

Epiphyte Contributions to Light Attenuation at the Leaf Surface

Building from the diagnosis and quantification of water-column contributions to attenuation of light, the present chapter focuses specifically on how changes in water quality variables alter the light available at SAV leaves and considers effects of light attenuation resulting from substances both in the overlying water column (phytoplankton, suspended particles and dissolved organics) and attached to SAV leaves (epiphytic algae, organic detritus and inorganic particles). A simple model is developed to calculate photosynthetically available radiation (PAR) at the leaf surface for plants growing at a given restoration depth (Z) under specific water quality conditions. The computed value for PAR at the plant leaves is compared to a target “minimum light requirement” for SAV survival, which is defined in Chapter VII of this report.

The overall objective is to apply this model using water quality monitoring data to estimate growing season mean light levels at SAV leaves for a particular site or geographic region. The calculated light levels at SAV leaves are then compared to the applicable minimum light requirement value to assess whether water quality conditions are suitable to support survival and growth of SAV. The relative contributions of water column vs. epiphytic substances in attenuating incident light to SAV leaves are also computed. The scientific basis of this model is described here in some detail.

Numerous models have been developed previously for making theoretical computations of SAV growth considering light attenuation by water-column materials only (e.g., Best 1982; Zimmerman *et al.* 1987) or water-column plus epiphytic substances (Wetzel and

Neckles 1986; Hootsman 1991; Bach 1993; Kemp *et al.* 1995; Madden and Kemp 1996; Fong *et al.* 1997). Other studies have described simple statistical models for predicting depth distribution of SAV in relation to variations in observed data on water column transparency (e.g., Rørslett 1987; De Jong and De Jong 1992; Scheffer *et al.* 1993). The model described in this chapter combines these approaches to calculate, from field observations, light available for SAV survival and growth, considering light attenuation from both water column and epiphytic materials.

APPROACH AND METHODOLOGY

To compute median PAR at the leaf surface of SAV, the model requires SAV growing season medians for four water quality variables: 1) dissolved inorganic nitrogen (nitrate + nitrite + ammonia), or DIN; 2) dissolved inorganic phosphorus (primarily phosphate), or DIP; 3) total suspended solids (TSS); and 4) diffuse downwelling PAR attenuation coefficient (K_d). Values for K_d are either obtained from direct measurements of PAR decrease with water depth using a cosine-corrected sensor, or they are calculated from observations on the depth at which a Secchi disk disappears (see Chapter III for the Secchi depth/ K_d conversion). An implicit assumption in this analysis is that light (PAR) availability is the primary environmental factor that limits SAV survival and growth in temperate coastal waters (Duarte 1991a; Dennison *et al.* 1993; Zimmerman *et al.* 1995). In the model, light is attenuated by dissolved and particulate materials in the water column (Chapter IV) and by biotic and abiotic epiphytic materials accumulated on SAV leaves.

The light attenuation to the SAV leaf surface is calculated using an exponential equation, with a depth-dependent term for water column shading and a mass-specific term for epiphyte attenuation. These are standard equations widely used in aquatic science (Kirk 1994) and ecosystem modeling (e.g., Hootsman 1991; Madden and Kemp 1996). The depth of the site is defined by the local bathymetry and the “target depth” for SAV restoration. Specific targets and formally adopted goals for restoration of SAV in Chesapeake Bay, originally defined and quantified in Batiuk *et al.* (1992) and Dennison *et al.* (1993), are summarized in Chapter VIII.

Specifically, the model calculates PAR at the SAV leaf surface for a given water depth (I_{zs}) as a fraction of the incident radiation at the water surface (I_o) using the following formulation:

$$[I_{zs}/I_o] = [e^{-(K_d)(Z)}][e^{-(K_e)(B_e)}] \quad (V-1).$$

There are four variables on the right side of this equation: 1) the water-column PAR attenuation coefficient, K_d ; 2) the depth of leaves growing up from sediments at the lower edge of a potential SAV habitat, Z ; 3) the biomass of epiphytic algae growing on SAV leaves, B_e ; and 4) the biomass-specific PAR attenuation coefficient for epiphytic algal material, K_e .

The model user defines Z with the assumption that SAV must grow upward from the sediment surface early in the growing season. As the plants grow upward and shoots get closer to the water surface, they begin to self-shade, which is not considered directly in this analysis. K_d is an input variable derived from field monitoring data. The model computes B_e from input water quality monitoring data on dissolved inorganic nitrogen, dissolved inorganic phosphorus, K_d and the selected value for Z . The fourth variable, K_e , is estimated from two statistical correlations derived from experimental data (Staver 1984) and field observations in oligohaline and mesohaline regions of the Potomac and Patuxent River estuaries (Carter *et al.*, unpublished data; Boynton *et al.*, unpublished data) and in the mesohaline and polyhaline reaches of the York River estuary (Neckles 1990). The first correlation is between K_e and the ratio B_e/B_{de} , where B_{de} is the total dry weight of epiphytic material (both algal and other material per dry weight of SAV leaf). The ratio, B_e/B_{de} , is itself calculated from a second statistical relationship with total suspended solids, using total suspended

solids water quality monitoring data as input to the computation.

MODEL DESCRIPTION

In this section, each step in the model calculation is explained and its derivation described (Table V-1). All key assumptions are stated explicitly, and their implications are discussed. The model is based on the relation described in Equation V-1, where light (as a fraction of that at the water surface) is attenuated by two exponential relations. One of these relations [$e^{-(K_d)(Z)}$] accounts for attenuation by the water overlying SAV leaves and dissolved and suspended materials contained in that water, and the other term [$e^{-(K_e)(B_e)}$] accounts for effects of materials accumulated on SAV leaves.

Most of the model description that follows explains how the second of these terms was derived from a combination of statistical relations and numerical model simulations. First, a description is provided on how an estimate of potential biomass of epiphytic algae is calculated from nutrient concentrations and other water quality measurements. Next, an approach is described for estimating a biomass-specific PAR attenuation coefficient for epiphytic material (K_e) in relation to the ratio of epiphytic algal biomass (B_e , as chlorophyll *a*) to total dry weight of material (B_{de}) on SAV leaves. Then a statistical correlation is described for estimating the ratio (B_e/B_{de}) in relation to water quality conditions.

Computing Epiphytic Algal Biomass (B_e) from Nutrient Concentration

A numerical ecosystem simulation computation is used in the first three steps of the overall model to compute growth of epiphytic algal biomass as a function of nutrient concentrations (e.g., Twilley *et al.* 1985; Borum 1985) and light availability (e.g., Short *et al.* 1995; Moore *et al.* 1996). This numerical submodel (adapted from Kemp *et al.* 1995 and Madden and Kemp 1996) is used to calculate mean epiphytic algal biomass from input data on dissolved inorganic nutrient concentrations, water depth and K_d . The numerical model also takes into account other environmental factors including temperature (Madden and Kemp 1996), grazing on epiphyte biomass (Hootsman and Vermaat 1985; Jernakoff *et al.* 1996) and water

TABLE V-1. Summary of the approach used to estimate photosynthetically available radiation at the leaf surface of submerged aquatic vegetation using water quality data routinely monitored in Chesapeake Bay.

Step in Model Calculation <i>Functional Relationship</i>	Input Data	Source of Model Relationship	Units
1) Decide limiting nutrient DIN/DIP > 16 , use DIP DIN/DIP ≤ 16 , use DIN	DIN, DIP	Fisher et al. 1992	μM
2) Derive general equation to calculate epiphyte biomass $B_e = (B_e)_m [1 + 208 (\text{DIN}^{-K_{N(OD)}})]^{-1}$ • $(B_e)_m$ = maximum B_e value • $K_{N(OD)}$ = characteristic coeff.	DIN, DIP	Numerical model (Madden and Kemp 1996)	B_e , gCgC ⁻¹ DIN, μM $K_{N(OD)}$, none
3) Calculate PAR effect on $K_{N(OD)}$ and $(B_e)_m$ $(B_e)_m = 2.2 - [0.251 (\text{OD}^{1.23})]$ • OD = Optical Depth = $K_d (Z)$ $K_{N(OD)} = 2.32 (1 - 0.031 \text{OD}^{1.42})$	K_d , Z	Numerical model (Madden and Kemp 1996)	K_d , m ⁻¹ Z, m
4) Calculate epiphyte dry weight $B_{de} = 0.107 \text{TSS} + 0.832 B_e$	TSS B_e	Regression from experimental data (e.g., Staver 1984)	TSS, mg l ⁻¹ B_e , mg chl gdw ⁻¹ B_{de} , gdw gdw ⁻¹
5) Calculate epiphyte biomass-specific PAR attenuation coeff. $K_e = 0.07 + 0.32 (B_e / B_{de})^{-0.88}$	B_e , B_{de}	Regression from experimental and field data	B_e , μg chl cm ⁻² B_{de} , mg dw cm ⁻² K_e , cm ² μg chl ⁻¹
6) Calculate PAR at SAV leaves (I_{ze}) Install Equation Editor and double-click here to view equation.	DIN, DIP, K_d , TSS, Z	Combining steps #1-5 (from above)	DIN, μM DIP, μM TSS, mg l ⁻¹ K_d , m ⁻¹
7) Compare SAV leaf PAR with Minimum Light Requirement	I_{ze} / I_o	See Chapter VII	%

exchange rate (Sturgis and Murray 1997). Earlier versions of this numerical model were calibrated using data from field sites in Chesapeake Bay (Kemp *et al.* 1995; Madden and Kemp 1996). The numerical model used in this analysis was calibrated using data from both field sites (e.g., Lubbers *et al.* 1990) and controlled mesocosm experiments (Sturgis and Murray 1997).

