

Habitat Requirements for Submerged Aquatic Vegetation in Chesapeake Bay: Water Quality, Light Regime, and Physical-Chemical Factors

W. MICHAEL KEMP^{1,*}, RICHARD BATTIUK², RICHARD BARTLESON¹, PETER BERGSTROM³, VIRGINIA CARTER⁴, CHARLES L. GALLEGOS⁵, WILLIAM HUNLEY⁶, LEE KARRH⁷, EVAMARIA W. KOCH¹, JURATE M. LANDWEHR⁴, KENNETH A. MOORE⁸, LAURA MURRAY¹, MICHAEL NAYLOR⁷, NANCY B. RYBICKI⁴, J. COURT STEVENSON¹, and DAVID J. WILCOX⁸

¹ *University of Maryland Center for Environmental Science (CES), Horn Point Laboratory, Cambridge, Maryland 21613*

² *U.S. Environmental Protection Agency, Chesapeake Bay Program Office, Annapolis, Maryland 21403*

³ *U.S. Fish and Wildlife Service, Annapolis, Maryland 21401*

⁴ *U.S. Geological Survey, Reston, Virginia 22092*

⁵ *Smithsonian Environmental Research Center, Edgewater, Maryland 21037*

⁶ *Hampton Roads Sanitation District, Virginia Beach, Virginia 23471*

⁷ *Maryland Department of Natural Resources, Annapolis, Maryland 21401*

⁸ *Virginia Institute of Marine Sciences, Gloucester Point, Virginia 23062*

ABSTRACT: We developed an algorithm for calculating habitat suitability for seagrasses and related submerged aquatic vegetation (SAV) at coastal sites where monitoring data are available for five water quality variables that govern light availability at the leaf surface. We developed independent estimates of the minimum light required for SAV survival both as a percentage of surface light passing through the water column to the depth of SAV growth (PLW_{min}) and as a percentage of light reaching leaves through the epiphyte layer (PLL_{min}). Values were computed by applying, as inputs to this algorithm, statistically derived values for water quality variables that correspond to thresholds for SAV presence in Chesapeake Bay. These estimates of PLW_{min} and PLL_{min} compared well with the values established from a literature review. Calculations account for tidal range, and total light attenuation is partitioned into water column and epiphyte contributions. Water column attenuation is further partitioned into effects of chlorophyll *a* (chl *a*), total suspended solids (TSS) and other substances. We used this algorithm to predict potential SAV presence throughout the Bay where calculated light available at plant leaves exceeded PLL_{min} . Predictions closely matched results of aerial photographic monitoring surveys of SAV distribution. Correspondence between predictions and observations was particularly strong in the mesohaline and polyhaline regions, which contain 75–80% of all potential SAV sites in this estuary. The method also allows for independent assessment of effects of physical and chemical factors other than light in limiting SAV growth and survival. Although this algorithm was developed with data from Chesapeake Bay, its general structure allows it to be calibrated and used as a quantitative tool for applying water quality data to define suitability of specific sites as habitats for SAV survival in diverse coastal environments worldwide.

Introduction

During the last several decades, the chronic loss of seagrasses and related submerged aquatic vegetation (SAV) has been a problem occurring with increasing frequency in shallow coastal ecosystems worldwide (Orth and Moore 1983; Walker and McComb 1992; Short and Wyllie-Echeverria 1996). Losses of SAV beds are of particular concern because these plants create rich habitat and food for animals, supporting growth of diverse waterfowl,

fish, and invertebrate populations (Lubbers et al. 1990; Heck et al. 1995). Seagrass and SAV communities also significantly modulate key biogeochemical (Caffrey and Kemp 1990), physical (Rybicki et al. 1997; Koch and Gust 1999), and sedimentological (Fonseca et al. 1982; Ward et al. 1984) processes. Although many factors such as climatic events (Pulich and White 1991), physical disturbance (Quammen and Onuf 1993), and herbicide toxicity (Kemp et al. 1985) may have contributed to these SAV declines, the most prevalent causes appear related to reductions in light availability associated with increased inputs of nutrients

* Corresponding author; tele: 410/221-8436; fax: 410/221-8490; e-mail: kemp@hpl.umces.edu

and suspended sediments (Kemp et al. 1983; Cambridge and McComb 1984; Borum 1985; McGlathery 1995; Tomasko et al. 1996).

