not supported commercial production due to excessive disease mortality (Jordan et. al. 1994), suggesting that the same problems may befall populations in adjacent regions of the mainstem. Oyster abundance in the Virginia mainstem appears to be below commercially viable levels as well. Hargis and Haven (1994) reported that 94% of 5,484 Va. bushels harvested in the 1993-94 season came from the James River. From this perspective, one may conclude that the commercial harvest does not provide useful evidence for average biomass or production of oysters per unit area in any region of the present-day Chesapeake Bay mainstem, other than to suggest that abundance is below levels in the commercially harvested tributaries.

If one assumes that the abundance of oysters in the mainstem Bay cannot be related to commercial landings, average biomass must be estimated as the product of the area of oyster bottom and the biomass density on those bottoms. The area of shell or "cultch" bottom was surveyed in 1976-1983 by the Maryland Bay Bottom Survey (MBBS) using patent tongs and/or a dragged microphone (Smith 2001). However, a re-examination of a subset of these areas using a sophisticated acoustic seabed classification system, underwater videography, and diver surveys showed that the MBBS could not distinguish between clean shell, suitable as oyster habitat, and shell covered with silt and mud, which is not suitable oyster habitat (Smith 2001). Moreover, of the mainstem oyster bars examined, 80-100% of the bottom was sand or mud, with no clean shell found. This suggests that a computation of the area of oyster bottom in the mainstem Bay based on the MBBS would be erronously high, perhaps

dramatically so. In fact, it seems to suggest that there is no significant area of oyster bottom in the mainstem Bay. This conclusion is also supported by examining the factors that have been associated with healthy oyster beds. For example, oyster bars have been associated with strong currents and high relief bottoms, which deter accumulations of silt. Some areas in the Maryland mainstem are associated with points of land and may be expected to have these characteristics. However, Smith (2001) examined some of these sites and found that none of them supported oyster populations. Although one cannot rule out the existence of oysters in the mainstem Bay, the area of suitable habitat may be minimal. Even if the oyster biomass at the remaining areas was substantial, which it may not be, overrall biomass would be be very low at the whole estuary scale. Compared to the near ubiquitous, even if depauperate, mesohaline infaunal communities, the oyster is probably not important in terms of carbon flow in the mainstem Chesapeake Bay food web. This constrasts with the wide perception of its present and past ecological importance. Where the oyster is present in greater abundances in the tributaries, different conclusions may easily be reached. However, this is beyond the scope of this study.

It is worth noting here that estimates of the biomass of oysters in the mesohaline Bay have been suggested in the past. Baird and Ulanowicz (1989), who described trophic networks for Chesapeake Bay during summer suggested an average mid Bay oyster biomass of 1100 mgC m^{-2}. The estimate was derived (apparently with some incorrect mass-mass conversions) from the biomass estimate of a well-known expert (S. Jordan, MD DNR), who suggested that the oyster biomass for the entire mesohaline oyster population in 1984 was equal to 4 10^6 bushels. Newell (1988)

cited an update for 1988 from the same expert, giving an estimated biomass of 1.1 10^6 kg dry weight, an ~50% decrease from the 1984 estimate (1 Md. bushel = 2.64 kg wet weight, dry weight= 20% of wet weight). Assuming hypothetically that all of the oyster biomass was in the mesohaline mainstem Bay (area=2338 km^2) and that 500 mgC = 1 g dry weight, the average biomass of oysters in the mainstem Bay is 235 mgC m^{-2}. This is 16% of the biomass estimate for the already degraded mid Bay infaunal community and (for comparison) 2% of the biomass estimate for the lower Bay infauna. In contrast to the hypothetical assumption, much of the biomass must be located in the tributaries rather than the mainstem, since this is where the commercial fisheries are concentrated. Thus, if one accepts these estimates of total biomass, the mainstem biomass must be very low. Moreover, commercial harvests in Maryland have declined further in recent years, to 50% of 1988 levels and biomass may have declined commensurately. From these results, it has been concluded that the oyster should be represented as functionally extinct in the mainstem Bay, even as this may not be strictly true, and even as this is arguably not the case in the tributaries, which support substantial ongoing harvests in association with repletion efforts there.

Finfish and Crabs

The Chesapeake Bay supports significant commercial and recreational fisheries. Despite some notable population collapses, total fisheries output has not declined over time indicating that the community continues to be productive (Houde et al. 1999). Species not supporting fisheries are likely to be ecologically important both as predators and prey, although this has not been demonstrated to the extent one might

expect. Good examples of such studies are available for bay anchovy (e.g. Luo and Brandt 1993). For this study, the fish community was analyzed as either individual species or taxonomically-based aggregations (e.g. alosids), primarily because this is the way that data have generally been collected and reported. The objective of this analysis was to characterize the biomass, bioenergetics, and diet of the most important species of fish and crabs in the ecosystem. Importance was determined primarily by relative summer biomass on a regional basis. Feeding guild (e.g. planktivore, benthivore, piscivore) was also considered to ensure representation of each guild. A few commercially and recreationally important species were included in the analysis specifically because of the fishery, although these species are probably ecologically important as well (e.g. striped bass).

To the extent possible, published data sources were utilized. However, additional fishery-dependent and fishery-independent data from unpublished sources were needed. Annual and monthly fisheries landings are reported by state on a National Oceanographic and Atmospheric Administration (NOAA) web site (http://www.st.nmfs.gov/st1/). These data are cited as "NOAA Fishery Statistics." The field component of a comprehensive multi-year assessment of finfish communities in Chesapeake Bay was recently concluded as part of the Chesapeake Bay Land-Margin Ecosystem Research Program (TIES). The resulting data, although still largely unpublished, have been compiled and summarized extensively by S. Jung, of Chesapeake Biological Laboratory. Results of these priliminary analyses were utilized for this study (S. Jung, unpublished data). These data were collected using 20-minute mid-water trawl tows conducted at night. The tows were stepped from the

surface to the bottom over the duration of the tow, scraping the bottom during the last several minutes of the tow. The results suggested size- and species-dependent gear selectivity. Larger piscivores (e.g. bluefish and striped bass) were caught rarely, suggesting net avoidance. Menhaden are known to form tight schools which also appeared to be able to avoid the net. It is also possible that demersal fishes were undersampled. Other studies such as stock assessments were used to supplement the TIES data.

The 5 most abundant species accounted for 86% of the average abundance estimated via TIES trawl data. The most abundant fish captured in these trawls was the bay anchovy (*Anchoa mitchilli*), followed (descending biomass) by white perch (*Morone americana*), Atlantic croaker (*Micropogonias undulatus*), weakfish (*Cynoscion regalis*), and spot (*Leiostomus xanthurus*). Addition of the herrings and shads (e.g. blueback herring, alewife, gizzard shad) accounts for an additional 4% of the total. Other important finfish include the Atlantic menhaden (*Brevoortia tyrannus*), which supports the largest commercial fishery in the Bay, and the striped bass (*Morone saxatilis*) and bluefish (*Pomatomus saltatrix*), which support significant recreational fishing. As noted, the relative biomass of these threee species may be underestimated by the TIES data due to net avoidance. The bottom-dwelling hogchoker (*Trinectes maculatus*) and the striped anchovy (*Anchoa hepsetus*) were also captured in significant biomass. The channel catfish (*Ictalurus punctatus*) and American eel (*Anguilla rostrata*) were captured in significant numbers in the upper Bay, but loss so elsewhere in the Bay. The blue crab (*Callinectes sapidus*) was not captured in great abundance in mid water trawls, but is known to be very abundant

throughout Chesapeake Bay. The discussion below is organized by species. Several species were examined in much greater detail than others, either because they are particularly abundant in the Bay, or because the quantity of relevant research data is greater, or both. All the estimated biomasses and bioenergetic parameters for the fish community are summarized in Table A-13.

Blue Crab

In recent years, the blue crab has supported the largest and most valuable fishery in Maryland. In Virginia, its fishery has been the third most important in Virginia in terms of weight and value (NOAA Fishery Statistics). The size of the fishery can be assumed to reflect the substantial biomass and production of the blue crab in Chesapeake Bay. The blue crab is also of great ecological importance via its substantial role as an epibenthic predator (e.g. Virnstein 1977, Hines et al. 1990 and references cited therein).

Because the blue crab is highly valued and exploited, ample fishery-independent and fishery-dependent abundance data have been collected. Rugolo et al. (1998) describe a detailed stock asessment, giving annual estimates of absolute abundance of the recruited stock and providing much of the basis for the population estimates described below. They estimated the 1985-1995 average recruited abundance to be ~500 10^6, with the age 1+ class 75% recruited and all older age classes fully recruited. Mean proportions at age were obtained from the theoretical stock described by Rugolo et al. (1998), assuming the total mortality rate Z=1.3 (Z=0.9, M=0.375) and aggregating the 4+ age group to include all older age classes

(Table A-13). Accordingly, the recruited stock accounts for 42% of total abundance, giving a total abundance of 1200 10^6 for the population as a whole. Although aging techniques have been developed recently for blue crabs (Ju et al. 1999), stock assessments have used length-based approaches, whereas mean carapace width at age are approximated. This study used the values suggested by Rugolo et al. (1998). No published, length-weight relationships could be found for blue crabs. However, relationships of the form $W=aL^b$ were derived here from a data set containing 493 observations on carapace width (mm) and wet weight (g) of male and female blue crabs collected in the Virginia winter dredge survey. For females, a=0.00672 and b=2.45. For males, which at larger sizes achieved slightly higher weight at a given length, a=0.000281 and b=2.66. The sex ratio was assumed to be 50:50, although the difference in weight at length was sufficiently small that any violation of this assumption would have a minimal effect. Summing the products of numbers and weights at age, the total biomass of the population was computed to be 150,000 tons, of which 125,000 tons was recruited to the fishery. The 1985-95 average landings, in which an unquantified recreational catch was assumed to equal 25% of the commercial landings (Rugolo et al. 1998), was estimated to be 48000 tons. The natural mortality rate is widely estimated to be 0.375, which results in an annual mortality equal to (150,000)(0.375)=56250 tons. At steady state, annual production equals natural plus fishing mortality, therefore, total production is approximately 104,250 tons and annual $P/\overline{B} = 0.7$. It is not clear how much of annual production occurs during summer. A value of 50% was assumed.