The molar ratio of concentrations (SAV growing season mean values) of dissolved inorganic nitrogen to dissolved inorganic phosphorus (DIN:DIP) is compared to the Redfield ratio of 16:1 (Redfield 1934) to select which nutrient should be used in the analysis (Table V-1). Here, a single limiting nutrient is assumed. If the molar ratio is ≤ 16 , dissolved inorganic nitrogen data are used; if the ratio is > 16 , dissolved inorganic phosphorus data are used. This assumption is generally consistent with observations from Chesapeake Bay algal bioassay and mesocosm experiments (D'Elia *et al.* 1986; Neundorfer and Kemp 1993; Fisher *et al.* 1992, 1998).

The numerical ecosystem simulation was used to compute a family of sigmoidal shaped curves relating nutrient concentration to epiphyte biomass, with different curves for different water column light regimes (Figure V-1). Model biomasses are calculated in terms of organic carbon, so epiphytes are reported here as g C epiphyte g C SAV⁻¹ (Table V-1). Light regimes are characterized by the "optical depth," which is the product of K_d times the water depth Z (e.g., Kirk 1994). It can be seen that changes in optical depth have a more pronounced effect on the maximum epiphyte biomass attained than on nutrient responses at low dissolved inorganic nitrogen concentrations. Consistent patterns are evident in the family of curves generated by this model, and these can be described by the following general function:

$$B_e = (B_e)_m [1 + 208(\text{DIN}^{-K_{N(\text{OD})})}]^{-1} \quad (\text{V-2})$$

where the two rate coefficients $(B_e)_m$ and $K_{N(\text{OD})}$ are the maximum possible epiphytic algal biomass (ultimately limited by space) and a shape coefficient describing the B_e vs. dissolved inorganic nitrogen (DIN) relationship, respectively. As the optical depth ($\text{OD} = Z \cdot K_d$) increases, values for $(B_e)_m$ decrease, while values for $K_{N(\text{OD})}$ increase.

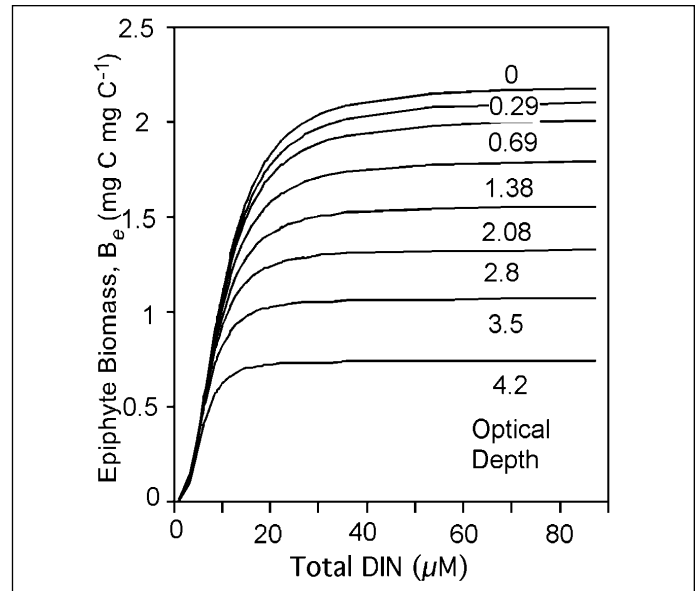


FIGURE V-1. Epiphytic Algal Biomass Responses to Varying DIN and Light Conditions. Calculated responses of epiphytic algal biomass (B_e , mg C/mg C SAV) to changes in dissolved inorganic nitrogen (DIN) concentration under varying light conditions in estuarine waters of Chesapeake Bay. Each curve represents estimated response under specific light regimes, characterized by different optical depths ($\text{OD} = K_d \cdot Z$). Relationships were generated from numerical ecosystem simulation model (modified from Madden and Kemp 1996) assuming constant biomass of host SAV plant over growing season (May-August). Similar functions are predicted for B_e versus dissolved inorganic phosphorus (DIP) concentrations, with $\text{DIP} = \text{DIN}/16$.

Statistically significant relationships were fit between model-generated values for the coefficient $(B_e)_m$ and input values for optical depth

$$(B_e)_m = 2.2 - [0.251 (\text{OD})^{1.23}] \quad (\text{V-3})$$

and between the coefficient $K_{N(\text{OD})}$ and optical depth,

$$K_{N(\text{OD})} = 2.32 (1 - 0.031 \text{OD})^{1.42} \quad (\text{V-4}).$$

The relationships described in equations V-3 and V-4 (Figure V-2) can then be substituted back into Equation V-2 to produce a single continuous function relating epiphyte biomass (B_e) to two input variables, dissolved inorganic nitrogen (or dissolved inorganic phosphorus) and OD. Although Equation V-4 predicts that $K_{N(\text{OD})} = 0$ at $\text{OD} = 11.55$, neither epiphytes nor SAV are capable of growing at such high values of OD.

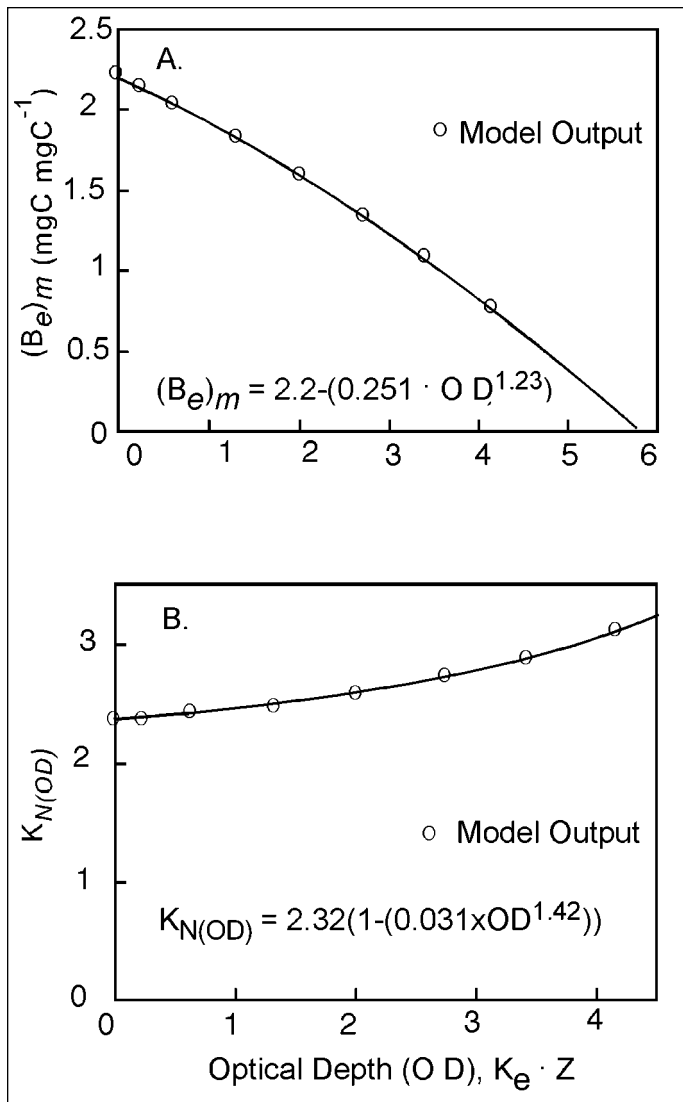


FIGURE V-2. Model Predicted Responses of Epiphytic Algal Biomass to Changes in Optical Depth and DIN Concentrations. Model predicted the effects of changing optical depth ($OD = K_d \cdot Z$) on coefficients describing response of epiphytic algal biomass B_e to changes in dissolved inorganic nitrogen (DIN) concentrations (see Fig. V-1). The coefficient $(B_e)_m$ is the maximum possible value for B_e at a given OD (upper panel, A), and $K_{N(OD)}$ is a coefficient describing the shape of the B_e versus DIN relationship (lower panel, B).

There are a limited number of complete data sets available for testing these relations between nutrient concentration, light availability and epiphyte biomass. This is, in part, because of the difficulty in obtaining nutrient data integrated over appropriate time scales to coincide with epiphytic algal growth (e.g., Sand-Jensen and Borum 1991; Duarte 1995). Data used as inputs to equations V-2 through V-4 to calculate

epiphyte biomass were measurements of dissolved inorganic nitrogen, dissolved inorganic phosphorus, K_d and Z (averaged over the course of the studies) from two field sites in Chesapeake Bay tidal tributaries—the Potomac River Estuary (Carter *et al.*, unpublished data) and the Patuxent River Estuary (Boynton *et al.*, unpublished data)—and from a recent mesocosm experiment (Sturgis and Murray 1997).