Health and survival of these plant communities in coastal waters depend on maintaining suitable environmental conditions that effectively define the SAV habitat. Previous studies have attempted to characterize these conditions quantitatively using simple statistical models that define, for selected water quality variables, threshold values beyond which SAV are absent (Batiuk et al. 1992; Dennison et al. 1993; Stevenson et al. 1993). This analysis used observations from sites throughout Chesapeake Bay to define critical SAV habitat requirements in terms of five water quality variables: dissolved inorganic nitrogen (DIN, μM) and phosphorus (DIP, μM), water column light attenuation coefficient (K_d , m^{-1}), planktonic chlorophyll *a* (chl *a*, $\mu\text{g l}^{-1}$), and total suspended solids (TSS, mg l^{-1}). Although these water quality variables relate to many aspects of SAV physiology and ecology, their influence on the plant's light climate was recognized to be of primary importance (Dennison et al. 1993). Although in recent years these SAV habitat requirements have been widely employed as a diagnostic tool to assess suitability of sites for plant growth or restoration, their use has met with mixed success in Chesapeake Bay (Moore et al. 1996; Landwehr et al. 1999) and many other coastal environments (Dunton 1996; Koch and Beer 1996; Tomasko et al. 1996; Valdes-Murtha 1997; Glazer 1999).

Alternative approaches have also been used for estimating habitat suitability for growth and survival of seagrasses and other SAV. For example, simulation models have been developed to compute plant growth based on ambient water quality conditions in many coastal habitats (Madden and Kemp 1996; Fong et al. 1997; Buzzelli et al. 1998; Cerco and Moore 2001; Burd and Dunton 2001). In most cases, these complex models are designed for estimating general trends in seagrass growth under scenarios of changing environmental conditions, rather than for directly assessing SAV habitat suitability at specific sites based on water quality measurements. Simple empirical correlations (Nielsen et al. 2002) have been used to predict depth of maximum SAV biomass or colonization from routine water clarity measurements (Rørslett 1987; Zimmerman et al. 1991; de Jonge and de Jong 1992). Although the widespread availability of water clarity data (e.g., Secchi disk depth) makes this a potentially useful approach, it does not account for light attenuation by epiphytes on SAV leaves, often a dominant factor in regulating plant growth (Twilley et al. 1985; Sand-Jensen 1990). One approach to account for epiphytic shading is

to monitor it directly in the field and to compute the combined effects of water clarity and epiphytes on total attenuation of light for SAV (Vermaat and de Bruyne 1993). This approach is limited by the fact that data on epiphyte shading are seldom collected as part of routine water quality monitoring programs (Stankelis et al. 2003).

The purpose of this paper is to use routine water quality data to compute potential availability of light for supporting SAV growth. This method integrates a combination of statistical relationships and numerical calculations to develop an algorithm for partitioning total attenuation of light (to SAV leaves) into water column and epiphyte contributions. The approach further partitions water column light attenuation into contributions from phytoplankton biomass, inorganic suspended solids, and other substances. Application of this approach required that we establish target values of minimum light requirements for SAV survival, which we derived through a literature review and by applying this algorithm to calculate available light under the empirically-derived minimum water quality conditions corresponding to SAV presence (Dennison et al. 1993). We address several questions including the following. How do the relative contributions to total light attenuation from epiphytes and water column vary with water depth and estuarine region? How well do predictions of SAV habitat suitability compare with actual SAV distributions throughout the estuary? Is this approach generally applicable to coastal systems beyond Chesapeake Bay?

Quantitative Approaches for Defining SAV Light Habitat

WATER QUALITY AND SAV HABITAT

The principal relationships between water quality conditions and the light regime required for growth of submerged plants are illustrated in a conceptual diagram (Fig. 1). Incident light, which is partially reflected at the water surface, is attenuated through the water column overlying submerged plants by particulate material (phytoplankton chl *a* and TSS), by colored dissolved organic substances, and by water itself. Light is also attenuated by epiphytic material (algae, bacteria, invertebrates, detritus, and sediments) accumulating on SAV leaves. This epiphytic light attenuation can be characterized by the exponential coefficient, K_e , which increases linearly with mass of epiphytic material (Twilley et al. 1985). The slope of this relationship depends on the composition (e.g., chl *a*-dry weight) of the epiphytic material (Losee and Wetzel 1983; Staver 1984). Dissolved inorganic nutrients (DIN and DIP) in the water column stim-