The blue crab is highly motile and exhibits large-scale seasonal migrations, particularly for females (e.g. Prager 1996). Consequently, assigning its ecological role on a regional and seasonal basis presents a problem. At this point, there does not appear to be a certain means of resolving this difficulty, except to examine the habitats preferred and/or required by the blue crab, and to assume that the blue crab does not occupy unsuitable habitats. In this regard, several observations can be made. Blue crabs are known to prefer well oxygenated water (>5 mg l^{-1}). Therefore, they are likely to avoid deeper habitats in summer, where oxygen is often depleted. Blue crabs have a wide salinity tolerance; studies have not shown strong population density gradients with salinity, except that males occupy lower salinity waters than do females (Miller et al. 1975). Thus, the area of the Bay in summer that might be excluded as habitat on the basis of salinity alone is minimal. It has been suggested that abundances of blue crabs are higher in the tributaries in summer than in the mainstem (references cited in Ulanowicz and Baird 1986). However, the crab pot fishery, which by law operates exclusively in the mainstem Bay in Maryland, accounts for 60% of the Maryland hard crab landings (EPA 1997), while the trotline fishery accounts for 40% of landings. While the pot fishery most likely intercepts migrating crabs which have utilized tributary habitats, blue crabs obviously do utilize mainstem Bay habitats as well. Lacking more certain data, it was assumed that during summer crabs have equal densities within all the suitable habitats. Unsuitable habitats were based on depth, whereas waters greater than 8 m in depth are more likely to have oxygen conditions below preferred levels for blue crabs. The surface area of the Chesapeake Bay and its tidal tributaries is ~18,200 km^2. Of this, 3,339 km^2 in the mainstem and 6 major

tributaries are at >8m depth. This leaves 14,861 km^2 of blue crab habitat. The upper Bay accounts for 3.6%, while the mid and lower Bay each account for 7.6% of the total habitat in the Bay and tributaries (Table A-14). In total, 18% of suitable blue crab habitat is in the mainstem Bay. The total biomass in each region was computed from the biomass of the entire population using these fractions. The average blue crab biomass in each region of the Bay was computed using total surface area rather than the surface area of suitable habitat. Accordingly, regional differences in average crab biomass reflect only differences in the proportion of habitat shallower than 8 m. Wet weight biomass was converted to carbon assuming ash-free dry weight (AFDW) is 16% of wet weight (Ricciardi and Bourget 1998) and 500 mgC=1g AFDW. Estimates of net growth efficiency (NGE) and assimilation effiency (AE) are as rare for blue crabs as for other taxa. Schroeder (1981) reported average values of 0.56 and 0.58, respectively, for aquatic invertebrate carnivores, and these values were adopted here.

Blue crab are known to be aggressive predators that can strongly affect prey populations (Virnstein 1977, Hines et al. 1990). While their diets can be varied, they are known to feed in Chesapeake Bay on bivalves such as *Mya arenaria*, and *Macoma balthica* and smaller *Rangia cuneata*. Large size provides a predation reguge for *Rangia* (Ebersole and Kennedy 1994). In summer, bivalve abundance in Chesapeake Bay can be reduced relative to spring, especially the numbers of vulnerable new recruits. In response to decreased bivalve abundance, blue crabs in Apalachicola Bay, FL, consumed a more varied diet in summer, increasing quantities of detritus, mysids, fishes, and small crabs (Laughlin 1982). Only larger blue crabs maintained a diet of bivalves, possibly because of their increased ability to pursue deeply buried prey.

Larger crabs also obtained as much as 10% of their diet via cannibalism (Laughlin 1982).

Larger blue crabs to not have many natural predators. Smaller crabs are consumed by striped bass (*Morone saxatilis*) and by larger blue crabs. Fisheries account for the majority of mortality in larger blue crabs. In Maryland, 60% of fishing results from the pot fishery in the mainstem (EPA 1997) and 55% of annual landings occur during summer (NOAA Fishery Statistics). Therefore, of the average annual Maryland landings of 20,000 tons, summer landings from the mainstem are 6,600 tons. The mesohaline mainstem accounts for 70% of the crab habitat in the Maryland mainstem, however, it was assumed that 85% of the Maryland mainstem landings were taken from this region because of the prevalence of crab potting near the mouths of the major tributaries of the mesohaline region. Based on the respective areas of the upper and mid Bay, landings amout to 1.82 and 2.09 mgC m^{-2} (Table A-13). Landings in excess of production suggest that the pot fishery intercepted crabs migrating from tributaries. In Virginia, summer landings account for 40% of the annual 16,700 tons of landings, reflecting the winter dredge fishery in Virginia. Since the Virginia pot fishery is operated throughout the tidal waters, landings were allocated according to the fraction of suitable crab habitat in Virginia, ~50% of which is in the mainstem Bay. Therefore, the summer landings from the mainstem were estimated to be 3340 tons, which was equal to 1.09 mgC m^{-2} $summer^{-1}$. Recreational crabbing was assumed to be restricted to the tributaries and was therefore neglected. Natural mortality (0.375 y^{-1}) was assumed to be constant over the year, amounting to 0.001 d^{-1}, or 0.63, 0.40 and 0.35 mgC m^{-2} d^{-1} during summer. The net migration was computed as the

difference between total mortality and production, neglecting changes in biomass over the course of summer (Table A-13). While the interpretation is not unambiguous, it is suspected that production in the Maryland tributaries as well as northward migrations subsidize the blue crab fishery in the mesohaline and upper Bay mainstem during summer.

Bay anchovy

Bay anchovy (*Anchoa mitchilli*) is the most abundant fish in Chesapeake Bay (by numbers), contributing as much as 40-50% of mid-water trawl catches Bay wide (S. Jung, unpublished data). Larval bay anchovy contribute an even larger fraction (67-88%) of the summertime larval fish assemblage (Rilling and Houde 1993a). Bay anchovy is a major component of piscivore diets (Hartman and Brandt 1995), while its diet consists almost entirely of crustacean mesozooplankton (Klebasco 1991). This makes bay anchovy one of the most ecologically important fishes in Chesapeake Bay, connecting phytoplankton production to piscivore production with as few as 3 trophic steps. The biomass, diet and bioenergetics of bay anchovy larvae and adults in Chesapeake Bay has been studied extensively in recent years, providing excellent data for describing the ecological role of this fish in Chesapeake Bay.

Estimating summer biomass and bioenergetic parameters is complicated by a strong change in age structure. Bioenergetic characteristics of the population are non-linear functions of individual weight, which changes subtly for the age 1+ cohort but dramatically for the young of the year (YOY) cohort. Consequently, both average biomass and the associated rates were estimated by separately modeling growth and

mortality of the two cohorts. The size of the age 1+ cohort in mid-summer was estimated from egg production models, while all other abundances were projected or back-calculated from that estimate.

For the age 1+ cohort, egg production models provide a robust means of estimating the biomass (Rilling and Houde 1993a). These models use measurements of egg abundance made using plankton net tows along with estimates of hourly egg mortality, batch fecundity, spawning fraction and sex-ratio to estimate the biomass of adult fishes. Using this approach Rilling and Houde (1999a) estimated that adult anchovy biomass was 23606 MT in 1993, an average density of 3.73 individuals m^{-2}. Biomass was estimated to be approximately the same in June and July, indicating that growth balanced mortality (Table A-15).

Using a similar egg production model Houde (unpublished data) estimated the biomass of age 1+ anchovy in Chesapeake Bay during summer of 1995-1999 (Table A-16). Biomass varied substantially among years, averaging 70% of the 1993 estimate. The regional distribution of biomass was strongly variable among years (Jung, unpublished data) and even within years (Rilling and Houde 1993a), making assigning an average regional distribution very difficult. A significant component of these changes in regional distributions may reflect ontogenetic and other migrations (Jung and Houde 2000, Kimura et al. 2000). Although Rilling and Houde (1993a) estimated a higher biomass density in the lower Bay, data from Jung (unpublished data) suggest that averaged over several years, densities may be approximately equal among regions. Thus, using a Bay-wide estimate of age 1+ biomass of 16,300 tons wet weight (WW), one obtains an average density of 2.6 g WW m^{-2}. Considering the

interannual variability, this estimate compares favorably with a slightly higher estimate for 1987 bay anchovy biomass in the mid-Bay (3-4 g WW m^{-2}) derived using fish acoustics (Luo and Brandt 1993). Wet weight was converted to carbon by assuming that dry weight is 20% of wet weight, 10% of dry weight is ash (Wang and Houde 1994) and carbon content is 42% of ash free dry weight. Thus, the average summer biomass of age 1+ bay anchovy is 197 mgC m^{-2} (Table A-17).

Using mean body size equal to 1.18 g (Rilling and Houde 1993a), the abundance of age 1+ anchovy in mid summer (assumed to be 7/15) is 2.20 m^{-2}, from which one can back-calculate the average weight (W_{jun1}) and abundance (N_{jun1}) for June 1 from corresponding values for July 15 (W_{jul15} and N_{jul15}) and estimates of rates of growth (G) and mortality (Z) using $N_{jun1} = \frac{N_{jul15}}{e^{-Z}}$ and $W_{jun1} = \frac{W_{jul15}}{e^{G}}$. Summer values for G and Z were computed by prorating April-June, June-Aug and Aug-Oct bimonthly estimates for G and Z (Wang and Houde 1995, see also Rilling and Houde 1999b). For example, G was computed as (0.25)(0.13)+(0.18)+(0.25)(-0.06)=0.1975. Similarly computed mortality rate was estimated to be 0.30. The back-calculated abundance, mean weight and biomass for June 1 were 2.56 m^{-2}, 1.07 g, 2.74 g m^{-2}, and respectively. Projecting these values through the summer, one observes that age 1+ biomass decreased by 20 mgC m^{-2} by the end of summer, an ~10% decrease (Table A-17).

The biomass of young-of-the-year (YOY) anchovy during summer is more difficult to measure directly than that of the age 1+ cohort. In part this arises from the fact that recruitment to trawl gear is partial at best, and egg production models cannot

be used to estimate the biomass of this sexually immature cohort. Thus, biomass was determined by modeling growth and mortality over time. The approach used was identical to that of Wang and Houde (1995), except that rates of growth (G) and mortality (Z) were prorated for July 15-September 1 from July-Aug and Aug-Oct bimonthly rates as described above. Total summer egg production was computed from the age 1+ abundance estimated above (2.2 m^{-2}). Following the approach of Wang and Houde (1995), it was assumed that all YOY belong to a single cohort spawned on July 15, the approximate date of peak spawning. Estimates of biomass for the cohort began with mean egg biomass. Changes in numbers and mean weight (via length-weight) were used to estimate cumulative mortality (Z) and growth (G), which were used to estimate mean biomass using

$$\overline{B} = \frac{B_t\left(e^{G-Z} - 1\right)}{G - Z}$$

where B_t is the total summer egg production. The population was assumed to be 50% females, which spawn an average of 50 times with a batch fecundity equal to 304.79+404.64 x female wt. (Wang and Houde 1995). Egg production was computed to be 43025 m^{-2} $summer^{-1}$, which is equal to 3.31 g WW m^{-2} (15.4 μg DW egg^{-1}, Tucker (1989), eggs are 80% water). The estimates of G and Z for July 15-September 1 are 7.01 and 6.29, which using eq. (1) gives an average YOY biomass in the second half of summer equal to 4.85 g WW m^{-2}. Since the YOY cohort was absent in the first half of summer, the YOY contribution to summer average biomass is half of the late summer average, or 184 mgC m^{-2} (Table A-17). At the end of the summer, YOY biomass is 518 mgC m^{-2}, an increase in biomass offset by a decrease of only 20 mgC

m^{-2} in the age 1+ cohort. Thus, summer Bay anchovy production contributed a net export to the Fall food web of 498 mgC m^{-2}, equal to a mean rate of 5.4 mgC m^{-2} d^{-1} (Table A-17).