Epiphyte biomass measurements are based on artificial substrates deployed and retrieved in the two referenced field studies and on direct measurements from leaves of *Potamogeton perfoliatus* in the referenced mesocosm experiments. All biomass measurements were converted from chlorophyll *a* to carbon units using measured chlorophyll *a*:carbon ratios. The model assumed a constant (mean) value for SAV biomass over the course of a 60-day simulation. Although there were only eight separate data points for this comparison, the “predicted” (PRED) biomass values compared well to measured (OBS) values (Figure V-3). There appears to be a slight bias, where the prediction tends to underestimate measured values at moderate biomasses; however, the relationship is statistically significant ($OBS = 0.21 + 0.93 \text{ PRED}$, $r^2 = 0.81$).

Relationships between epiphytic algal biomass and nutrient concentrations or loading rates previously have been reported for a wide range of conditions. While most of these are from experimental manipulations (Philips *et al.* 1978; Twilley *et al.* 1985; Neundorfer and Kemp 1993; Neckles *et al.* 1993; Williams and Ruckelshaus 1993; Short *et al.* 1995; Sturgis and Murray 1997), several field studies also revealed positive relations between nutrients and epiphytic algal biomass (Borum 1985; Cattaneo 1987; Lapointe *et al.* 1994). Many recent studies have emphasized the importance of invertebrate grazing as a control on epiphytic algal biomass (e.g., Cattaneo 1983; Orth and van Montfrans 1984; Hootsman and Vermaat 1985; Howard and Short 1986), and other studies suggest that heavy grazing pressure may preclude epiphytic algal responses to nutrients (Neckles *et al.* 1993; Jerinakoff *et al.* 1996; Alcoverro *et al.* 1997). Results of other recent studies have indicated that muted epiphytic algal responses to nutrient enrichment may also result from shading associated with phytoplankton growth (e.g., Taylor *et al.* 1995; Short *et al.* 1995; Lin *et al.* 1996) or other sources of turbidity (Moore *et al.*

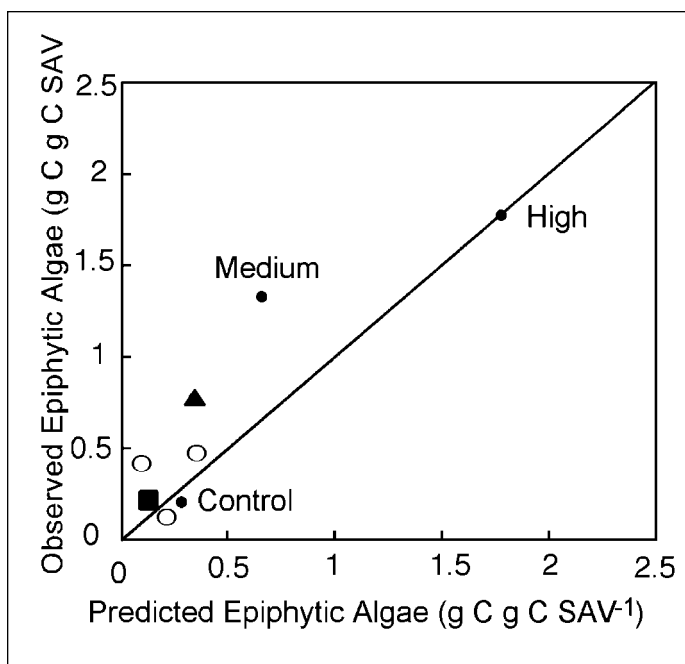


FIGURE V-3. Observed vs. Predicted Epiphytic Algal Biomass. Comparison of observed epiphytic algal biomass and predicted values (from Equation V-2 and Figure V-1) using inputs of data for dissolved inorganic nitrogen (or dissolved inorganic phosphorus) and optical depth ($OD = K_d \cdot Z$). Data and model predictions were averaged over duration of field deployments of artificial substrates (2 weeks) or mesocosm experiments (6 weeks), and data are averaged over multiple sites and replicate mesocosms. Values for B_e were from four sources: 1) *Potamogeton perfoliatus* plants in mesocosm studies (closed circles, Sturgis and Murray 1997); 2) artificial substrates from field studies in the Potomac River estuary (triangles, Carter *et al.*, unpublished); 3) artificial substrates from field studies in the Patuxent River estuary (squares, Boynton *et al.*, unpublished); and 4) artificial substrates from field studies in the York River estuary (open circles, Neckles 1990). High, Medium, and Control refer to nutrient treatments in mesocosm studies.

1996). Shear stress associated with waves can also reduce the accumulation of epiphytes on SAV leaves, with open exposure to waves leading to reduced accumulation of epiphytes (Strand and Weisner 1996; Kendrick and Burt 1997). Finally, there is growing evidence that epiphyte responses to nutrient enrichment may vary with the residence time of water flushing SAV beds (Kemp *et al.* 1983; Sturgis and Murray 1997; Murray *et al.* unpublished), as regulated by physiographic characteristics of the site (Kemp *et al.* 1983) and by SAV abundance (Ward *et al.* 1984; Rybicki *et al.* 1997).

The structure of the numerical ecosystem simulation model used in this study allows for sensitivity analyses of how light, grazing and flushing rate might alter the relationship between nutrient concentration and biomass of epiphytic algae. Effects of light availability in concert with water depth were discussed previously, and model simulation results (Figure V-2) illustrate that epiphytic algal growth will be relatively unaffected by nutrient enrichment in low light environments (e.g., the bottom curve in Figure V-1 at $OD = 4.2$). Light effects are already directly captured in the present version of the Figure V-1 model algorithm described here. Both grazing rates on epiphytes and in water exchange rates are fixed at baywide average values in the present version of this algorithm. Potential effects of these two factors on the calculated nutrient-epiphyte relationship can be investigated using numerical model simulations.

Model simulations revealed that high grazer biomass (e.g., 1 g C m^{-2}) can completely mask the relationship between epiphytic algal biomass and dissolved inorganic nitrogen (Figure V-4, upper panel). By contrast, at lower grazer biomass (0.2 g C m^{-2}), epiphytic algae accumulate sharply with increasing dissolved inorganic nitrogen concentrations, reaching biomass levels that exceed two grams C (g C SAV^{-1}) at $30 \mu\text{M}$ dissolved inorganic nitrogen (Figure V-4, upper panel). The model suggests that the dissolved inorganic nitrogen-epiphyte relationship is highly sensitive to grazing effects at herbivore biomass levels between 0.8 and 1.0 g C m^{-2} (assuming a mean grazer size of 1 mg dw).

Field data on herbivorous epifaunal abundances are available from the early 1980s for one *Z. marina* site in the lower Chesapeake Bay (Fredette *et al.* 1990) and for two sites (dominated by *Potamogeton spp.* and *Ruppia maritima*) in the mesohaline Chesapeake Bay (Lubbers *et al.* 1990). Using these data, along with reported allometric relations between epifaunal size and consumption (Cattaneo and Mousseau 1995), potential grazing rates on epiphytes in these SAV beds were estimated. At the *Z. marina* site, calculated grazing rates appear to have been capable of controlling epiphyte growth, while moderate-to-low grazing rates at the mesohaline Bay sites would have been incapable of regulating epiphyte biomass. This is consistent with observed trends in SAV abundance at these two Chesapeake Bay sites in recent decades, where SAV populations have declined more in the mesohaline than in the polyhaline regions of the estuary. More

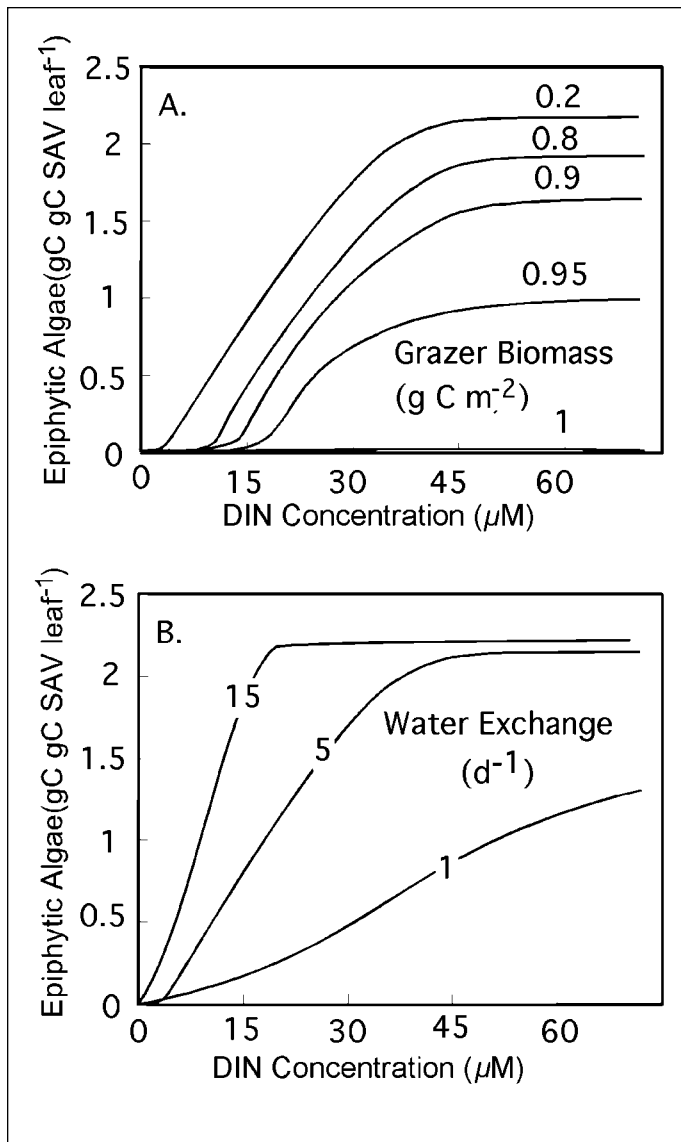


FIGURE V-4. Modeled DIN vs. Epiphytic Algal Biomass Responses Under Varying Grazer Biomass and Water Exchange Rates. Model calculated changes in the relationship of dissolved inorganic nitrogen (DIN) versus epiphytic algal biomass in response to variations in biomass of herbivorous epiphyte grazers (upper panel, A) and rates of water exchange with adjacent environments (lower panel, B).

recent mesocosm experiments, where epifaunal grazing rates were comparable to those at this eelgrass site in the 1980s, revealed that grazing effectively precluded epiphyte response to nutrient enrichment (Neckles *et al.* 1993), further demonstrating the ability of these model calculations to simulate the impact of grazing.