Conceptual Model of Light/Nutrient Effects on SAV Habitat

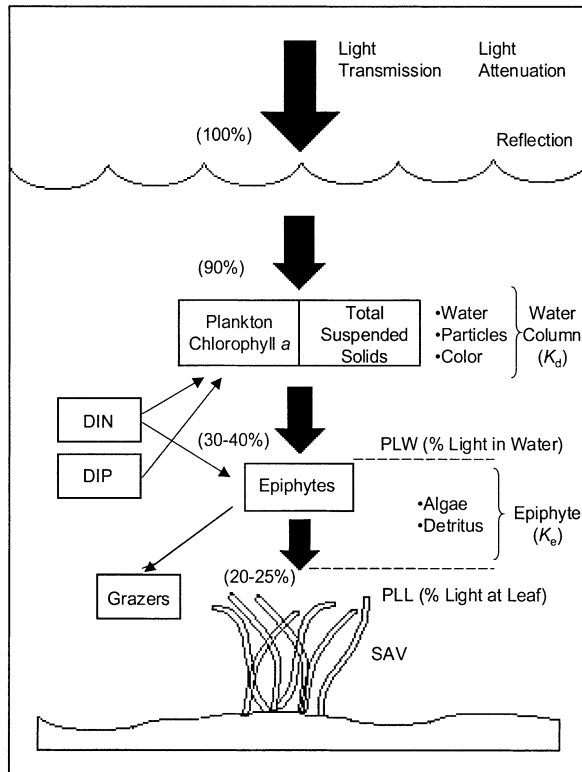


Fig. 1. Conceptual representation illustrating how availability of light to support photosynthesis of seagrasses and other SAV is influenced by dissolved and particulate material in the water column and by epiphytic material accumulating on plant leaves. Dissolved inorganic nitrogen and phosphorus (DIN and DIP, respectively) stimulate growth of planktonic and epiphytic algae, which can be controlled by herbivorous grazers (modified from Batiuk et al. 1992; Dennison et al. 1993).

ulate growth of both phytoplanktonic and epiphytic algae, and suspended solids can settle onto SAV leaves to become part of the epiphytic matrix (Vermaat and de Bruyne 1993; Guarraci 1999). The percent surface light reaching SAV leaves depends on water depth and on key water quality variables (DIN, DIP, chl *a*, TSS, K_d) defining SAV habitat requirements (Batiuk et al. 1992; Dennison et al. 1993). Because epiphytic algae also require light to grow, water depth and K_d constrain algal accumulation on SAV leaves, and light attenuation by epiphytic material (K_e) depends on the mass of both algae and TSS settling on leaves.

An extensive monitoring program in Chesapeake Bay has provided the data needed to relate distributions of water quality and SAV (Chesapeake Bay Program unpublished data). Water quality conditions have been measured at 2–4 wk intervals since 1985 at ~50 stations in the mainstem of

Chesapeake Bay and at another 90 stations in Bay tributaries. Aerial photographs (Moore et al. 2000; Wilcox et al. 2000), taken and analyzed annually since 1989 to monitor the spatial distribution and relative abundance of SAV throughout the estuary, are also used in our analysis.

WATER COLUMN DEPTH

Our approach to defining SAV habitat requirements explicitly considers water column depth. For any site, the minimum water quality conditions needed for SAV survival will tend to vary with water column depth. Chesapeake Bay is characterized by broad shoals flanking a narrow channel such that large increases in benthic habitat suitable for SAV growth will result from relatively small changes in light penetration into the water column (Kemp et al. 1999). As a consequence of the estuary's bottom morphology, the doubling of SAV depth penetration from 1–2 m results in a 50% increase in potential bottom area of SAV coverage in Chesapeake Bay, from 165,380–250,400 ha (Table 1). As of the 1998 aerial survey, however, actual SAV coverage represented only 16% and 10% of the 1 m and 2 m restoration targets, respectively.

In this paper we have used mean tidal level (MTL) as the reference point from which mean water column depth is measured. MTL is the mean depth over all tidal cycles during the year. Although SAV restoration depths were previously (Batiuk et al. 1992) referenced to mean low water (MLW), these have been adjusted to MTL by adding half the diurnal tidal range to restoration depth chosen. Tidal amplitudes in Chesapeake Bay vary from approximately 120 cm in the upper York River to 39 cm just south of the Rappahannock River. Tidal ranges on the Bay's eastern shoals tend to be higher by 10–15 cm than those on the western side, and ranges are generally 40–50 cm higher in tidal fresh regions of tributaries than at their mouths (Hicks 1964). SAV are generally excluded from intertidal areas because of physical stress (waves, desiccation, freezing), and the shallow depth-limit for SAV distribution therefore tends to be deeper in areas with higher tidal range (Koch and Beer 1996). The deeper depth limit is generally reduced at sites with larger tidal range because of increased light attenuation through the longer average water column (Koch 2001), resulting in an inverse relationship between tidal range and the range of SAV depth distribution (Fig. 2).

DEFINING LIGHT ATTENUATION PARAMETERS

We define two parameters that measure different components in transmission of incident light to SAV (Fig. 3). The first of these parameters is a measure of the light transmitted through the water

TABLE 1. Restoration target areas for coverage of submerged aquatic vegetation (SAV) in major salinity regions of Chesapeake Bay, and comparisons to 1998 aerial surveys of SAV distribution.