Summer production by the age 1+ cohort can be computed from the summer average biomass ($\overline{B}$) and the growth rate (G) using $P = G\overline{B}$. For June 1-September 1, G=0.1975 as described above. Thus, summer production is (2.6)(0.1975)=0.51 g WW m^{-2}, or 38.8 mgC m^{-2}. This estimate reflects only somatic production, however. Egg production amounted to 3.31 g m^{-2} $summer^{-1}$; therefore somatic and reproductive production totals 3.82 g m^{-2}, or 290 mgCm^{-2}. The equivalent daily rate is 3.15 mgC m^{-2} d^{-1}.

Summer production for the YOY cohort can also be estimated from average biomass ($\overline{B}$) and the growth rate (G) using $P = G\overline{B}$. For July 15 - September 1, G has been estimated to be 7.01, while $\overline{B}$ =368 mgC m^{-2}. Thus, summer production is (7.01)(367)=2573 mgC m^{-2}, in the same range as reported by Wang and Houde (1995). The combined production of the age 1+ and YOY cohorts is 2863 mgC m^{-2} $summer^{-1}$, an average daily production equal to 31 mgC m^{-2} d^{-1}.

The diet composition of bay anchovy consists almost completely of zooplankton (Klebasco 1991). However, the diet changes during summer as the zooplankton assemblage and the age structure of the bay anchovy population changes (Table18). The effect of the zooplankton assemblage is particularly obvious in June, when copepod abundance in Chesapeake Bay is typically low, but abundance of meroplankton (e.g. barnacle cyprids) and small macrobenthic animals (e.g., amphipods) is greater. During the remainder of the summer, however, the diet

consists almost exclusively of copepods. Small anchovy (<40 mm, probably YOY) appear to be limited in their ability to eat large prey such as adult copepods by their esophageal diameter (Klebasco 1991). Therefore, these individuals prey on abundant copepodites. In general, though, bay anchovy exhibit a particle feeding mechanism that prefers larger prey. Even very small anchovy (i.e. 8 mm) prefer larger particles, leaving behind copepod nauplii in favor of copepodites in experimental studies (Detwyler and Houde 1970, cited in Klebasco 1991). Rotifers constitute a large fraction of juvenile bay anchovy diets in numerical terms, but due to their small size do not constitute a large fraction by biomass. The largest fraction of identified copepods were *Acartia* spp., although a substantial fraction was identified only as "calanoid copepods" or "unidentified copepods" (Klebasco 1991).

The daily ration of bay anchovy appears to be weakly food limited, with food limitation most likely in June when copepod abundance is low. In the other summer months, food is sufficiently abundant that daily ration does not depend appreciably on food abundance (Klebasco 1991). Using a bioenergetics model compared to growth estimates, Luo and Brandt (1993) also concluded that consumption was close to maximal (60-70%) most of the time. For July and August, Klebasco (1991) found that adult bay anchovy consumed ~17.8% of dry body weight per day (Table A-19), 60% of maximum possible consumption (Luo and Brandt 1993). Juveniles consumed 30.3% and 39% of their dry body weight in July and August, respectively (Klebasco 1991, Table A-19), also consistent with weight- and temperature-dependent maximum consumption (Luo and Brandt 1993). Daily consumption was computed as the product of estimated daily biomass for each cohort and the appropriate specific

consumption, then totaled for each month and for the summer. The summer average specific consumption for the entire population was estimated to be 0.26 d^{-1} (Table A-19). The amount of consumption for each diet component was computed from the diet fraction and total consumption, then aggregated into several prey categories (Table A-20).

Egestion (E) was computed as a temperature-dependent fraction of consumption (Luo and Brandt 1993). At 27°C, 20.6% of consumption is egested. Excretion (U) is 15% of consumption minus egestion, or 11.9% of consumption. Total egestion plus excretion (E&U) is 2957 gC m^{-2} $summer^{-1}$. The resulting assimilation efficiency is 68%.

Respiration depends on weight, temperature and consumption according to $R = a_r W^{b_r} f(T)A + S(C - F)$, with parameters defined in Luo and Brandt (1993). Accordingly, respiration was computed at a daily time increment for each cohort, then summed for the summer (Table A-21).

According to the initial estimates developed in the above description, the estimated production, excretion, egestion and respiration exceed consumption by 1278 mgC m^{-2} or 14% of consumption (Table A-17). To balance the carbon budget, small adjustments were made to the initial values, with uncertainty in the likely direction and magnitude of initial estimates considered (Table A-22). Because the estimated consumption was significantly below maximum (~60% of maximum) consumption was revised upward. Similarly, respiration was estimated assuming temperature conditions leading to a maximal estimate, therefore respiration was revised downward slightly. Production was not changed, while egestion and excretion were adjusted to

maintain constant assimilation efficiency. The balanced carbon budget resulted in net growth efficiency equal to 42% and assimilation efficiency equal to 68%, consistent with average rates for carnivorous fish (Schroeder 1981).

Menhaden

Atlantic menhaden (*Brevoortia tyrannus*) is a migratory clupeid fish found along the entire Atlantic seasboard from Florida and Maine. Spawning in the mid Atlantic region occurs from May to October. Eggs hatch at sea and larvae are moved into estuaries where larvae grow and metamorphose into juveniles. Menhaden occupy much of the Chesapeake Bay and its tidal tributaries. In late fall, juveniles migrate seaward out of estuarine areas to large Bays or to the open waters of the coastal zone. This highly migratory nature complicates the task of estimating their trophic role in Chesapeake Bay during summer.

Menhaden support a substantial purse-seine fishery on the Atlantic coast, with landings during the 1990's between ~170,000 and 400,000 tons (Vaughn et al. 2001). The quantity of this catch attributable to removals from Chesapeake Bay cannot be known directly due to fishing practices and confidentiality restrictions on reporting of landings. However, Vaughn et al. (2001) reported estimates of this fraction derived from Captain's Daily Fishing Reports. Annual removals of menhaden from Chesapeake Bay by the purse-seine fleet between 1985 and 1999 averaged 150,000 tons, which was obtained entirely from the Virginia portion of the mainstem Bay. These landings amounted to ~50% of the entire Atlantic coast landings for the purse-seine fleet. Additional landings occur in Maryland as the result of the pound net

fishery. Average Maryland landings during 1985-1999 amounted to 2,000 tons, which is entirely due to the pound net fishery operating in both tributary regions and the mainstem. Landings by the pound net fishery were about 2,000 tons in recent years (NOAA Statistics). This can be neglected as it is well within the variability for the purse-seine landings.

Vaughn et al. (2001) used virtual population analysis to estimate the abundance of each age class of the Atlantic coast menhaden stock. Biomass was estimated as the product of average abundance at age (Vaughn et al. 2001) and weight at age. Average weights at age for age 1+, 2+ and 3+ individuals was obtained from Vaughn et al. (2001), while weight at age for age 0+ in mid-summer was assumed to be 10 g WW (Luo et al. 2001). Accordingly, the Atlantic coast stock has a biomass equal to ~743,000 tons. Assuming that the exploitation rate within Chesapeake Bay is the same as outside the Chesapeake, the Chesapeake stock is (1/0.39)(150000)=385,000 tons. This may be an upper limit. If the exploitation rate within Chesapeake Bay was higher than for the Atlantic coast as a whole, then the biomass would be lower. However, there is no evidence to indicate that this is the case. Age 0+ individuals, which have a different diet from that of adults (see below), were estimated on the basis of the VPA to account for 43% of abundance, but only 5% of summer biomass, as individual weight reaches a maximum in late fall (Luo et al. 2001). The distribution of menhaden within the Chesapeake Bay is broad and appears to exclude very little of the surface area. Therefore, the average biomass of menhaden was distributed over 18,000 km^2, the approximate surface are of the Bay and its

tributaries. The resulting biomass estimate is 21 g m^{-2}, or 2136 mgC m^{-2} (Table A-13).

Consumption by menhaden was estimated by applying the menhaden foraging model described by Luo et al. (2001). It was assumed that menhaden occupied water with an average chlorophyll-a concentration of 10 μg l^{-1} which was converted to carbon assuming C:Chl-a=50. Water temperature was assumed to be 25°C. The estimated age structure derived from Vaughn et al. (2001) was applied to estimated specific consumption at age to derive a population average specific consumption rate of 0.1 d^{-1} (Table A-13).

Menhaden growth rate depends on the habitat in which it grows. Luo et al. (2001) show that menhaden apparently seek out and occupy habitat with suitable food density, achieving average growth rates of ~0.025 d^{-1} during summer. Suitable habitat apparently consists of substantial phytoplankton blooms, which the schools of fish may identify through chemosensory abilities (Friedland et al. 1989). Menhaden assimilate their diet with very high efficiency, ~87% (Durbin and Durbin 1981).

Landings of menhaden from Chesapeake Bay by the purse-seine fleet, as noted above, amount to 150,000 tons y^{-1}. Other menhaden landings amount to ~4,000 tons y^{-1} and were assumed to come predominantly from outside the mainstem Bay and were therefore neglected. Approximately 50% of purse-seine landings occur during summer (NOAA Statistics), and all of the landings are from the lower Bay region of the Chesapeake Bay mainstem, which has a surface area of 2,661 km^2. Thus, daily removals during summer amount to 0.3 g m^{-2} d^{-1}, or 30.6 mgC m^{-2} d^{-1} (Table A-13). This is equal to 57% of estimated daily production by the Chesapeake Bay stock in the

lower Bay. Production in the upper and middle portions of the mainstem Bay is largely unexploited by the fishery.