The present model also suggests strong effects of water exchange rate on epiphyte responses to nutrient

enrichment. The initial slope of the relationship between epiphyte biomass and dissolved inorganic nitrogen concentration declines with water exchange rate (Figure V-4, lower panel). While exchange rate has little influence on this relationship at high nutrient levels, the effect is substantial at concentrations below 30 μM. This relationship arises primarily because at low flushing rates, the relatively high initial (spring) biomass of SAV compared to epiphytes confers a competitive advantage to the plants. In addition, biomass-specific nutrient uptake rates tend to saturate at much higher concentrations for SAV leaf uptake compared to uptake by epiphytic algae (e.g., Day *et al.*, 1989). Thus, at low water exchange rates, the rapid uptake and storage of nutrients by macrophytes is sufficient to lower local (at the plant leaves) nutrient concentrations substantially, and consequently epiphyte growth. Under these conditions of relatively high SAV biomass and slow water exchange, nutrient concentrations tend to be much lower inside than outside the bed. At higher flushing rates, the ability of plants to regulate local nutrient concentrations is swamped by rapid water exchange, such that there is little gradient in nutrient concentrations from outside to inside the SAV bed. Limited available field data support the idea that nutrient concentration gradients can be maintained by plant uptake under conditions of high SAV biomass and rapid growth, coupled with relatively slow water exchange rates (e.g., Bulthuis *et al.* 1984; Moore 1996).

In summary, these sensitivity analyses (Figure V-4) illustrate that the present numerical model is relatively robust in its ability to simulate the effects of a wide range of environmental factors on nutrient-epiphyte relationships. It is also evident that refined application of this model analysis to specific field sites must be attentive to the nutrient-epiphyte relationship that may be affected by other factors such as grazing and flushing rates. There is a pressing need for field data on these factors to better calibrate these effects.

Epiphyte Biomass-Specific PAR Attenuation Coefficient

An extensive review of the published literature and unpublished reports was conducted to compile data on direct measurements of light attenuation attributable to epiphytic material on SAV leaves. A limited number of studies were identified with direct estimates of

epiphytic algal biomass-specific PAR attenuation coefficient, K_e ($\text{cm}^2 \mu\text{g chl a}^{-1}$). These studies were associated with various SAV species, including *Potamogeton perfoliatus* (Staver 1984; Twilley *et al.* 1985; Neundorfer and Kemp 1993), *P. pectinatus* (Vermaat and Hootsman 1994; van Dijk 1993), *R. maritima* (Twilley *et al.* 1985), *Z. marina* (Sand-Jensen and Borum 1983; Neundorfer and Kemp 1993; Neckles *et al.*, unpublished), *Heterozostera tasmanica* (Bulthuis and Woelkerling 1983a), *Posidonia australis* (Silberstein *et al.* 1986) and *Thalassia testudinum* (Kemp *et al.* 1989; Dixon and Leverone 1995).

Unfortunately, these studies used four different conventions for units of measure of epiphyte abundance: 1) μg chlorophyll *a* cm^{-2} (leaf); 2) mg dry weight cm^{-2} (leaf); 3) mg ash-free dry weight cm^{-2} (leaf); 4) g dry weight epiphyte per g dry weight (SAV leaves). Information on plant morphology was used to convert between leaf area and dry weight (e.g., Duarte 1991b), and observed carbon:chlorophyll *a* ratios (e.g., Staver 1984) were used to convert between μg chlorophyll *a* and mg ash-free dry weight for epiphytic material.

Although it was anticipated that values of attenuation coefficients would converge from the different sources, this was not the case. Estimates of K_e varied as much as two- to threefold, expressed either in terms of epiphytic algal chlorophyll *a* or total dry weight of epiphytic material.

One factor contributing to the widely varying estimates of K_e appears to be the composition of epiphytic material in terms of relative contributions of algal biomass, detritus and inorganic particles. Although the ratio of epiphytic algal biomass to detrital epiphytic matter may vary somewhat over the course of a growing season (Staver 1984), it was assumed that epiphytic algal biomass would serve as an index of contributions of both living and non-living organic matter to total K_e . However, because of the highly dynamic nature of resuspension and deposition (e.g., Ward *et al.* 1984), it was assumed that the contribution of inorganic solids to K_e could vary widely from site to site, depending on hydrographic and sedimentological conditions. Presumably, these inorganic materials are resuspended from bottom sediments, transported into SAV beds and deposited onto SAV leaves, where they may be incorporated into the epiphytic matrix (e.g., Brown and Austin 1973; Ward *et al.* 1984; Kendrick and Burt 1997).

In an experimental study, Staver (1984) considered how K_e varied with the ratio of epiphyte biomass (B_e , mg chlorophyll *a* cm^{-2} substrate) to total dry weight (B_{de} , g dw cm^{-2} substrate). Here, nearly 100 simultaneous observations of K_e , B_e , and B_{de} were separated into four groups based on this ratio ($B_e : B_{de}$). While Staver (1984) found great variance when all observations were pooled, highly significant correlations between B_e and PAR attenuation (the slope of which is K_e) were observed when the data were separated (according to the ratio of biomass to dry weight) into the four groups.

Recent field studies in two tidal tributaries of Chesapeake Bay—the Potomac River estuary (Carter *et al.* unpublished) and the Patuxent River estuary (Boynton *et al.* unpublished)—have provided an expanded data base. These field data were combined with the previously described mesocosm data (Staver 1984) to generate a significant inverse relationship between K_e and $B_e : B_{de}$ (Figure V-5),

$$K_e = 0.07 + 0.322 (B_e / B_{de})^{-0.88} \quad (\text{V-5}).$$

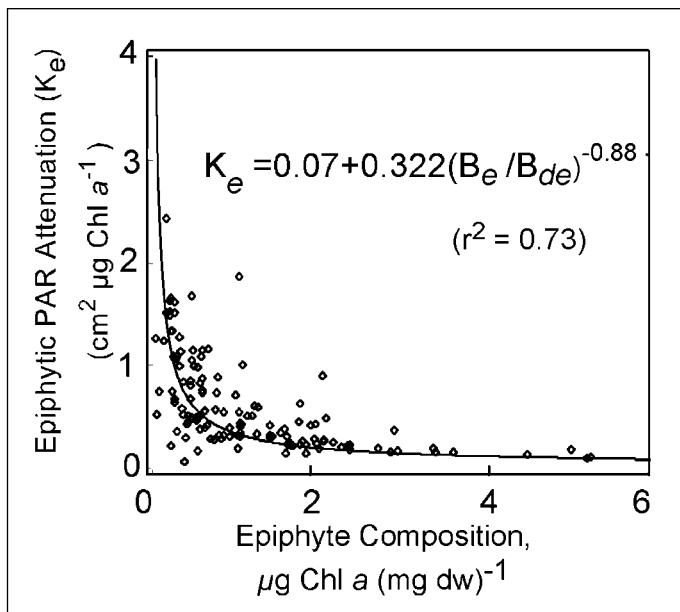


FIGURE V-5. Epiphytic Composition vs. Epiphytic PAR Attenuation. Relationship between the composition of epiphytic material (μg chlorophyll-*a* (mg dry weight) $^{-1}$) and the biomass-specific PAR (photosynthetically available radiation) attenuation coefficient ($\text{cm}^2 \mu\text{g chl a}^{-1}$) for epiphytes. Data are pooled from a pond mesocosm experiment (Staver 1984) and from field studies in Patuxent River estuary (Boynton *et al.*, unpublished) and Potomac River estuary (Carter *et al.*, unpublished). In all cases, epiphytic material was measured on artificial substrates.

Equation V-5 expresses a complex relationship in that its slope is essentially a ratio of ratios. However, it clearly indicates that the chlorophyll *a*-specific attenuation coefficient, K_e , increases (in a non-linear way) as the relative contribution of chlorophyll *a*-bearing material decreases. Since light attenuation is measured per unit algal chlorophyll *a*, the increase in K_e with decreasing values of $B_e: B_{de}$ ($\text{mg chl-}a \text{ g dry wt}^{-1}$) is due to the light-attenuating effects of non-algal materials. Thus, while K_e appears to vary widely among sites depending on physical conditions, it can be predicted with confidence from data on the ratio of epiphyte biomass to dry weight.