Potential SAV Coverage		Restoration Targets (hectares)		
Region	Area ^a	Tier I ^b	Tier II ^c	Tier III ^d
Tidal Fresh and Oligohaline Region	Area (hectares)	9,550	36,740	61,010
	% 1998 survey	75	20	12
Mesohaline Region	Area (hectares)	24,860	101,880	155,930
	% 1998 survey	41	31	7
Polyhaline Region	Area (hectares)	11,620	26,760	33,460
	% 1998 survey	87	31	30
Total Bay	Area (hectares)	46,030	165,380	250,400
	% 1998 survey	56	16	10

^a Indicates areas are derived from Geographic Information System analysis of bathymetric maps of the Bay, and these are compared to actual SAV coverage calculated from aerial surveys in 1998.

^b Indicates restoration of SAV to areas currently or previously inhabited by SAV as mapped through regional and baywide aerial surveys, 1971–1998.

^c Indicates restoration of SAV to all shallow water areas delineated as existing or potential SAV habitat down to the 1 m depth contour, excluding areas identified as unlikely to support SAV based on historical observations, recent surveys and physical exposure regimes.

^d Indicates restoration of SAV to all shallow water areas delineated as existing or potential SAV habitat down to the 2 m depth contour, excluding areas identified under the Tier II target as unlikely to support SAV and several additional areas between 1 and 2 m depths.

column to the depth of SAV growth, referred to as Percent Light through the Water (PLW). The second light parameter, which considers the additional light attenuation by epiphytic materials, is referred to as Percent Light at the Leaf (PLL). PLW is calculated as an exponential relationship to depth of SAV growth (Z) and attenuation coefficient (K_d) in accordance with the standard Lambert-Beer relationship,

$$PLW = 100 \exp [(-K_d)(Z)]. \quad (1)$$

PLL is calculated from PLW plus variables estimating epiphyte biomass (B_e) and biomass-specific epiphytic light attenuation coefficient (K_e), both of which are derived from numerical and empirical relationships (Kemp et al. 2000),

$$PLL = (PLW) \exp [(-K_e)(B_e)]. \quad (2)$$

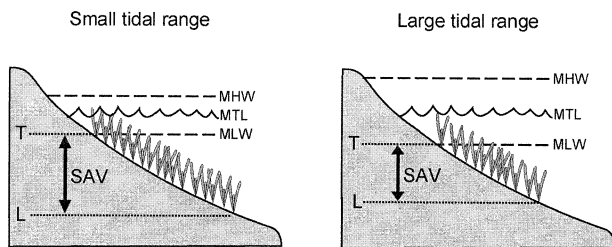


Fig. 2. Illustration of how tidal range influences vertical depth distribution of SAV. The vertical range for plant distribution can be reduced with increased tidal range. The minimum depth of SAV distribution is limited by the low tide (T), while the maximum depth of SAV distribution is limited by light (L). The SAV fringe (arrow) decreases as tidal range increases. A small tidal range results in a large SAV depth distribution, whereas a large tidal range results in a small SAV depth distribution. Mean high water (MHW), mean tide level (MTL) and mean low water (MLW) are also illustrated.

Previous studies have made quantitative distinctions between water column and epiphytic contributions to total light attenuation (Twilley et al. 1985; Vermaat and de Bruyne 1993).

MINIMUM LIGHT REQUIREMENT FOR SAV SURVIVAL

In general, for all SAV species there is a strong positive relationship between water clarity and the maximum water column depth to which plants grow (Chambers and Kalff 1985; Duarte 1991; Abal and Dennison 1996; Olesen 1996). Numerous statistical models have been reported describing relationships between maximum SAV colonization depth (Z_c) and water transparency measured by K_d or Secchi depth (Canfield et al. 1985; Vant et al. 1986; Duarte and Kalff 1987; Carter et al. 2000). Virtually all of these models are similar in shape and trajectory, and two representative examples are given (Fig. 4) for freshwater plants (Chambers and Kalff 1985) and seagrasses (Duarte 1991). Although it appears that freshwater plants survive better than seagrasses in relatively turbid waters ($K_d^{-1} < 2.5$ m) whereas seagrasses grow deeper in clear waters ($K_d^{-1} > 3$ m), these differences are small and perhaps unimportant. Percent of surface light reaching bottom at the maximum SAV colonization depth (PLW_c) can be calculated from $PLW_c = 100 \exp [(-K_d)(Z_c)]$, where regression equations such as those in Fig. 4, are used to compute Z_c in relation to K_d . Values for PLW_c tend to range from 10–30% for both marine and lacustrine habitats. This calculation represents a quantitative index of the minimum light required for SAV survival. Results from in situ experiments involving seagrass shading suggest a similar range of mini-