Herrings and Shads

A diverse assemblage of herrings and shads were captured in Chesapeake Bay mid-water trawls (S. Jung, unpublished data). These include include the American shad (*Alosa sapidissima*), blueback herring (*Alosa aestivalus*), alewife (*Alosa pseudoharengus*), hickory shad (*Alosa mediocris*), gizzard shad (*Dorosoma cepedianum*), Atlantic thread herring (*Opisthonema captivai*), as well as unclassified Clupeidae belonging to various genera. These species make annual spawning migrations to fresh waters in summer (EPA 1989) and were found in greatest abundance in the upper Bay (S. Jung, unpublished data). Most individuals that were captured were young of the year. Based on trawl data, S. Jung estimated the YOY abundance in the upper Bay during summer to have varied between near zero in the apparently failed recruitments of 1999 and 2000 up to 1.25 million in 1996. Typical summer abundances YOY were 200-400 million (S. Jung, unpublished data). Based on the summer length-frequency, YOY blueback herring were about 6.0 cm while YOY alewives were slightly larger, 8-10 cm. These lengths correspond to weights of 2 and 9 g, respectively. Assuming that the combination of these species had an average weight per individual in between these values, total biomas can be estimated to have been 750-1500 tons.

Another approach to estimate the biomass of herrings and shads is based on their mortality rate and estimated demand by predators. It was estimated that

consumption of alosids amounts to 1.64 mgC m^{-2} d^{-1}, or 151 mgC m^{-2} $summer^{-1}$. Based on a maximum longevity of 8 years, Hoenig's (1983) model suggests a natural mortality rate of ~0.7. However, young-of-the year may be assumed to be subject to higher mortality. Hoenig's model predicts M=2.0 for a nearly annual fish such as Bay anchovy, while Wang and Houde (1995) estimated M=6.29 for the young-of-the year Anchovy during late summer. Assuming that YOY mortality for alosids was ~0.5 for the summer, then 39% of the biomass is consumed by predation each summer and the average biomass is equal to 382 mgC m^{-2}, or ~1800 tons (Table A-13).

A third approach to obtain a minimum estimate of alosid biomass is to assume that summer production by alosids is at least equal to the predation demand. Based on the growth characteristics for *Alosa pseudoharengus* (Froese and Pauly 2001), specific growth for an individual ~6 cm in length is roughly 0.01 d^{-1}. Therefore, a biomass of 163 mgC m^{-2} is required to support a predatory demand of 1.63 mgC m^{-2} d^{-1}. Over the area of the upper Bay, this is equal to a biomass of 771 tons.

Based on these three approaches, the biomass of young of the year alosids in the upper Bay was estimated to be about 1000 tons, or 212 mgC m^{-2} (Table A-13). Production was assumed to be 0.01 d^{-1}, with assimilation and net growth efficiencies equal to 0.68 and 0.41, respectively (Schroeder 1981). The YOY alosids were assumed to be primarily zooplanktivorous (Froese and Pauly 2001).

Striped Bass

The striped bass (*Morone saxatilis*) is an important piscivore in Chesapeake Bay and supports substantial recreational and commercial fisheries (EPA 1995). In

Maryland, commercial landings from the Bay averaged about 240 tons y^{-1} in the early 1990's (EPA 1994). Recreational landings accounted for an additional 374 tons y^{-1}. Landings from the Potomac River averaged 74 and 69 tons y^{-1} for commercial and recreational landings for a total of 144 tons y^{-1}. In Virginia, commercial and recreation landings averaged 100 and 235 tons y^{-1} for a total of 335 tons y^{-1}. Thus, overall Bay wide landings of striped bass in the early 1990's were about 1000 tons y^{-1}.

Maryland landings, which include the coastal landings, increased 4.5-fold in the late 1990's relative to the early 1990's as the stock continued to recover from long term lows and a fishing moratorium in the 1980's. For the period 1985-1999, average Maryland landings were about 2-fold greater than the early 1990's levels. Therefore, Chesapeake Bay landings during this period may have averaged about 2000 tons y^{-1}. EPA (1995) reported on the basis of tag-recapture studies that the fishing mortality rate in recent years was F=0.09. Based on that estimate and assuming natural mortality rate is M=0.15, then the exploitation rate ($\mu = \left[F\left(1 - e^{-M+F}\right)\right]/(M + F)$) is 0.08 y^{-1}, giving an estimate of stock biomass equal to 25,000 tons via $B = C/\mu$.

The striped bass stock was assumed to be distributed over the entire surface area of Chesapeake Bay and its tidal tributaries (18,000 km^2), giving an average density of 1.38 g m^{-2}, equivalent to 172 mgC m^{-2} (DW=0.25WW, Hartman and Brandt 1995c, 1 g DW=500 mgC) (Table A-13).

An estimate of growth for the population was derived by constructing a theoretical population structure. A von Bertalanffy growth equation ($L_t = L_\infty\left(1 - e^{-K(t-t_0)}\right)$ with the parameters L_∞=139 cm, K=0.117, and t_0=0 (Mansueti

1961, Froese and Pauly 2001) was used to estimate length at age and annual growth increment for each age. Length (cm) and growth increment was converted to weight (g) via $W = aL^b$ where a=0.0061 and b=3.153 (Mansueti 1961, Froese and Pauly 2001). Weight-specific growth decreased from 2 y^{-1} for age 0-1 fish to 0.08 y^{-1} for a 15 year old fish. These functions show that striped bass do not reach legal size until age 3-4. Therefore, fishing mortality on those age classes was reduced to zero. The resulting age structure assuming M=0.15 and F=0.09 for recruited age classes (Age 4+) and the computed growth at age gives a specific growth estimate for the population equal to 0.3 y^{-1}. However, summer production may be more or less than the annual mean rate.

Specific rates of production, consumption, respiration as well as the assimilation efficiency were obtained by applying coefficients reported by Hartman and Brandt (1995b) to the estimated age structure of a Chesapeake Bay striped bass population assuming a water temperature of between 25-28°C. At these temperatures, temperature-dependent specific consumption should be near the maximum, which distributed over the age structure gives an average of 0.034 d^{-1}, similar to that of an age-7 individual. Assimilation was found to be 83% of consumption. Active respiration rates, derived as g O_2 g^{-1} d^{-1} were converted to g WW d^{-1} assuming 3240 cal g^{-1}, 4.184 J cal^{-1} (Hartman and Brandt 1995b) and 4000 J g^{-1} WW (Hartman and Brandt 1995c). For the estimated age structure, the average specific respiration rate at 25°C is 0.016 d^{-1}. Specific dynamic action amounts to 17.2% of assimilation and is also a component of the respiration rate. Assuming maximal consumption the scope for growth is 0.0076 d^{-1}, ~9 times greater than the annual mean rate. If the striped

bass population is able to achieve only 75% of maximum consumption, then the summertime specific growth is 0.0018 d^{-1}, twice the annual mean rate. At that rate of consumption, active metabolic and SDA equal 0.019 d^{-1}, giving NGE=0.083 (Table A-13). At $C=C_{max}$, NGE=0.27.

Striped bass undergo ontogenetic shifts in their diets during summer (Hartman and Brandt 1995d). Age-0 fish in early summer ate primarily small invertebrates, but by late summer ate a substantial fraction of juvenile naked goby. By age 1+, bay anchovy and menhaden accounted for 50% of the summer diet, with the remainder invertebrates. Age 2+ and older fish primarily ate fish (80%), but obtained about 20% of the diet from benthic and epibenthic invertebrates (Hartman and Brandt 1995d). Hollis (1938) came to similar conclusions after examining the stomachs of 1,738 striped bass in Chesapeake Bay in 1936-37. In the upper Bay (Rock Hall and Conowingo) the diet also included shad, white perch, eel, and yellow perch (Hollis 1952). Biomass was estimated to be overwhelmingly dominated by age 2 and older fish. Therefore, the diet for the population was assumed to reflect their diet (50% menhaden, 20% bay anchovy, 10% other fish, 20% invertebrates).

Bluefish

Abundance of bluefish (*Pomatomus saltatrix*), a piscivorous predator, in the Bay peaked in the late 1970's and is known to be highly variable. The bluefish stock is highly exploited, principally as a recreational fishery (>80% of total exploitation). Based on figures presented by EPA (1990), recreational landings in the Bay have been estimated to average 1360 tons in Maryland, with a similar figure in Virginia. The

commercial fishery includes both inshore and offshore components. EPA (1990) reported that from 1970-1986 the Bay landings dominated the total, but accounted for a decreasing fraction. Analysis of landings by gear type for 1985-1999 suggests that Bay landings accounted for a smaller fraction of the total in recent years (~30%). Accordingly, commercial landings in the Bay were estimated to average 64 tons y^{-1} in Maryland and 154 tons y^{-1} in Virginia. The total landings of bluefish from the Bay where therefore estimated to average 2940 tons y^{-1} over the past 15 years. In Maryland, hook and line fishing accounted for two-thirds of commercial landings, with the remaining fraction coming from pound nets. In Virginia, the vast majority of the commercial landings were due to the pound net fishery. All the bluefish fisheries were concentrated during May-October, when Bluefish are resident in the Bay.

Fishery utilization of the bluefish resource was computed by assuming that Maryland Chesapeake Bay landings were from the upper and mid Bay and that 50% of these landings were from the mainstem Bay. Half of the landings were assumed to occur during the three months of summer, since the season lasts 6 months, from May-October. Maryland landings were allocated to the upper and mid Bay on a relative area basis. Half of the Virginia Chesapeake Bay landings were assumed to come from the lower mainstem Bay, with the balance coming from Virginia tributaries.

Growth and mortality rate estimates for bluefish were derived from Barger (1990, cited by Froese and Pauly, 2001) and EPA (1990). Bluefish have an estimated lifespan of 10-12 years. Natural mortality has been estimated to be 0.35 y^{-1} for younger bluefish and 0.6 y^{-1} for older fish. Fishing mortality rates in for the Atlantic stock as a whole have been estimated to be 0.7 y^{-1} for younger fish and 0.27 y^{-1} for

older fish. Increased fishing pressure on smaller fish is due to their increased presence in inshore areas. An approximate age structure and weight at age was computed using these figures, and assuming the coefficients of the von Bertalanffy growth equation are L_∞= 115 cm and K=0.135 and the weight-length relation has coefficients a=0.0131 and b=2.934 (Barger 1990, Froese and Pauly 2001). Based on the age-structured fishing mortality rate and the estimated total exploitation, the average exploitation rate is μ=0.36 and total biomass is 8130 tons. Young of the year and adult bluefish are known to occupy all salinities (EPA 1990), while the relative distribution among regions was unknown. Therefore, the average biomass was assumed equal through out the Chesapeake Bay and tributaries (18,000 km^2) and was estimated to be 0.45 g WW m^{-2}, or 68 mgC m^{-2} assuming dry weight is 30% of wet weight (Hartman and Brandt 1995c) and 1 g DW=500 mgC (Table A-13).