Similar hyperbolic relationships can be produced for each of the three separate field and mesocosm data sets. There was no statistically significant difference among any of these, nor between any particular site and the relationship illustrated in Figure V-5 for the pooled data. At low values of the epiphyte composition ratio, $B_e: B_{de} < 0.5 \text{ mg chl-}a \text{ g dry wt}^{-1}$, Equation V-5 is highly sensitive to small changes in that ratio. However, applying field data on $B_e: B_{de}$ to Equation V-5 illustrated that calculated values of K_e rarely exceeded $1.5 \text{ cm}^2 \mu\text{g chl } a^{-1}$.

The option of calculating the biomass-specific epiphyte attenuation coefficient (K_e) in terms of total dry weight of epiphytic material rather than algal chlorophyll *a* was also explored. The dry weight-specific coefficient yielded a significant, but slightly weaker, relationship compared to that for chlorophyll *a*-specific attenuation. Therefore, the chlorophyll *a*-specific attenuation coefficient was retained in the model because chlorophyll *a* is a better measure of algal biomass, which is what is being predicted in Equation V-2.

Estimating the Ratio of Epiphyte Biomass to Total Dry Weight

The next step of the analysis involves deriving a means for computing, from available water quality monitoring parameters, the ratio of epiphytic algal biomass to total dry weight of epiphytic materials. Toward this end, it was postulated that the contribution of inorganic particles to total dry weight of epiphytic material would increase with sediment resuspension and associated water-column concentrations of total suspended solids.

Previous studies in Chesapeake Bay have shown that rates of total suspended solids deposition in SAV beds

are proportional to SAV biomass and to total suspended solids load (Ward *et al.* 1984). It was further assumed that sedimenting particles would tend to be trapped in the organic matrix of epiphytic material in proportion to the biomass of algal epiphytes. In hydrodynamically active coastal environments, where SAV plants are in constant motion, very little of the sinking particles would adhere to leaves without the organic 'glue' associated with algal biomass. In fact, in a Swedish lake, the total dry weight of epiphytic materials (B_{de}) was inversely related to wave exposure (Strand and Weisner 1996).

While there is no published quantitative description of the relationship between total suspended solids, B_e and B_{de} , the assumed pattern is consistent with numerous observations with SAV in field and experimental conditions (e.g., Kemp *et al.* 1983; Twilley *et al.* 1985). An existing data set was used to develop an empirical relationship to calculate B_{de} [(g dw epiphytic material) (g dw SAV)⁻¹] from data on B_e [(mg epiphyte chl-*a*) (g dw SAV)⁻¹] and concentrations of total suspended solids (mg l^{-1}) in the adjacent water. This relationship would allow values for a biomass-specific epiphytic PAR attenuation coefficient (K_e) to be estimated from the previous step in the analysis.

Simultaneous measurements of total suspended solids, B_{de} and B_e were available from a set of studies in experimental ponds (Twilley *et al.* 1985; Staver 1984). A significant ($r^2 = 0.85$) relationship was observed using the data,

$$B_{de} = 0.107 \text{ TSS} + 0.832 B_e \quad (\text{V-6})$$

To test the robustness of Equation V-6, values for dry weight of epiphytic material (B_{de}) predicted from the equation were compared with measured values. A highly significant fit was observed between model and data ($r^2 = 0.85$, Figure V-6), although predicted values tend to underestimate observed values at intermediate values of B_{de} ($2\text{-}4 \text{ mg dw mg dw}^{-1}$). An alternative non-linear formulation with an interactive term ($\text{TSS} \cdot B_e$) on the right side of the equation provided a substantially poorer statistical fit.

Field data with simultaneous measurements of total suspended solids, B_{de} and B_e were much harder to identify. Attempts were made to use data collected in the Potomac and Patuxent River estuaries, where observations were made on one- to three-week intervals; however, these data yielded substantially weaker

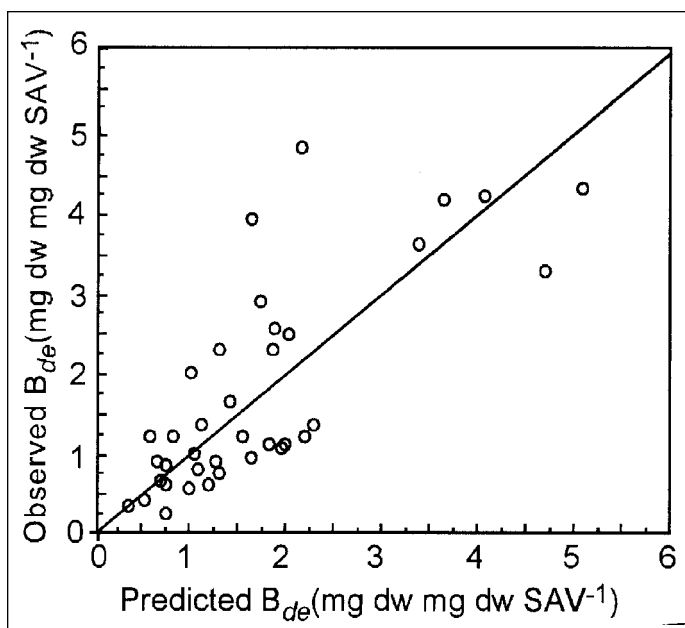


FIGURE V-6. Observed vs. Predicted Dry Weight Epiphytic Material. Comparison of observed values for total dry weight of epiphytic material (B_{de}) accumulating on artificial substrates and predicted values (from Equation V-6, $B_{de} = 0.107 \text{ TSS} + 0.832 B_e$), using inputs of data for total suspended solids, TSS (mg l^{-1}) and epiphytic algal biomass, B_e ($\text{mg chl-a g dw}^{-1}$), from experimental pond studies (Staver 1984, Twilley et al. 1985). Line indicates one-to-one correspondence between predicted and observed epiphyte mass.

relationships. In the experimental pond studies (Staver 1984), data were collected at much higher frequencies—two to three times per week. The increased sampling frequency is thought to have contributed to the relative success in developing this relationship (Equation V-6), compared to attempts to detect similar functions from field sampling, where total suspended solids (and, perhaps, B_{de}) tend to be highly variable over short time periods, such as days.

With the relationship indicated in Equation V-6, we have a complete, calibrated, statistically significant algorithm, which can be computed in a spreadsheet format or statistical package. This spreadsheet model solves the original Equation V-1 to estimate light levels (as percent of surface PAR) at SAV leaf surfaces (I_{zs}) for any site at a particular depth that has data for dissolved inorganic nitrogen, dissolved inorganic phosphorus, K_d , and total suspended solids. The model defines percent light at the SAV leaf surface (PLL) and percent light in the water directly overlying leaves

(PLW). The computations in this model can be summarized into seven steps, which require different data inputs and user decisions (Table V-1). A computer spreadsheet program for performing these calculations has been developed and is available for access and downloading in conjunction with this report through the Chesapeake Bay Program web site at www.chesapeakebay.net/tools.

SENSITIVITY ANALYSIS OF THE MODEL

The model was used to calculate PAR levels at SAV leaves for different values of dissolved inorganic nitrogen, dissolved inorganic phosphorus, K_d and total suspended solids to consider the relative contributions of each to light attenuation at 1-meter depth. The 1992 SAV habitat requirements were selected as a reference point (Batiuk *et al.* 1992; Dennison *et al.* 1993) for this analysis; plankton chlorophyll *a* was omitted from this analysis because its effect on light attenuation is accounted for with K_d . The relevant habitat requirement values (expressed in micromolar or M units for dissolved inorganic nitrogen and dissolved inorganic phosphorus) are: DIN = 10 M (mesohaline and polyhaline); DIP = 0.67 M (tidal fresh, oligohaline and polyhaline) and DIP = 0.33 M (mesohaline); K_d = 1.5 m^{-1} (mesohaline and polyhaline) and K_d = 2 m^{-1} (tidal fresh and oligohaline); and TSS = 15 mg l^{-1} . Each parameter value was varied by factors of 0.5 and 2 to calculate the percent of incident light levels in the water directly overlying SAV leaves (PLW) and the percent of incident light available at the leaf surface (PLL). This sensitivity analysis was performed for each of the Bay salinity regimes (tidal fresh/oligohaline, mesohaline and polyhaline).

The percent of surface light level available in the water overlying the SAV leaves (PLW) is regulated by K_d , varying from 22 percent in mesohaline and polyhaline regions to 13 percent in the tidal fresh and oligohaline regions. The percent surface light available at the leaf surface (PLL) ranges from 9 percent in tidal fresh and oligohaline regions to 17 percent in mesohaline and 14 percent in polyhaline regions. These differences in PLL and PLW among salinity regimes derive from differences in the habitat requirements listed above. Results of the sensitivity analysis are presented in Figure V-7, with horizontal dashed lines indicating values of PLL and PLW calculated for these habitat requirement values (Batiuk *et al.* 1992).