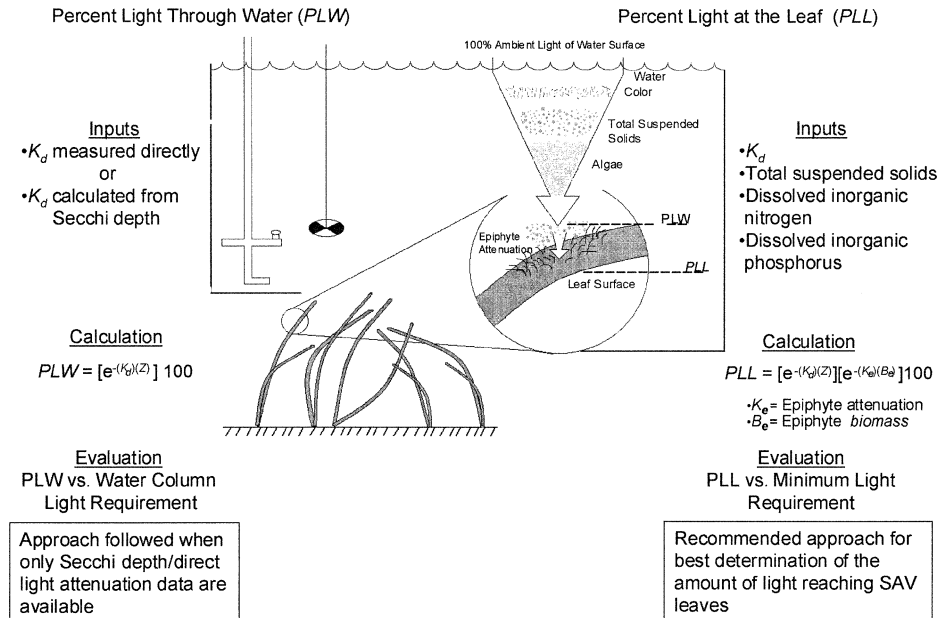
Calculation of *PLW* and *PLL* and Comparisons with their Respective Light Requirements

Fig. 3. Conceptual representation of how percent surface light through the water (*PLW*) and percent surface light at the leaf (*PLL*) are calculated and how these parameters are used to evaluate a site as a potential habitat for SAV.

imum light values (10–35% surface irradiance) at which plants can survive (Congdon and McComb 1979; Gordon et al. 1994; Czerny and Dunton 1995; Lee and Dunton 1997).

Neither of these approaches for estimating SAV light requirements accounts for shading by epiphytes, which grow at all depths on SAV leaves including experimentally shaded plants. Studies in various estuarine habitats indicate that light attenuation by epiphytic material contributes an additional 15–50% shading on SAV (Bulthuis and Woelkerling 1983; Sand-Jensen and Borum 1983; van Dijk 1993; Vermaat and Hootsmans 1994). A recent detailed study of *Thalassia testudinum* beds in Florida coastal waters (Dixon 2000) showed that, while light levels at the maximum depth of seagrass colonization averaged about 22% of surface irradiance, epiphytic attenuation reduced this to approximately 15% of surface light actually available to the plants. This represents an average of ~30% additional shading by epiphytes.

Whereas seagrasses tend to be meadow-forming species with blade-shaped leaves that grow up from their base (basal meristem), most freshwater plants are canopy-formers that have leaves growing out from the tips of stems (apical meristem). Under low-light conditions, the canopy-forming species often exhibit rapid vertical growth by stem-elongation, and they retain only their uppermost leaves near the water surface (Goldsborough and Kemp

1988; Maberly 1993). Canopy-formation and stem-elongation are two shade-adaptation mechanisms (Vermaat et al. 1996; Middelboe and Markager 1997) that allow these species to survive considerably better than meadow-forming seagrasses in turbid shallow environments (Fig. 4). Because SAV species inhabiting shallow, turbid tidal fresh and oligohaline regions of estuaries such as Chesapeake Bay tend to be canopy-formers, we might anticipate that the apparent minimum light requirements for SAV survival would be relatively lower in these areas than in higher salinity areas dominated by meadow-forming seagrass.