Bioenergetics of bluefish were described by Hartman and Brandt (1995b). Temperature dependent consumption was equal to 98% of Cmax when temperature was between 23 and 28 °C, therefore consumption was assumed to not be temperature limited. Active respiration rates were computed as for striped bass, but using coefficients for bluefish. Moderate food limitation was assumed by estimating consumption to be only 75% of the temperature-dependent maximum. Accordingly, summer average scope for growth was ~2-fold greater than annual mean growth derived from the age-length and weight-length relations. Using these assumptions, population average specific rates of growth, consumption and respiration (including specific dynamic action) were estimated to be 0.0069, 0.094, and 0.052 d^{-1}, respectively. Net growth efficiency (NGE) was 0.12 (Table A-13), less than the food-

replete NGE under the same assumptions, which is 0.29. Assimilation efficiency for bluefish was assumed to be the same as for striped bass, 0.83 (Hartman and Brandt 1995b).

Unlike striped bass, bluefish ate a diet consisting almost exclusively of fish. Age 0+ bluefish consumed almost exclusively bay anchovy and silversides during summer (Hartman and Brandt 1995a), but this age class was estimated to account for only 3% of biomass. Age 1+ bluefish, which were estimated to account for 21% of biomass, obtained the largest fractions of their diet from bay anchovy and spot, but also significant contributions from silversides, menhaden, and other fish. Age 2+ fish, unlike their younger counterparts, obtained a significant fraction of their summer diets (60%) from Atlantic croaker. The average diet, accounting for the fraction of biomass at each age was approximately: Bay anchovy 31%, Menhaden 8%, Spot 15%, Croaker 46%. In fall, however, the diet of larger bluefish consisted almost exclusively of menhaden, while that of younger bluefish consisted of bay anchovy and menhaden (Hartman and Brandt 1995a). Hence, the dependence on bluefish on spot and croakers was limited to summer.

Weakfish

Weakfish (*Cynoscion regalis*), like striped bass and bluefish, is a major Chesapeake Bay piscivore that supports both commercial and recreational fisheries. Commercial landings in Maryland and Virginia included a substantial coastal component. Chesapeake Bay commercial landings were estimated to have been about 804 tons y^{-1} in the 1980s (EPA 1990b), of which 726 tons y^{-1} were from Virginia

waters. Recreational landings were about 2-fold greater, 1556 tons y^{-1}, of which 1406 were from Virginia waters. Total landings of weakfish amounted to 2360 tons y^{-1}. Most (90%) of the commercial weakfish landings in Maryland occurred in April, October and November, while in Virginia, 32% of the landings occurred during summer. It was assumed that about half the the summer landings in both states were from tributary waters, rather than the mainstem Bay.

The total biomass of the resident Chesapeake Bay population was estimated using the total landings from the Bay, information about the ages subject to fishing, available growth and mortality data, and approximate estimates of young-of-the-year abundance based on trawl data (S. Jung, unpublished data). There is no estimate of the total mortality rate for the weakfish stock. Natural mortality rate was estimated to be ~0.7 y^{-1} based on Hoenig's (1983) model and a longevity of about 6 years for weakfish in the mid Atlantic region (EPA 1990b). The parameters of the von Bertalanffy growth equation ($L\infty$=67, K=0.35) and the length weight parameters (a=0.0091, b=2.984) used to estimate length and weight at age. These results, combined reports of the length-frequency and age-frequency in the catch (Sadzinski et al. 1999) were used to estimate that fishing mortality on age 2+ fish was ~0.6. Accroding, obtaining the annual landings from the Chesapeake Bay requires a young-of-the-year (YOY) abundance equal to ~45 million individuals. Projecting this abundance throught the age structure gives a total weakfish biomass of about 6000 tons. Based on reported life history characteristics (EPA 1990b), the TIES trawl data (S. Jung, unpublished data) and the relative contribution of Virginia and Marytland landings to the total, it was estimated that 75% of the population resided in Virginia

waters. In Maryland YOY biomass was concentrated in the upper Bay (S. Jung, unpublished data). Older fish were in greater abundance in the mid Bay than the upper Bay, reflecting their salinity preferences (EPA 1990b). Lacking better data, it was assumed that the biomass of the Maryland portion of the population was equally distributed between the upper Bay and the mid Bay. Half of the biomass in both regions was assumed to inhabit tributary waters rather than the mainstem Bay. The same assumptions were applied to Virginia (lower Bay) waters. Accordingly, the average weakfish biomass in the upper and mid Bay during summer was estimated to have been 67 mgC m^{-2}, while biomass in the lower Bay was estimated to have been 211 mgC m^{-2} (0.25 gDW= 1 g WW, Hartman and Brandt 1995d, 1g DW=500 mgC) (Table A-13).

Detailed age-structured bioenergetics data for weakfish were obtained from Hartman and Brandt (1995b) and were used to compute scope for growth for the age-structured weakfish population at summertime temperatures. Summer scope for growth was found to be 14 times greater than the annual mean growth rate computed from the von Bertalanffy growth parameters and the length-weight relationship. Since scope for growth for weakfish is negative at temperatures below 15°C (Hartman and Brandt 1995b) and is nearly maximal at 25°C, it was assumed that summer scope for growth was 3-fold greater than annual mean growth, which was achieved when consumption was ~60% of C_{max}. Accordingly, specific consumption was computed to be 0.068 d^{-1} and specific growth was 0.0088 d^{-1}. Assimilation efficiency was reported to be 0.83 (Hartman and Brandt 1995b). The computed values implied that net growth efficiency was 0.16. Biomass accumulation was computed as summer production

minus the sum of summer landings and summer mortality (M=0.7/365 d^{-1}) and was estimated to be 0.42 mgC m^{-2} d^{-1} for the upper and mid-Bay and 1.03 mgC m^{-2} d^{-1} for the lower Bay.

The summer diet of age-0 and age-1 weakfish consists of about 75% bay anchovy with the remaining fraction coming from small invertebrates. At age 1+ the diet consists of 70% bay anchovy, 8% menhaden, 10% other fish, with the balance obtained from invertebrates. Hartman and Brandt (1995b) did not report the mid summer diet for age 2+ weakfish in the mid Bay. However, based on the May-Jun and Sep-Oct diets of age 2+ weakfish, it can be inferred that the diet includes about 40% menhaden, 30% spot, about 20% other fish, and and 10% invertebrates. The average diet was computed from the proportion at age and the age-specific diets. It was assumed that a relatively larger fraction of the population was YOY in the upper and mid Bay and that a larger fraction was age 2+ in the lower Bay. Average diet was computed accordingly.

Atlantic Croaker and Spot

Atlantic croaker (*Micropogonias undulatus*) and spot (*Leiostomus xanthurus*) are important demersal feeders in Chesapeake Bay. They are an important component of the diet of striped bass and bluefish (Hartman and Brandt 1995a, see above), and also support commercial and recreational fisheries during summer (EPA 1991A). Atlantic croaker spawn on the continental shelf, then both juveniles and adults move into estuarine areas in late spring through mid fall. Young of the year are distributed throughout the estuary, while adults are more abundant when salinity >5 ppt (EPA

1991A). Croaker have been in relatively low abundance in recent years, however, mid-water trawl surveys (S. Jung, unpublished data) suggested that strong recruitments occurred in 1996 and 1998, leading to increased abundance and landings in the late 1990's (S. Jung, unpublished data, NOAA Landings Data).

Commercial landings of croakers were dominated in the Bay by the pound net fishery. Average pound net landings during 1985-2000 were 884 tons, of which 782 tons was in Virginia. The recreational fishery was of similar magnitude, with total Chesapeake Bay landings of ~1.5 million pounds (EPA 1991A, equal to 682 tons). Virginia recreational landings typically accounted for about 75% of the recreational landings, thereby giving a figure of 511 tons in Virginia and 170 tons in Maryland. Thus, average total landings of croaker in the past 15 years was estimated to have been ~1565 tons y^{-1}.

EPA (1991) suggested that an appropriate total mortality rate for Atlantic croaker was Z=1.15, while Ross (1988) estimated Z=1.3 from catch curve analysis. Natural mortality was estimated to be ~ 0.5 y^{-1} by assuming a longevity of of 8 years (EPA 1991A) and applying Hoenig's (1983) model. This implies an exploitation rate of 0.38, and therefore a total biomass of 4,118 tons. Given growth parameters for croaker (Ross 1988), population production based on this estimate was not sufficient to account for estimated bluefish predation, which was ~2.2 mgC m^{-2} d^{-1}. Assuming summer growth was 2-fold greater than the annual mean rate and assuming a population dominated in numbers by age 0+ and age 1+ individuals, specific growth in summer may be ~0.01 d^{-1}. Thus, a biomass of 222 mgC m^{-2} d^{-1} is required to support bluefish predation. An additional biomass is required to support the fishery.

Assuming half the Maryland landings were from the mid Bay mainstem and that half the landings removed summer production, landings amounted to 0.032 mgC m^{-2} d^{-1}, which would require an additional 3.2 mgC m^{-2}. In Virginia, landings were greater, amounting to 0.13 mgC m^{-2} d^{-1} under the same assumptions, requiring 13 mgC m^{-2} additional biomass. Thus, a minimum estimate of croaker biomass was computed to be 225 and 235 mgC m^{-2} in the mid and lower Bay, respectively (Table A-13). Croakers were much less abundant in the upper Bay in TIES mid-water trawls. Therefore, it was assumed that croakers were not abundant there. Lacking specific bioenergetic data for croakers, assimilation and net growth efficiencies were assumed to be 0.68 and 0.41, reasonable values for carnivorous fish (Schroeder 1981). Consumption, respiration and excretion plus egestion were computed using these ratios.

Spot (*Leiostomus xanthurus*) is distributed throughout the salinity range of Chesapeake Bay (EPA 1991A) and were caught in the TIES mid water trawls (S. Jung, unpublished data) in interannually varying abundance in all regions of the Bay. Spot supports both a commercial and recreational fishery, which are most important in Virginia where spot are generally larger. The largest catches in Virginia occur in late summer to early fall when migrating spot are captured in Virginia. Annual commercial landings in Virginia averaged 1330 tons, about a third of which was landed in summer. Landings in Maryland averaged about 78 tons, about 50% of which was in summer. EPA (1991) reported that recreational landings in Maryland were about 1.3 million fish in 1980, which is equal to about 91 tons of age 2 fish. In Virginia, recreational landings in the mid-1980's were 1.6 million pounds, or 727 tons,

in 1986 and about twice that in 1985 (EPA 1991A). Thus, total annual landings of spot are probably 950 tons y^{-1}, about 330 tons of which was landed in summer. Commercial and recreational landings of spot in Maryland were assumed to come from the mid Bay. Per unit area these landings were equal to 0.003 and 0.021 mgC m^{-2} d^{-1}, respectively. In Virginia, recreational and commercial landings per unit area were equal to 0.089 and 0.015 mgC m^{-2} d^{-1}, respectively (Table A-13).