In terms of total light reduction, this analysis revealed that PAR levels were most sensitive, by far, to changes in K_d . This is not surprising, given the fact that K_d is an exponential coefficient. Calculated values for PLL were also responsive to variations in total suspended solids, dissolved inorganic nitrogen and dissolved inorganic phosphorus (Figure V-7).

The asymmetry of these sensitivities results from the highly nonlinear nature of the spreadsheet model. Sensitivities to dissolved inorganic phosphorus and dissolved inorganic nitrogen were the same for the polyhaline and oligohaline areas, but PLL did not respond to changes in dissolved inorganic nitrogen in the mesohaline because DIN:DIP ratio was greater than 16 for the 1992 SAV habitat requirements in that salinity regime (Batiuk *et al.* 1992). For both the mesohaline and polyhaline regions, changes in nutrient concentration had somewhat greater effect ($\pm 1-4$ percent) on PLL than did changes in total suspended solids ($\pm 1-2$ percent). Note, however, that this analysis only considers effects of total suspended solids on epiphyte attenuation of light. The direct impact of total suspended solids on K_d (which is great; see Chapter IV) was not taken into account. In the tidal fresh/oligohaline region, calculated PLL was less sensitive to changes in total suspended solids and nutrients but more responsive to changes in K_d than in other salinity regimes.

Another way to consider the relative contributions of total suspended solids and dissolved inorganic nutrients to light attenuation by epiphytic material is illustrated by plotting isolumes (lines of constant light) calculated by the spreadsheet model under conditions where total suspended solids and dissolved inorganic nitrogen concentrations are varied simultaneously (Figure V-8). In general, at $Z = 1$ meter, changes in dissolved inorganic nitrogen have a substantial effect on the light climate (crossing isolumes) at all but the lowest total suspended solids concentrations, while decreases in total suspended solids have a significant impact only at very high dissolved inorganic nitrogen concentrations and very low PLL values. For example, at a total suspended solids concentration of 15 mg l^{-1} , a reduction in dissolved inorganic nitrogen from 15 to 5 M improves light conditions from 12 to 17 percent surface irradiance; however, at a dissolved inorganic nitrogen concentration of 20 M, a reduction in total suspended solids from 15 to 5 mg l^{-1} improves light at the SAV leaf surface only from 11 percent to 12 percent. It is obvious that such changes in total suspended

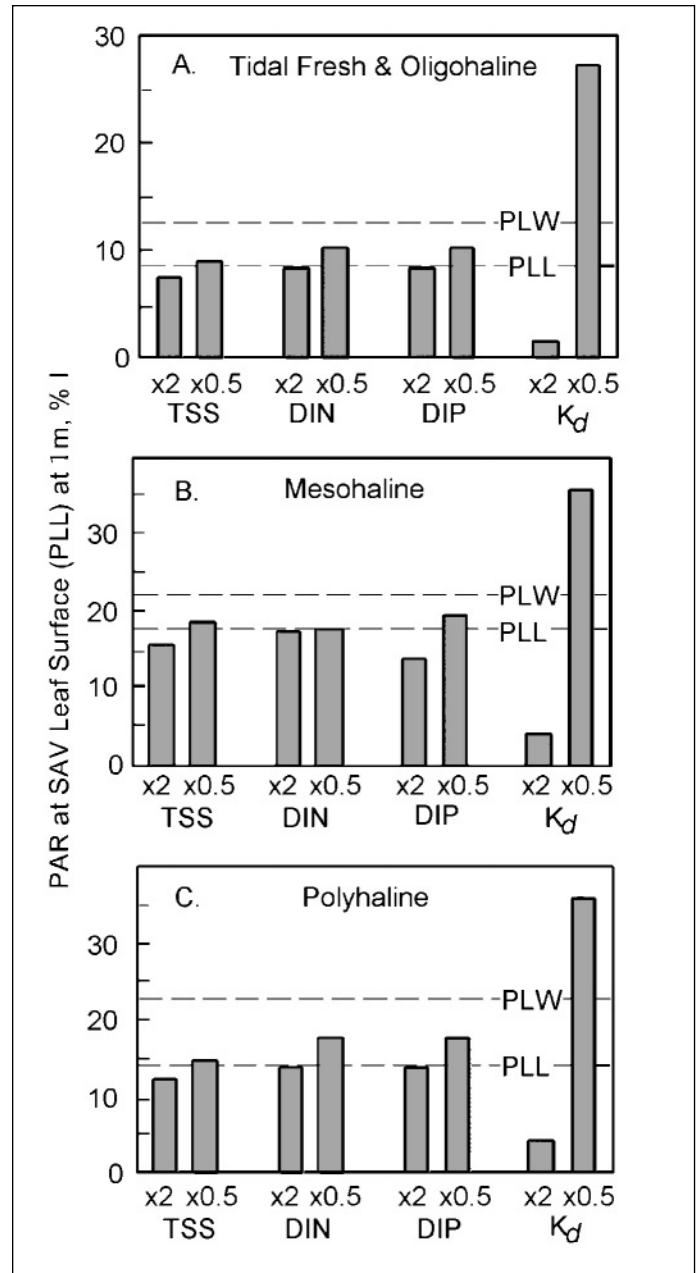


FIGURE V-7. Percent Light at the Leaf Sensitivity Analysis. Sensitivity analysis for values of percent of incident light at SAV leaf surface (PLL) calculated from the spreadsheet model (Table V-1) in response to doubling (x 2) and halving (x 0.5) concentrations of total suspended solids (TSS), dissolved inorganic nitrogen (DIN), and dissolved inorganic phosphorus (DIP), and values for light attenuation coefficient (K_d). Calculated values based on previously published SAV habitat requirements (Batiuk *et al.* 1992) are used as references, with values of PLL and percent incident light in water overlying SAV (PLW) shown as horizontal dashed lines for A) tidal fresh and oligohaline, B) mesohaline and C) polyhaline regions of Chesapeake Bay.

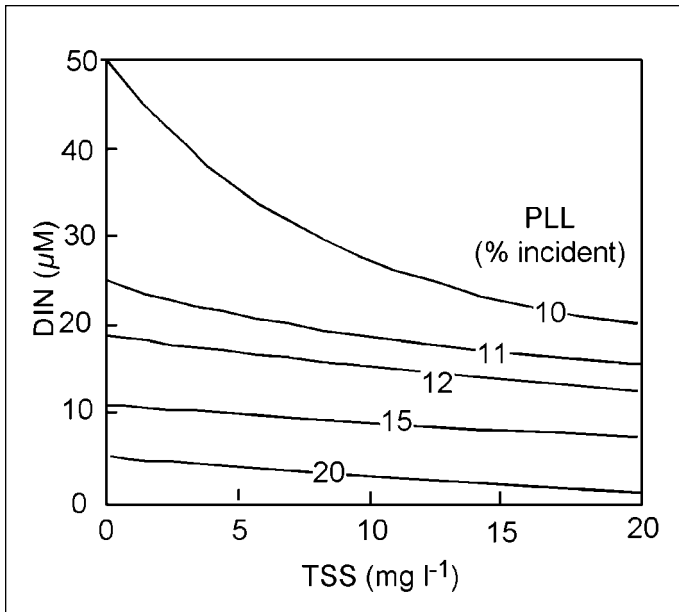


FIGURE V-8. Effects of DIN and TSS on Percent Light at the Leaf. Interacting effects of dissolved inorganic nitrogen (DIN) and total suspended solids (TSS) concentrations on percent incident light at SAV leaf surface (PLL). Family of isolumes (lines of constant light) for PLL of 10-20 percent calculated from the model described in this report for a restoration depth of 1 m (see Table V-1).

solids would also impart substantial effects on K_d ; however, the purpose of this analysis was to isolate the effects on epiphytic attenuation only.

The relative contribution of epiphytic material to total PAR attenuation varies with depth and water column turbidity. In the 1992 SAV habitat requirements for the mesohaline and polyhaline regions of Chesapeake Bay (DIN = 10 M, $K_d = 1.5 \text{ m}^{-1}$; Batiuk *et al.* 1992), PAR attenuation by epiphytic material is approximately 25 percent of the total at 0.5 m and 10 percent of the total at 1-meter depth (Figure V-9, upper panel). This contribution decreases substantially at lower ambient nutrient concentrations. At lower values of K_d (1.0 m^{-1}) and 0.5 m water depth, epiphyte contribution to total PAR attenuation increases to almost 40 percent at DIN = 10 M and 20 percent at DIN = 2 M (Figure V-9, lower panel). These sensitivity calculations emphasize the fact that at $Z > 0.5 \text{ m}$, epiphytic material contributes substantially less to the total shading of SAV than do materials suspended and dissolved in the overlying water. However, in many cases the additional reductions in ambient light associated with epiphytic accumulations is sufficient to