For the present analysis, we estimated the minimum light for SAV survival required at canopy height (PLW_{min}) and at leaf surface (PLL_{min}) by inserting into Eqs. 1 and 2, respectively, appropriate values for K_d , DIN, DIP, and TSS (Table 2) previously shown to be maximum thresholds beyond which SAV did not occur in Chesapeake Bay (Dennison et al. 1993). This resulted in values for PLW_{min} of 22% for mesohaline and polyhaline regions ($K_d = 1.5 \text{ m}^{-1}$) and 13% for the tidal fresh and oligohaline segments of the Bay ($K_d = 2 \text{ m}^{-1}$). Using our algorithm for calculating epiphyte shading (Fig. 5, Eqs. 2, 8, and 9), we estimated values for PLL_{min} to be 15% and 9% surface light for the mesohaline-polyhaline and tidal fresh-oligohaline regions, respectively (Table 2). Consistent with earlier discussion, this calculation suggests that epi-

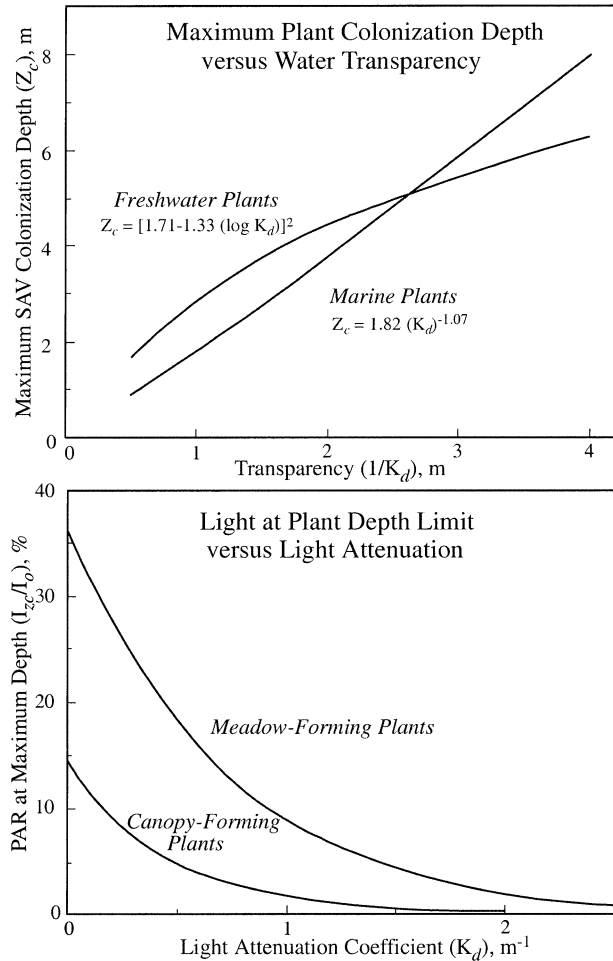


Fig. 4. Empirical relationship (after Chambers and Kalfs 1985; Duarte 1991) between the maximum depth of seagrass and submerged freshwater plant colonization and water column transparency (upper panel), and empirical relationship (after Middleboe and Markager 1997) between photosynthetically active radiation (PAR) at the maximum colonization depth and the diffuse down-welling light attenuation coefficient (K_d) for meadow-forming and canopy-forming plants (lower panel).

phytes contribute an average of 30% additional shading [$100 (PLW_{min} - PLL_{min})/PLW_{min}$] to water column attenuation. These values for PLL_{min} are remarkably similar to those suggested from our review of the literature (see above).

Partitioning Light Attenuation from Water Surface to SAV Leaf

WATER COLUMN LIGHT ATTENUATION

Attenuation of light within the water column is attributable to light absorption and scattering by dissolved and suspended substances in water and by water itself (Kirk 1994). As a first approximation, the diffuse attenuation of light measured by K_d can be partitioned into contributions from wa-

ter and dissolved organic matter ($K_{(W+DOC)}$), from phytoplankton chl a (K_{chl}), and from total suspended solids (K_{TSS}). Although wavelength-specificity of absorption by any substance and interactions with absorption by other substances would theoretically preclude linear partitioning of diffuse light attenuation (Gallegos 1994; Kirk 1994), we have assumed these non-linearities to be unimportant for most management applications (Gallegos 2001). The basic relationships can be described by the following simple equations:

$$K_d = -\ln(PLW/100)/Z \quad (3)$$

$$K_d = K_{(W+DOC)} + K_{chl} + K_{TSS} \quad (4)$$

We derive Eq. 3 by rearranging Eq. 1; Eq. 4 describes a linear partitioning of diffuse attenuation. The values for K_{chl} and K_{TSS} can be approximated as linear functions of chl a and TSS concentrations, respectively. For this analysis, values of the three partial attenuation coefficients were derived for Chesapeake Bay from the large monitoring database that includes simultaneous observations on K_d , chl a , and TSS (Gallegos 2001), as follows:

$$K_d = 0.32 + 0.016[\text{chl } a] + 0.094[\text{TSS}]. \quad (5)$$

By combining Eq. 3 and 5, we obtain:

$$-\ln(PLW/100) = Z(0.32 + 0.016[\text{chl } a] + 0.094[\text{TSS}]), \quad (6)$$

where Z is the target depth penetration selected for SAV restoration.