Since fishing mortality rates are not known, there is no direct means of estimating the abundance of spot in the Bay. Given an estimate of specific growth rate, minimum biomass can be estimated as that required to support landings and estimated consumption by dominant predators. Growth parameters of spot were reported by Froese and Pauly (2001), apparently inferred from data in Pacheco (1962). Maximum longevity is 4-5 years, in which time a maximum size of ~24 cm and ~150 g (K=0.725, a=0.0092, b=3.072; Froese and Pauly 2001). Most individuals are age 0 to age 2 (Pacheco 1962), and growth in this time is rapid (K=0.725), declining from ~0.02 d^{-1} to 0.006 d^{-1}. At a specific growth rate equal to 0.01 d^{-1}, the biomass required to balance summer landings in the mid and lower Bay is 3.9 and 25.2 mgC m^{-2}, which summed over those regions is equal to a wet weight of 763 tons. Estimated consumption of spot by striped bass, bluefish and weakfish requires a biomass of 195, 217 and 545 mgC m^{-2} in the upper, mid and lower Bay, respectively, which is equal to a total wet weight of 20,506 tons. Total biomass is therefore 20,268 tons. The above noted estimate of specific growth (0.01 d^{-1}) was assumed, while growth efficiencies were estimated to be the same as for croaker (AE=0.68, NGE=0.41) (Table A-13).

White Perch

Behind bay anchovy, white perch (*Morone americana*) contributed the second largest biomass to TIES mid water trawls. Based on the TIES data, the presence of this species in the mainstem Bay was limited to the upper Bay, however, it is also known to be present in the upper reaches of the mesohaline Bay. This reflects the salinity preferences and spawning migrations of this species (Mansueti 1961). White perch abundance in the mid Bay may be greater than suggested by the TIES data if it was abundant in shallower waters than were sampled by TIES.

Commercial landings in Maryland averaged 466 tons during 1985-2000, with landings increasing through the period, especially in the 1990's following strong recruitments. It is not known what fraction of these landings were from the mainstem Bay, however, a figure of 50% seems plausible and was adopted. Recreational landings were ~200 tons y^{-1} in Maryland in 1998 (Sadzinski et al. 1999) and were assumed to be ~100 tons in the upper Bay. The vast majority of commercial landings occurred during November through May, with summer landings <3% of peak spring landings. Virginia landings averaged 14% of Maryland landings and were assumed to have been obtained from the tributaries due to high salinity in the Virginia mainstem.

Biomass in the upper Chesapeake Bay was estimated by modeling growth and mortality of a hypothetical stock. Growth was modeled assuming L_∞=35 cm and K=0.2 y^{-1}, which was increased from the estimate reported by St. Pierre and Davis (1972) to match the length frequencies observed in the upper Bay TIES data in 1997. Length-weight parameters were estimated to be a=0.007 and b=3.17. Natural mortality was estimated to be 0.6 based on the catch curve analysis of St. Pierre and

Davis (1972) and Hoenig's (1983) regression model. To obtain landings of 250-350 tons y^{-1} with a size structure consistent with data reported by Webb and Zlokovitz (1999) and with commercial size restrictions (>20.3 cm), recruitment must be ~50 million y^{-1} with fishing mortality rate equal to ~0.4 on age 3+ fish and negligable on younger individuals. This level of recruitment is consistent with the smaller, but not failed recruitments suggested by the TIES data (S. Jung, unpublished data. Based on the estimated recruitment, growth and mortality, total biomass is about 2000 tons. Larger landings (i.e. if recreational fishing is more substantial than suggested) would require greater recruitment since the yield was near the calculated maximum yield-per-recruit. One third of the biomass was assumed to be in the upper mesohaline Bay, while the reamaining was assumed to be distributed over the surface area of the upper Bay. Accordingly, the biomass density is equal to 282 mgC m^{-2}, similar in abundance to bay anchovy. The average mid Bay abundance is estimated to be 29 mg m^{-2}, which is low due to the large surface area of the mid Bay region.

Consistent with the age structure of the population, the biomass-weighted average age in the stock was ~3, for which specific growth is ~0.002 d^{-1} (Table A-13). If the average age is somewhat younger, production could be much greater, as high as 0.008 if the population was dominated by age 1 fish. Total summer production was estimated to be 52 and 5.3 mgC m^{-2} in the upper and mid Bay, respectively. Natural mortality in the two regions during summer was ~14% of biomass $= \overline{B}\left(1 - e^{-M/4}\right)$, or 39 and 4 mg m^{-2}. Since fishing mortality during summer was negligable, biomass accumulation must be ~0.14 and 0.01 mgC m^{-2} d^{-1} in the two regions. White perch have been reported to be primarily consumers of zoobenthos as adults (Froese and

Pauly 2001); however, significant consumption of bay anchovy by white perch has also been observed in the upper Bay, suggesting that these fish may also be a major diet component when abundant. Juvenile bay anchovy are also zooplanktivores. Consumption and egestion was computed assuming AE=0.68 and NGE=0.41 (Schroeder 1981).

Catfish

The channel catfish, *Ictalurus punctatus* and other catfishes occupy low salinity habitats and were captured in significant abundance in TIES mid-water trawls in the upper Bay (S. Jung, unpublished data). Commercial landings in Maryland average 760 tons y^{-1}, 50% of which was assumed to have come from tributary populations. Virginia landings of 477 tons y^{-1} were assumed to have been obtained entirely from tributaries and are ignored here (NOAA Landings, Sadzinski et al. 1999). Recreational landings in Maryland were reported to have been ~200 tons y^{-1}, of which 50% were also assumed to have been been obtained from the tributaries. Thus, total removals from the mainstem Bay were estiamated to be 480 tons y^{-1}. Catfish landings occur throughout the year at a fairly constant rate (NOAA Landings). Therefore, 25% of annual landings were assumed to occur in summer.

The channel catfish has a maximum reported age of 16 years, with growth parameters K=0.06 and L_∞=119 and length-weight parameters a=0.0042 and b=3.132 (Pauly and Froese 2001). Natural mortality for catfish was estimated to be 0.2 based on maximum longevity (Hoenig 1983), while Sadzinski et al. (1999) reported that total mortality of the Choptank River stock was 0.8 for recruited age classes. Minimum

marketable size is 48 cm (Sadzinski et al. 1999), which corresponds approximately to an age-8 catfish. Thus, fishing mortality was assumed to be 0.6 on age 8+ catfish. Age 6 and 7 fish were assumed to be partially recruited (F=0.1, 0.2, respectively), consistent with size-structued pound net landings reported by Sadzinski et al. (1999). These estimates of fishing mortality at age gave close to maximum yield-per-recruit, indicating that annual recruitment to age 1+ was ~6 million. Based on estimated growth and mortality, total biomass was estimated to be 3,200 tons. As with white perch, it was assumed that a fraction of the catfish population inhabits the upper mesohaline zone of the Bay. A figure of 30% was assumed. Distributed over the upper Chesapeake Bay, two-thirds of the population has a biomass density of 450 mgC m^{-2}. In the mesohaline Bay, one-third of the population has an average density of 45 mgC m^{-2} (Table A-13).

The mean biomass-weighted age of fish in the population is 6 y, for which specific growth is 0.001 d^{-1}. Average assimilation and growth efficiencies were used (AE=0.68, NGE=0.41) to compute production. The diet of smaller catfish includes mostly benthic invertebrates, however, as catfish grow they apparently consume an increasing fraction of small fish (Poe et al. 1991).

Hogchoker

The hogchoker (*Trinectes maculatus*) is known to be abundant in the Bay, but because it is unexploited and little studied, certain estimates of it's biomass throughout the Bay will be elusive. Average baywide abundance, estimated via the TIES trawl surveys was 260 tons (S. Jung, unpublished data). Most likely, this is an

underestimate of the biomass of this fish, which is is closely associated with the bottom and may not be well-sampled by mid-water trawls. The trawl-based estimate is 20% of the trawl-based estimate for spot, for which the mainstem biomass was estimated to be ~20,000 tons. Accordingly, the biomass of hogchokers in the mainstem Bay may be 4,300 tons. Dovel et al. (1969) report that hogchokers spawn in higher salinity waters and that the young juveniles migrate to lower salinities before returning as they growth toward maturity. This pattern is reflected in the length-frequencies reported for different salinity zones by Derrick and Kenndy (1997). Accordingly, one may suspect that summer average biomass is higher in low and high salinity zones than in the mesohaline region. This may also be suspected due to the relatively larger area of unsuitable habitat in the mid Bay (due to hypoxia) and the larger macrobenthic biomass in the upper and lower Bay, which constitute the diet of the hogchoker (Derrick and Kenndy 1997). Pro-rated over the surface areas of these regions, the estimated biomass in the respective regions is 100, 50 and 100 mgC m^{-2} (Table A-13).

Peters and Boyd (1972) estimated the feeding rate of hogchokers at summer temperatures to be about 0.15 g g^{-1} d^{-1} in 0-15 ppt salinity and 0.21 g g^{-1} d^{-1} in when salinity was 30 ppt. Gross growth efficiency (P/C) increased with salinity from 0.23 to 0.27. Accordingly, growth rate increased from about 0.025 d^{-1} when salinity was 0-15 ppt to 0.04 d^{-1} at higher salinity. The diet of hogchokers includes polychaetes and amphipods, in accordance with their abundance. They also consume the siphons of bivalves, but not whole bivalves (Derrick and Kennedy 1997).

American Eel

American eel (*Anguilla rostrata*) was captured in greatest numbers in the upper Bay in TIES mid water trawls (S. Jung, unpublished data). Being catadromous, eels spawn in the Sargasso Sea and migrate into the Bay in late spring as elvers. Elvers migrate to lower salinity areas, including freshwater, oligohaline, and mesohaline areas of the Bay (Wenner and Musick 1975, EPA 1991b), reaching these areas by their first summer in the Bay. Once into the Bay, eels reside for as long as 24 years before migrating back to the open sea to spawn, during which time they do not eat, and from which they do not return (EPA 1991b).