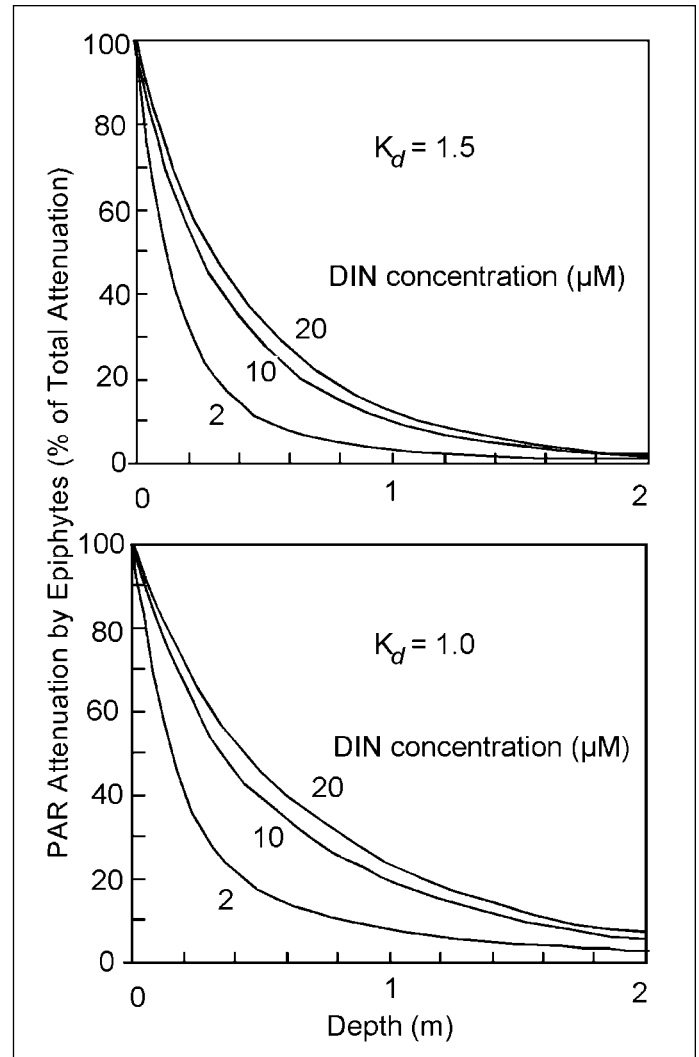


FIGURE V-9. Effects of Water Depth, DIN, and K_d on Epiphyte Contribution to PAR Attenuation. Effects of water depth, dissolved inorganic nitrogen concentration (DIN) and light attenuation (K_d) on relative contributions of epiphytes to total PAR attenuation to SAV leaves. Lines calculated from the model developed in this report (see Table V-1).

reduce SAV growth below the minimum levels needed for plants to survive (e.g., Kemp *et al.* 1983; Twilley *et al.* 1985).

This spreadsheet model calculation of the percent light reaching SAV leaf surface (PLL) was applied to sites in the mainstem and tidal tributaries of Chesapeake Bay for field verification and to explore regional patterns in the estuary. Growing season median values for dissolved inorganic nitrogen, dissolved inorganic phosphorus, total suspended solids and K_d measured at Chesapeake Bay water quality monitoring stations

within 2 to 5 km of existing and potential nearshore SAV habitats were compiled from the period 1985-1996 for stations in the mainstem Bay and from all monitored tidal tributary and embayment estuaries. These data are updated versions of those used for field verification analyses presented previously (Batiuk *et al.* 1992).

Results of model computations are summarized (Figure V-10) in bar graphs as mean light levels calculated at the SAV leaf surface (PLL, including epiphyte attenuation) for all sites in the estuary. Values for PLL were calculated at water depths of 1 meter and 0.5 meters (upper panel only). Results are summarized for five categories of SAV abundance: 1) “always none”; 2) “usually none”; 3) “sometimes some”; 4) “always some”; and 5) “always abundant.” These categories are defined precisely in Chapter VII. Calculations are also parsed into three salinity regions of the Bay: 1) tidal fresh/oligohaline; 2) mesohaline and 3) polyhaline. No sites qualified for the “always none” category in the polyhaline region, where SAV is generally most abundant. Calculations are provided for water depth of 0.5 m in the tidal fresh/oligohaline region because of the prevalence of relatively shallow, broad and protected sites in the upper Bay.

In general, there is a consistent pattern of increasing light (PLL) with increasing probability of SAV occurrence (Figure V-10). The one exception is for the “always abundant” category in the oligohaline region (Figure V-10, upper panel). It is assumed that minimum light required for SAV survival should fall between the mean light levels associated with the “sometimes some” and “always some” categories of SAV abundance.

For the mesohaline and polyhaline regions, the mean calculated PLL values range from 20-25 percent surface irradiance for sites having SAV occurrence characterized between “sometimes” and “always.” This analysis suggests that the target value of 15 percent surface irradiance for SAV minimum light requirement derived from analysis of the literature serves as a conservative but robust index of SAV habitat suitability for these regions of Chesapeake Bay.

Light requirements in the tidal fresh and oligohaline regions are more difficult to discern; however, for the same SAV occurrence categories, calculated values for PLL range from 4 to 7 percent at 1-meter water depth

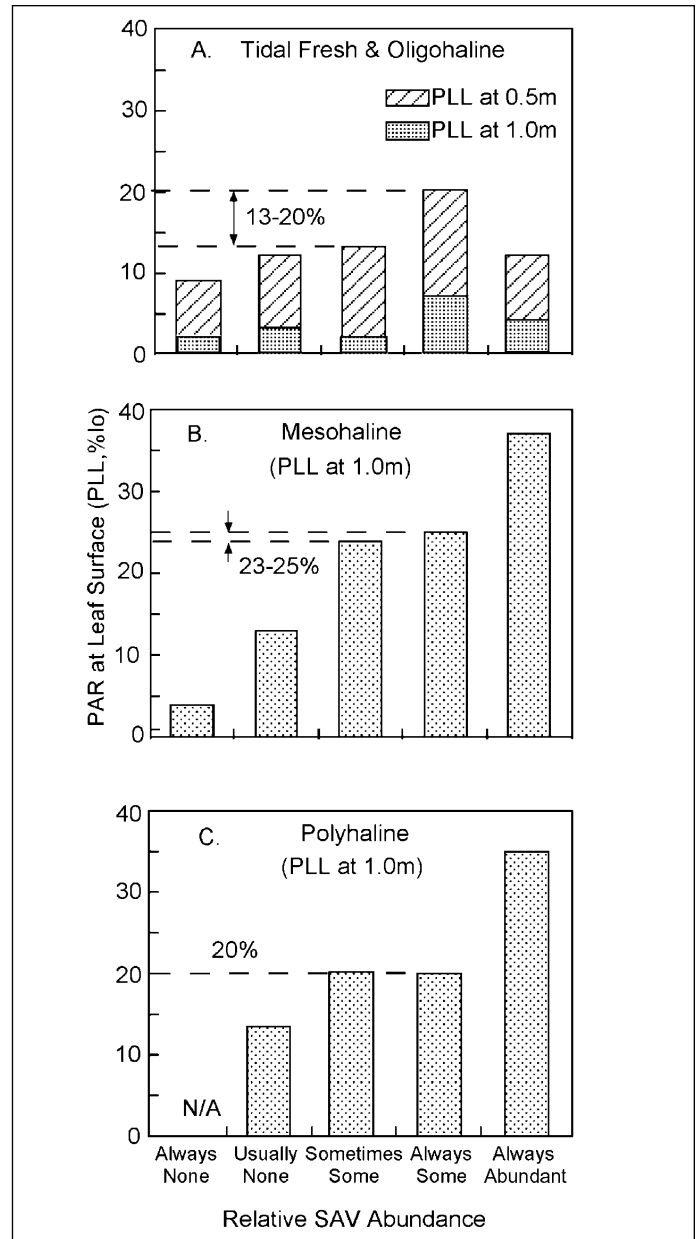


FIGURE V-10. Calculated Percent Light at the Leaf Values by Relative SAV Abundance by Salinity Regime. Calculated mean values for percent incident light at SAV leaf surface (PLL) for all water quality monitoring stations in the mainstem, tidal tributaries and embayments of Chesapeake Bay during 1985-1996 grouped into five categories of relative SAV abundance or occurrence and three salinity regimes. Values of PLL were calculated for water depth of 0.5 and/or 1.0 m using the model described in this report (see Table V-1) with input data (total suspended solids, dissolved inorganic nitrogen, dissolved inorganic phosphorus, K_d) for SAV growing season (April-October for tidal fresh, oligohaline, and mesohaline and March-May and September-November for polyhaline) of each year from the Chesapeake Bay Program water quality monitoring program. N/A indicates that there were no sites in the polyhaline region without occasional SAV presence.

and from 13-20 percent at 0.5 meters. Since the mean water depths for sites with SAV growing in these Bay regions tend to fall between 0.5 meters and 1 meter, the target value (derived from the literature review) of 9 percent surface irradiance is also very consistent with mean light conditions calculated to support minimal SAV growth. The tidal fresh and oligohaline regions of the Bay are generally the most turbid (e.g., Schubel and Biggs 1969; Keefe *et al.* 1976; Smith and Kemp 1995). The reduced consistency between light variability and SAV occurrence in this turbid region of the Bay (Figure V-10, upper panel) is consistent with observations in turbid lakes (Middleboe and Markager 1997).

Regional variations in the relative contributions of water-column and epiphyte attenuation for defining potential SAV habitats can be seen by comparing calculated values for PLL and PLW at sites pooled into different salinity regimes (Figures V-11 and V-12). In general, values of both PLL and PLW tend to increase as one moves from lower to higher salinity regions (Figure V-11; upper, middle and lower panels, respectively). Although Figure V-11 presents data for Virginia portions of the Bay only, similar patterns are evident for the Maryland waters of the Bay.