This equation can be rearranged to calculate linear combinations of chl a and TSS concentrations that just meet the water column light requirement target (PLW_{min}) for a particular depth (Fig. 6) at any site or season as follows

$$[\text{TSS}] = -(0.32 + 0.016[\text{chl } a] + \ln(PLW/100)/Z)/0.094. \quad (7)$$

It can be used to consider management options for meeting SAV habitat requirements.

The range of management strategies can be illustrated with four alternatives for meeting the PLW_{min} requirement by reducing TSS or chl a or both (Fig. 6). The first option involves reducing both chl a and TSS along a projection from the existing median water quality conditions toward the origin, until the respective PLW_{min} value is met. In the second option, chl a and TSS reductions are balanced by moving along a trajectory perpendicular to the PLW_{min} target. The third option is to reduce TSS only, moving existing median values down a vertical projection to PLW_{min} . The final option, which focuses on reductions in chl a only (plus algal contribution to TSS), moves the median

TABLE 2. Statistically-derived water quality thresholds beyond which submerged aquatic vegetation (SAV) are not present, and calculated minimum light requirements for SAV survival.^a

Salinity Regime ^b	Growing Season ^c	Light Required at SAV Leaf (%), PLL_{min}	Light Required through Water (%), PLW_{min}	Water Column Light Attenuation (K_d m ⁻¹)	Total Suspended Solids (mg l ⁻¹)	Plankton Chlorophyll <i>a</i> (μg l ⁻¹)	Dissolved Inorganic Nitrogen (mg l ⁻¹)	Dissolved Inorganic Phosphorus (mg l ⁻¹)
Tidal Freshwater	April–October	>9	>13	<2	<15	<15	—	<0.02
Oligohaline	April–October	>9	>13	<2	<15	<15	—	<0.02
Mesohaline	April–October	>15	>22	<1.5	<15	<15	<0.15	<0.01
Polyhaline	March–May	>15	>22	<1.5	<15	<15	<0.15	<0.01
	September–November							

^a Indicates that these are statistically-derived water quality threshold values, beyond which SAV were found to be absent, based on intensive field studies at selected sites in Chesapeake Bay (Batiuk et al. 1992; Dennison et al. 1993). Minimum light requirement for SAV survival given as a percent of surface light through the water column (PLW_{min}) and percent of surface light at leaves (PLL_{min}) based on Eqs. 1 and 2 (see text).

^b Regions of the estuary defined by salinity regime, where tidal freshwater means < 0.5 psu, oligohaline means 0.5–5 psu, mesohaline means 5–18 psu, and polyhaline means >18 psu.

^c Medians calculated over this growing season should be used to check the attainment of any of these habitat requirements, and raw data collected over this period should be used for statistical tests of attainment. For polyhaline areas, the data are combined for the two periods shown.

values along a path parallel to the line describing the minimum contribution of chl *a* to TSS. The potentially serious theoretical and practical limitations to this linear model (Eqs. 4, 5, and 6) can be

partially overcome with calibration to the particular study site (Gallegos 2001).

EPIPHYTE LIGHT ATTENUATION

Central to this revised approach for computing potential light available at SAV leaves is a relationship developed to compute biomass of epiphytic

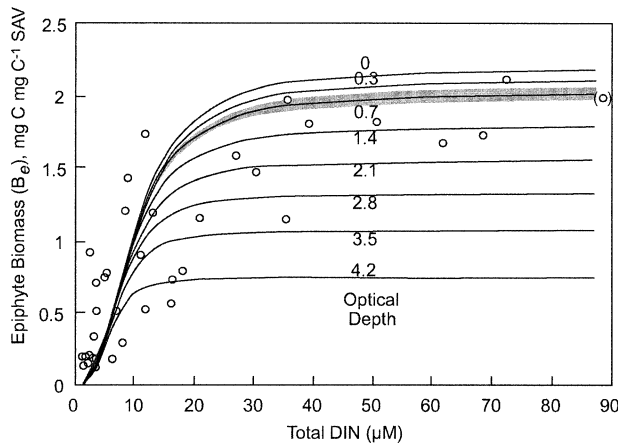


Fig. 5. Calculated responses of epiphytic algal biomass (B_e , mg C/mg C SAV) to changes in dissolved inorganic nitrogen (DIN, μM) concentration under various light (PAR, μE m⁻² s⁻¹) conditions in estuarine waters. Each curve is described by the equation, and each represents computed response under different light regimes, characterized by the dimensionless optical depth ($OD = K_d Z$). These curves, which are described by $(B_e)_m = (B_e)_m [1 + 208 (DIN^{-KN(OD)})^{-1}]$ (where $(B_e)_m = 2.2 - [0.251 (OD^{1.23})]$ and $K_{N(OD)} = 2.32(1 - 0.031OD^{1.42})^{-1}$), were generated from numerical model calculations (modified from Bartleson 1988) assuming constant biomass of host SAV plant over the growth season (May–August). The model was calibrated to data (open circles) from mesocosm studies (Murray unpublished data) for experimental light conditions (shaded area). Equations were fit to model calculations using a statistical curve-fitting routine (Kemp et al. 2000). Similar functions are predicted for B_e versus dissolved inorganic phosphorus (DIP) concentrations, with $DIP = DIN/16$.