Eels are subject to two fisheries in the Chesapeake Bay, both of which use pots. One fishery targets smaller eels, >25 cm, for use as crab bait. The other fishery captures them live for human consumption overseas. The latter fishery requires larger eels, >33 cm (EPA 1991b). Landings for the bait fishery have not been well documented due to minimal reporting requirements; however, EPA (1991b) describe a scheme for estimating landings as a ratio of crab harvests and reported use of eels as bait by crabbers using trotlines (chicken necks are now widely used as well). Based on these figures, the estimated Maryland landings are about 455 tons y^{-1}. Landings in Virginia are better documented due to reporting requirements by the Potomac River Fisheries Commission. Virginia landings from the Potomac River have averaged ~140 tons y^{-1} (EPA 1991b), and on that basis combined landings from other rivers were estimated to a have been a similar amount. Thus, total Virginia landings may have been 280 tons y^{-1}. EPA (1991b) reported that waterman in the live fishery have complained that the average size of eels is decreasing and that many of the eels that

have been captured are undersized. On this basis, is has been assumed that fishing mortality is high, sufficient to achieve this size structure. The fishing mortality rate was inferred by modeling growth using estimated growth parameters derived using length-weight and maximum length data reported by Froese and Pauly (2001). The growth coefficient K was estimated from EPA (1991b) which noted that the annual growth increment for market size eels, estimated using tagging studies, was about 60 mm. Accordingly, K was estimated to be 0.08 y^{-1}. Assuming natural mortality is 0.2 based on a maximum age of 25 years, growth overfishing such that most of the harvest is of marginal size for the live eel fishery occurs when F≈0.8. The biomass necessary to support the catch (735 tons y^{-1}) is 1692 tons. Of the total surface area of the Chesapeake Bay and tidal tributaries, about 25% was assumed to be low mesohaline to freshwater and favored habitat for eels. Thus, the eels were computed to have an average density within that habitat of 35 mgC m^{-2} d^{-1} (0.2 gAFDW=1 g WW, 500 mgC=1g AFDW). Only 25% of the mesohaline mainstem Bay was assmed to be favored habitat. Therefore, biomass in the mid Bay was computed to be 8.75 mgC m^{-2}. The lower Bay was assumed to not have any habitat in summer for eels and biomass was set to zero.

The average age of eels, weight by biomass was 4.8 y, for which annual average P/B is 0.0015 d^{-1}. Summer average P/B was assumed to be 2-fold greater, or 0.003 d^{-1}. Average values for assimilation efficiency and net growth efficiency obtained from values reported by Schroeder (1981) for carnivorous fish (AE=0.68, NGE=0.41, Table A-13). At this rate of production, annual eel production in the Bay is estimated to be 926 tons, of which the fishery removed 80%. During summer, eels

production was estimated to be 467 tons. Since maximum demand for eels occurs during summer, it was assumed that 75% of the landings (551 tons) occurred during summer, or 120% of summer production. Therefore, fisheries removals from the upper Bay were estimated to be 0.126 mgC m^{-2} d^{-1}, while the same for the mid Bay was 0.032 mgC m^{-2} d^{-1}. Thus, summer mainstem landings were 124 tons, or 22% of the annual baywide landings. To balance the excess landings, it was assumed that biomass decreased during summer by 0.021 mgC m^{-2} d^{-1} in the upper Bay and 0.006 mgC m^{-2} d^{-1} in the mid Bay.

Other Fish

It is important to note here that the upper Bay has been characterized here as having more fish species than the mid Bay, which has more than the lower Bay. In fact, the lower Bay may have a more diverse fish assemblage (e.g. TIES data, S. Jung, unpublished data). This dicrepancy reflects an artifact of data analysis: to suitably represent a species in a network model requires adequate knowledge of its biomass, diet and predators. If the species assemblage is more diverse, this becomes a more arduous if not impossible. For example, fish that are not abundant may be pooled as "other fish" in studies of predator diets. Although it may be possible to quantify the abundances of this diverse assemblage, this substantial task has not been undertaken here. Rather, the possible ramifications of such an oversight are discussed in the analysis of the flow networks.

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Table A-1. Storage and physical input and export of detrital dissolved organic carbon (DOC) and detrital particulate organic carbon (POC). Total POC and DOC are indicated in parentheses. Storages have units mgC m^{-2} while transport fluxes have units mg C m^{-2} d^{-1}.

	DOC			POC		
Region	Storage	Import	Export	Storage	Import	Export
Upper Bay	12180	263	286	2933	90	0
	(12504)			(5249)		
Mid Bay	27000	79	85	5130	0	0
	(28207)			(10324)		
Lower Bay	26286	93	220	5156	0	0
	(26915)			(8309)		

Table A-2. Estimates of summer average primary production rates derived from Harding et al. (2001) and Kemp et al. (1997). (A) Net ^{14}C-PP was obtained directed from Table 2 in Harding et al. (2001), averaging regions as follows: Upper Bay=Region 6; Mid Bay=Average of Region 3-5.; Lower Bay=Average of Region 1 and 2. (B) Gross ^{14}C-PP was computed as (1.48/1.2)(1.229)(Net ^{14}C-PP). (C) Summer average daily gross O_2-PP was computed from data in Kemp et al. (1997) assuming PQ=1.2 (Stokes 1996). (D) Euphotic zone integrated phytoplankton biomass was computed from chl-a obtained from Harding et al. (2001) assuming C:Chl-a=50.

Region	(A) Net ^{14}C-PP (mg C m^{-2} d^{-1})	(B) gross ^{14}C-PP (mg C m^{-2} d^{-1})	(C) gross O_2-PP (mg C m^{-2} d^{-1})	(D) PP Biomass mg C m^{-2}
Upper Bay	811	1230	570	1595
Mid Bay	2176	3298	3030	3913
Lower Bay	1406	2131	3070	2485

Table A-3. Summer phytoplankton biomass, gross phytoplankton production (GPP), algal respiration (R), extracellular release of DOC (ER), and net POC production by phytoplankton (PP).

	Biomass (mg C m^{-2})	GPP (mg C m^{-2} d^{-1})	R (mg C m^{-2} d^{-1})	ER (mg C m^{-2} d^{-1})	PP (mg C m^{-2} d^{-1})
Net Plankton					
UB	1356	984	271	71	642
MB	3326	2638	665	197	1776
LB	2112	1705	422	128	1154
Picoplankton					
UB	239	246	60	19	168
MB	587	660	147	51	462
LB	373	426	93	33	300
Total					
UB	1595	1230	331	90	809
MB	3913	3298	812	249	2237
LB	2485	2131	516	162	1454

Table A-4. Biomass, gross primary production, algal respiration, extracellular DOC release and net production by microphytobenthos in three regions of Chesapeake Bay during summer.

Region	Biomass ($mg\ C\ m^{-2}$)	GPP ($mg\ C\ m^{-2}\ d^{-1}$)	R ($mg\ C\ m^{-2}\ d^{-1}$)	ER ($mg\ C\ m^{-2}\ d^{-1}$)	PP ($mg\ C\ m^{-2}\ d^{-1}$)
UB	293	234	59	16	159
MB	265	212	53	15	144
LB	293	234	59	16	159

Table A-5. Coverage of submersed aquatic vegetation (SAV) in Chesapeake Bay by region. %Veg.= percent of total area vegetated, B-VA=Average biomass in vegetated areas, P-VA=average production in vegetated areas, Biomass=regional average biomass, Production=regional average production.

Region	SAV Area (ha)	%Veg.	B-VA ($mgC\ m^{-2}$)	P-VA ($mgC\ m^{-2}\ d^{-1}$)	Biomass ($mgC\ m^{-2}$)	Production ($mgC\ m^{-2}\ d^{-1}$)
UB	2495	3.86	54000	406	2086	16
MB	3136	1.45	135000	1260	1952	18
LB	3967	1.47	135000	1260	1986	19

Table A-6. Biomass, production, consumption and respiration of free-living and particle attached bacteria in Chesapeake Bay during summer. Bacterial growth efficiency: UB=0.43, MB=0.52, LB=0.39 (del Giorgio and Cole 1998)

Region	Biomass ($mgC\ m^{-2}$)	Production ($mgC\ m^{-2}\ d^{-1}$)	Consumption ($mgC\ m^{-2}\ d^{-1}$)	Respiration ($mgC\ m^{-2}\ d^{-1}$)
Free Bacteria				
Upper Bay	649	349	811	462
Mid Bay	2415	1417	2725	1308
Lower Bay	1258	740	1897	1157
Particle-Attached Bacteria				
Upper Bay	36	28	65	37
Mid Bay	73	83	159	77
Lower Bay	39	41	105	64

Table A-7. Estimates of biomass (B), production (P), respiration (C), consumption (C) and and egestion plus excretion (U) for the zooplankton in the upper, mid and lower Bay. Biomass has units mgC m^{-2}. The rates (P, R, C, U) have units mgC m^{-2} d^{-1}.

	B	P	R	C	U
Upper Bay					
Heterotrophic Microflagellates	30.2	100	66	285	119
Ciliates	65.9	165	97	330	68
Rotifers	13.7	4.11	4.11	13.70	5.48
Meroplankton	3.2	1.62	1.62	5.41	2.16
Mesozooplankton	282	106	35	256	115
Ctenophores	17.0	2.30	1.30	5.80	2.20
Sea Nettles	0.00				
Mid Bay					
Heterotrophic Microflagellates	149.3	418	279	1194	498
Ciliates	147.0	366	215	733	151
Rotifers	23.4	7.02	7.02	23.39	9.36
Meroplankton	18.0	9.01	9.01	30.02	12.01
Mesozooplankton	526	263	88	637	287
Ctenophores	126	16.00	10.00	42.00	16.00
Sea Nettles	6.29	0.10	0.30	3.90	
Lower Bay					
Heterotrophic Microflagellates	43.1	142	95	407	169
Ciliates	86.7	217	127	434	89
Rotifers	0.0	0.00	0.00	0.00	0.00
Meroplankton	38.4	19.20	19.20	64.01	25.60
Mesozooplankton	1073	268	89	650	293
Ctenophores	108	14.00	8.00	36.00	14.00
Sea Nettles	0.00				

Table A-8. Biomass, consumption, respiration and egestion for copepod nauplii and mesozooplankton. Biomass has units mgC m^{-2}. The rates have units mgC m^{-2} d^{-1}. P=production, R=respiration, C=consumption, U=egestion.

Region	Nauplii Biomass	Meso-zooplankton Biomass	P	R	C	U
UB	31	251	106	35	256	115
MB	83	443	263	88	637	287
LB	107	966	268	89	650	293

Table A-9. Geometric mean biovolumes (ml m^{-2}) of the ctenophore *Mnemiopsis leidyi* for summer in three regions of Chesapeake Bay. Unpublished TIES data courtesy of J.E. Purcell. Biomass as carbon (mg m^{-2}), in parentheses, was computed using 1 ml = 1.012 mg wet weight = 0.485 mgC (Nemazie 1991).

Year	Upper-Bay	Mid-Bay	Lower-Bay
1995	26 (13)	38 (20)	202 (104)
1996	10 (5)	721 (372)	585 (302)
1997	93 (48)	167 (86)	90 (46)
2000	156 (80)	226 (117)	9 (4.6)
TIES Average	71 (36)	288 (149)	223 (115)
CBMP Average	0 (0)	240 (124)	
Best Estimate	36 (18)	264 (126)	223 (115)

Table A-10. Geometric mean biovolumes (ml m^{-2}) of *Chrysaora quinquecirrha* for summer in three regions of Chesapeake Bay. Biomass (mg C m^{-2}) is indicated in parentheses. Unpublished data courtesy of J.E. Purcell. Biovolume to carbon conversions were made using 1 ml = 1.75 mgC (Purcell 1992; Purcell, J. E., personal communication).