Sites in the tidal fresh and oligohaline regions appear to have greater potential effects of light attenuation by epiphytic material, as indicated by the data points falling well below the 1:1 line (Figure V-11). In these low salinity regions, almost half of the total attenuation is attributable to epiphytic materials. This is because of the higher nutrient concentrations and total suspended solids levels in lower salinity areas.

There is little difference in the relative contribution of epiphytes in the mesohaline and polyhaline regions, where the epiphyte effect $[(PLW-PLL)/PLL]$ tends to range from 25-40 percent and increases as PLL decreases (Figure V-12). While there is a clear pattern of changing contribution of epiphyte attenuation along the estuarine salinity gradient, there is less of a marked difference in the PLL vs. PLW relationship for upper Bay (Maryland waters) compared to lower Bay (Virginia waters) areas (Figure V-12). In both cases, mean epiphyte contributions $[(PLW-PLL)/PLL]$ range from about 20-50 percent, and they are greatest at more turbid sites. Thus, it is clear that at 1-meter water depth, potential accumulation of epiphytic material represents a significant fraction of total potential light attenuation at sites throughout Chesapeake Bay.

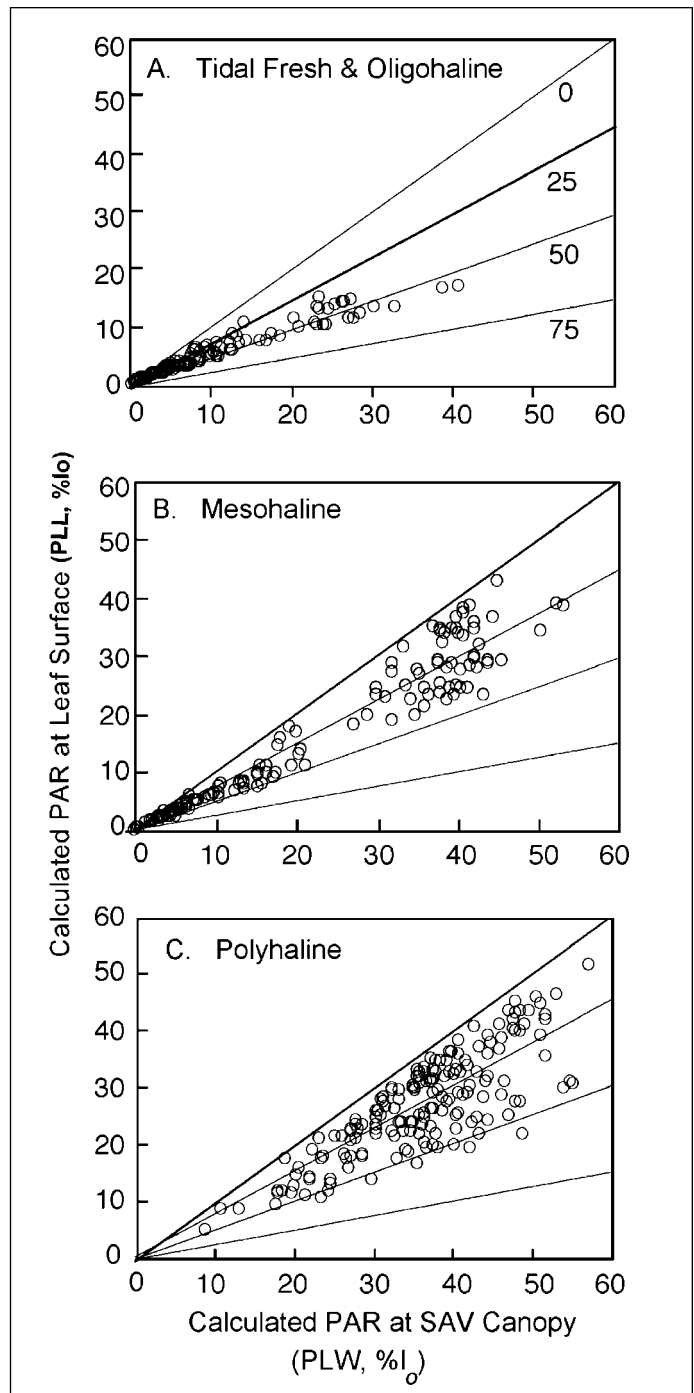


FIGURE V-11. Percent Light at Leaf vs. Percent Light Through the Water Column by Salinity Regime.

Comparing values for percent surface light at SAV leaf surface (PLL) and percent surface light in water just above the SAV leaf (PLW) calculated for restoration depth $Z = 1$ m from the model described in this report (Table V-1) for water quality monitoring stations in Virginia portion of Chesapeake Bay for 1985-1996 in three salinity regimes. Lines indicate position of points where epiphyte attenuation reduced ambient light levels at the leaf surface by 0, 25, 50 and 75 percent.

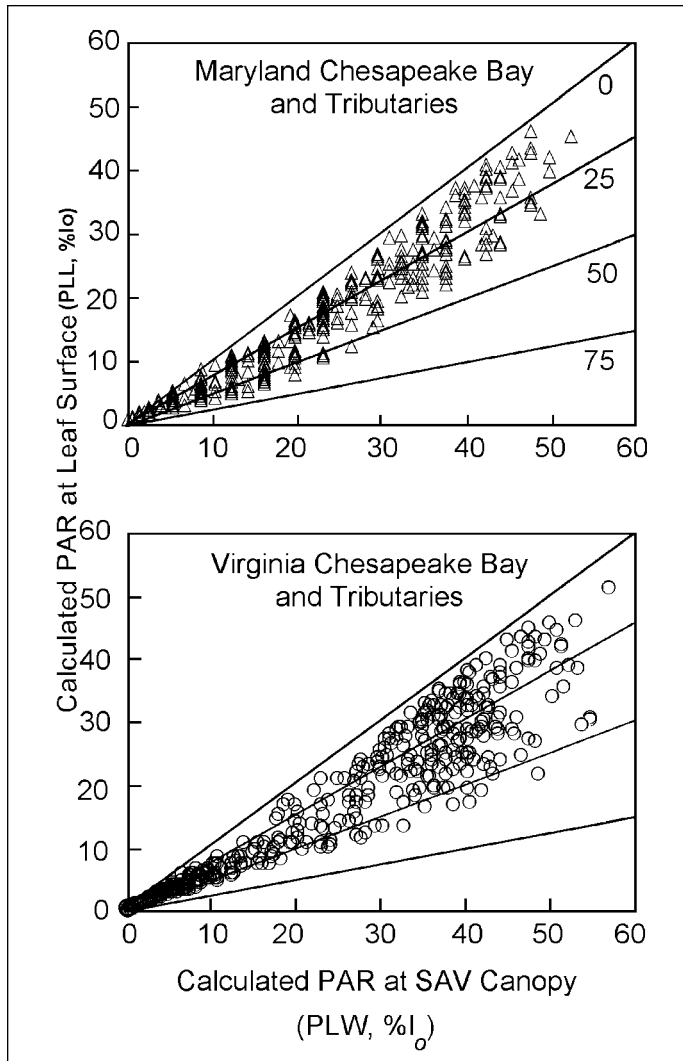


FIGURE V-12. Percent Light at the Leaf vs. Percent Light Through the Water Column, by State.

Comparing values for percent surface light (PAR) at SAV leaf surface (PLL) and percent surface light in water just above SAV leaf (PLW) for all monitored sites in the main-stem, tidal tributaries and embayments of Chesapeake Bay during 1985-1996 grouped into upper (Maryland) and lower (Virginia) estuary regions. Values of PLL and PLW were calculated for water depth of 1 m using the model described in this report (Table V-1) with input monitoring data (total suspended solids, dissolved inorganic nitrogen, dissolved inorganic phosphorus, K_d) for the SAV growing season of each year. Lines indicate position of points where epiphyte attenuation reduced ambient light levels at the leaf surface by 0, 25, 50 and 75 percent.

CONCLUSIONS

The model developed in this chapter to calculate contributions of water-column and epiphytic materials to light attenuation under different water quality conditions works well for sites throughout Chesapeake Bay, including its tidal tributaries across all salinity regimes. Values for PLL calculated from water quality data vary widely among sites throughout the Bay. The model relies on a combination of empirical relationships derived from field studies and experimental systems and numerical computations from a well-calibrated ecosystem process model. Much of the information on which the model is based comes from the measurements and analyses done in the mesohaline and polyhaline regions of Chesapeake Bay; particularly studies of two SAV species—*Potamogeton perfoliatus* and *Z. marina* (e.g., Staver 1984; Twilley *et al.* 1985; Goldsborough and Kemp 1988; Neckles 1990; Moore 1996; Sturgis and Murray 1997). This is due to limited comparable data from lower salinity tidal habitats.

The model is easily used and is amenable to simple spreadsheet computations on diverse platforms. It has substantial utility as a screening tool to assess trends in SAV habitat conditions at individual sites, based on changes in water quality variables. In ecosystems such as Chesapeake Bay, where a broad monitoring program exists to support efforts to improve water quality for restoring SAV to degraded habitats, this model provides an additional important tool to guide management efforts.