Year	UB	MB	LB
1995	0.48 (0.84)	8.40 (14.7)	0.14 (0.25)
1996	0.10 (0.18)	0.89 (1.56)	0.33 (0.58)
1997	0.67 (1.17)	5.07 (8.87)	0.00 (0.00)
2000	0.00 (0.00)	0.01 (0.02)	0.00 (0.00)
TIES Average	0.31 (0.55)	3.59 (6.29)	0.12 (0.00)

Table A-11. Active sediment carbon pool size, and rates of sediment bacterial metabolism. Sediment oxygen consumption (SOC) was estimated by Cowan and Boynton (1996) for stations in the channel of each region. Integrated benthic sulfate reduction was estimated by Marvin-DiPasquale and Capone (1998) and was converted to O_2 assuming $S:O_2=2$. Total channel metabolism was estimated as SR+0.5SR and was converted to carbon assuming respiratory quotient =1.0. Regional average benthic metabolism was computed from channel rates assuming appropriate rates outside the channel were 50% of channel rates (Kemp et al. 1997).

Region	Sediment Carbon (mgC m^{-2})	SOC (g O_2 m^{-2} d^{-1})	SR (mmol S m^{-2} d^{-1})	Channel Average (mgC m^{-2} d^{-1})	Region Average (mgC m^{-2} d^{-1})
UB	346500	0.58	4.64	220	130
MB	202400	0.18	50.2	1240	839
LB	77000	0.72	26.4	770	559

Table A-12. Biomass and bioenergetic rates for benthic bacteria, meiofauna, suspension feeders and deposit feeders. UB=Upper Bay, MB=Mid Bay, LB=Lower Bay. Biomass has units mgC m^{-2}, all rates are mgC m^{-2} d^{-1}.

Region	Biomass	Production	Respiration	Consumption	Egestion
Benthic Bacteria					
UB	30	34	80	114	0
MB	298	337	787	1124	0
LB	220	249	580	829	0
Meiofauna					
UB	700	49	49	196	98
MB	476	33	33	133	67
LB	700	49	49	196	98
Suspension Feeders					
UB	27232	218	327	1089	545
MB	421	6	9	29	15
LB	6962	98	146	488	244
Deposit Feeders					
UB	2368	33	41	166	92
MB	1030	14	21	71	36
LB	4089	57	86	287	143

Table A-13. Estimates of biomass (B, mgC m^{-2}), specific growth rate (P/B, d^{-1}), gross growth efficiency (GGE=P/C), net growth efficiency (NGE), assimilation efficiency (AE), biomass accumulation (BA), net migrations (immigration-emigration), and removals by recreational fishing (RF) and commercial fishing (CF). Unless otherwise indicated, rates have units mgC m^{-2} d^{-1}. Efficiencies are unitless.

	B	P/B	GGE	NGE	AE	BA	I-E	RF	CF
Upper Bay							0.13		1.82
Blue crab	610	0.004	0.33	0.57	0.58		-48		
Menhaden	2136	0.025	0.25	0.29	0.87				
Bay anchovy	287	0.081	0.28	0.40	0.69	4.00			
Herrings and Shads	212	0.010	0.28	0.41	0.68				
White Perch	282	0.002	0.29	0.42	0.68	0.14			
Spot	195	0.010	0.28	0.41	0.68				
Croaker	50	0.010	0.28	0.41	0.68				
Hogchoker	100	0.025	0.17	0.25	0.68			0.146	0.038
Catfish	450	0.001	0.25	0.37	0.68				
Striped Bass	172	0.002	0.08	0.10	0.83	0.24			
Bluefish	68	0.007	0.10	0.12	0.83			0.197	0.009
Weakfish	67	0.009	0.13	0.16	0.83	0.42		0.036	0.002
American eel	35	0.003	0.28	0.41	0.68	-0.02			0.126
Mid Bay							1.25		2.09
Blue crab	390	0.004	0.33	0.57	0.58				
Menhaden	2136	0.025	0.25	0.29	0.87	48			
Bay anchovy	381	0.081	0.28	0.40	0.69	5.41			
White Perch	29	0.002	0.29	0.42	0.68	0.01			
Spot	222	0.010	0.28	0.41	0.68			0.021	0.018
Croaker	226	0.010	0.28	0.41	0.68			0.020	0.012
Hogchoker	50	0.025	0.17	0.25	0.68				
Catfish	45	0.001	0.25	0.37	0.68			0.015	0.004
Striped Bass	172	0.002	0.08	0.10	0.83	0.24			
Bluefish	68	0.007	0.10	0.12	0.83			0.197	0.009
Weakfish	67	0.009	0.13	0.16	0.83	0.42		0.036	0.002
American eel	9	0.003	0.28	0.41	0.68	-0.006			0.032

Table A-13, continued.

	B	P/B	GGE	NGE	AE	BA	I-E	RF	CF
Lower Bay							0.14		1.09
Blue crab	342	0.004	0.333	0.575	0.58				30.6
Menhaden	2136	0.025	0.25	0.29	0.87				
Bay anchovy	381	0.081	0.28	0.46	0.60	5.41			
Spot	570	0.010	0.28	0.41	0.68		0.12	0.089	0.163
Croaker	236	0.010	0.28	0.41	0.68			0.050	0.080
Hogchoker	100	0.040	0.19	0.28	0.68				
Striped Bass	172	0.002	0.08	0.10	0.83	0.24			
Bluefish	68	0.007	0.10	0.12	0.83			0.210	0.020
Weakfish	211	0.009	0.13	0.16	0.83	1.03		0.359	0.059

Table A-14. (A) The fraction of all blue crab habitat located in the Chesapeake Bay and its tributaries that is located in each region of the mainstem Bay. (B) The total blue crab biomass in each region. (C) The total surface area of each region (includes non blue crab habitat area). (D) The blue crab biomass per unit of bottom area.

Region	(A) Habitat Area	(B) Biomass (tons)	(C) Total Area (km^2)	(D) Biomass ($mgC\ m^{-2}$)
UB	0.024	3597	472	610
MB	0.076	11389	2338	390
LB	0.076	11389	2661	342

Table A-15. Biomass (MT wet-wt) of adult Bay anchovy in Chesapeake Bay during summer of 1993. Data from Rilling and Houde (1999) as recomputed from raw data (G. C. Rilling, personal communication).

	Upper Bay	Mid Bay	Lower Bay	Total
June	2653	8556	12808	24017
July	142	4956	18096	23194
Average	1398	6756	15452	23606
($g\ m^{-2}$)	(1.94)	(3.59)	(4.14)	(3.73)

Table A-16. Preliminary estimates of biomass (tons wet-wt) of adult Bay anchovy in Chesapeake Bay during summer of 1995-1999. Data obtained from E. Houde (personal communication).

Year	Bay-Wide Biomass (tons wet-wt)	% 1993 Estimate
1993[1]	23606	100
1995	5597	24
1996	3058	13
1997	25236	107
1998	26331	112
1999	13969	59
Average	16300	69

[1] Data as reported in Table A-15.

Table A-17. Age-structured carbon balance for bay anchovy in Chesapeake Bay during summer. Biomass has units mgC m^{-2}. Rates have units mgC m^{-2} $summer^{-1}$. Specific rates have units d^{-1} and were computed from $summer^{-1}$ rates assuming 92 days for the age 1+ cohort and 46 days for the age 0+ cohort.

	Age 0+	Age 1+	Combined
Average Biomass	368	197	381[1]
Change in Biomass	+518	-20	+498
Production	2573	290	2863
Somatic	2573	39	2612
Reproductive	0	252	252
Consumption	6524	2575	9099
Egestion+Excretion	2120	837	2957
Respiration	2799	1758	4557
C Balance	-967	-311	-1278
Specific Rates			
P/B	7.0	1.5	
P/R	0.92	0.17	
Specific Cons. (d^{-1})	0.39	0.14	
Specific Resp. (d^{-1})	0.17	0.10	

[1] computed as half of age 0+ biomass plus age 1+ biomass.

Table A-18. Diet composition (%) by weight of adult bay anchovy during June in mid-Chesapeake Bay. Data from Klebasco (1991).

Diet Component	June	July	August
Copepods	6.0	96.1	97.5
Barnacles (cyprids)	56.2	0.3	1.8
Polychaetes	3.5		
Amphipods	20.6		
Unid. Crustaceans	13.0	2.3	
Other	0.7	1.3	0.7

Table A-19. Specific consumption and total consumption for bay anchovy. Specific consumption from Klebasco (1991).

Cohort	June	July	August	Summer
Specific consumption (d^{-1})				
Age 0+ (YOY)	n/a	0.303	0.393	n/a
Adults (Age 1+)	0.07	0.184	0.172	n/a
Consumption (mgC m^{-2} $period^{-1}$)				
Age 0+ (YOY)		1468	5056	6524
Adults (Age 1+)	430	1128	1018	2575
Whole Population	430	2596	6074	9099
(specific rate, d^{-1})				(0.26)

Table A-20. Consumption for the combined bay anchovy cohorts with diet allocated to diet components according to diet composition in Table A-18. The division of copepod composition into mesozooplankton and microzooplankton is approximate and based on the age structure of the bay anchovy population. Young-of-the-year anchovy were assumed to eat copepodites (Klebasco 1991), which are a component of the microzooplankton.

Diet Component	June	July	August	Summer (% of total)
Mesozooplankton	85	1812	4175	6071 (67%)
Microzooplankton	0	776	1789	2566 (28%)
Meroplankton	257	8	109	374 (4%)
Benthic Susp. Feeders	89	0	0	89 (1%)
TOTAL	430	2596	6074	9099

Table A-21. Monthly and summer total respiration (mgC m^{-2}) by bay anchovy. Rates were converted from O_2 consumption using respiratory quotient =1.0.

Cohort	June	July	August	Summer (d^{-1})
YOY	0	669	2130	2799
Age 1+	418	694	646	1758
Total	418	1363	2776	4557
				(50)

Table A-22. Adjustments to initial bioenergetic estimates for bay anchovy to achieve carbon balance for the summer. nc = no change.

Rate	Initial Value	Final Value (% difference)	Daily Rate (C specific rate, d^{-1})
Consumption	9099	10191 (+12%)	111 (0.29)
Respiration	4557	4016 (-12%)	46 (0.12)
Egestion+Excretion	2957	3312 (+12%)	36 (0.09)
Production	2863	2863 (nc)	31 (0.08)

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