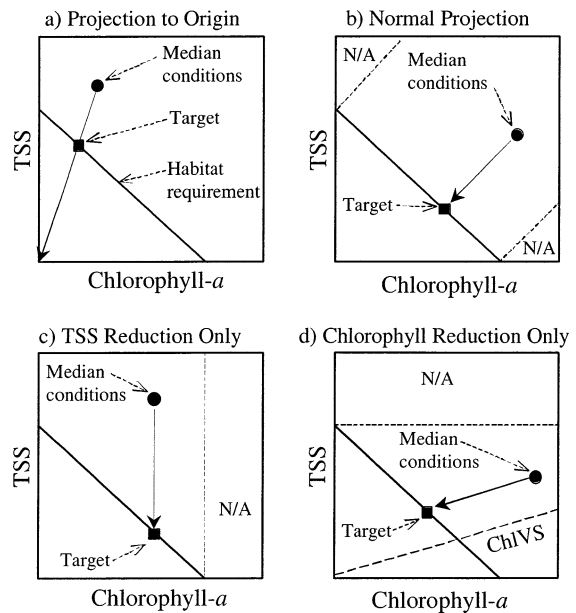


Fig. 6. Illustration of the use of a diagnostic tool to calculate target concentrations for TSS and chl *a* (growing season means) for restoration of SAV to a given depth (Gallegos 2001). Target concentrations are calculated as the intersection of the minimum water column light levels required for SAV habitat (PLW_{min}), with a line describing the reduction of median chl *a* and TSS concentrations calculated by one of four strategies (a–d). See text for explanation.

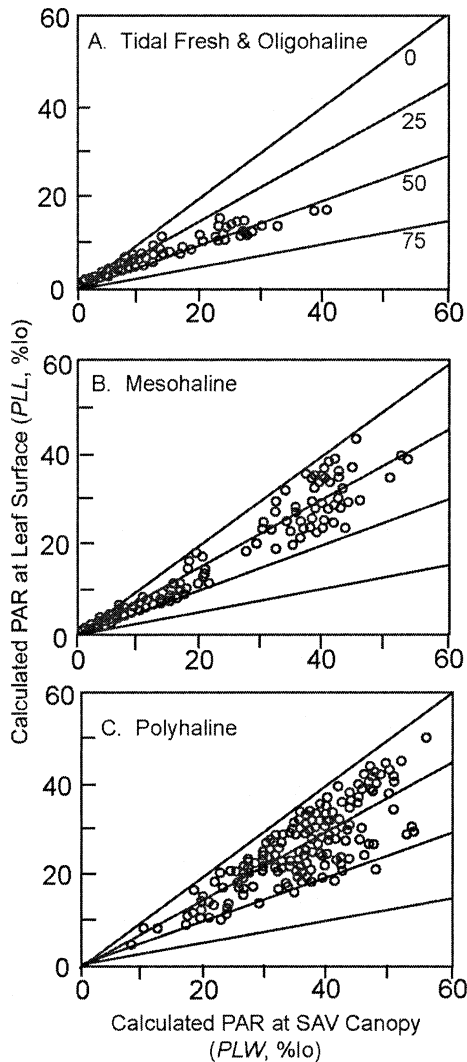


Fig. 7. Relationships between values for percent of surface light at SAV leaves (PLL) and percent of light in water just above epiphytes on SAV leaves (PLW) calculated from water quality monitoring data for $Z = 1$ m in Virginia portion of Chesapeake Bay in 1985–1996 in three salinity regimes. Lines indicate position of points where epiphyte attenuation reduces ambient light levels at the leaf surface by 0, 25, 50, and 75%.

materials and to estimate associated light attenuation (Kemp et al. 2000). Although the relative contribution of epiphytic material to total light attenuation for SAV can be measured directly (Twilley et al. 1985), widespread monitoring of epiphyte attenuation (Stankelis et al. 2003) would be prohibitively expensive for large estuaries such as Chesapeake Bay. We developed a quantitative function to estimate potential epiphyte contribution to total light attenuation for SAV at a particular depth from monitored water quality data for K_d (m^{-1}), TSS ($mg\ l^{-1}$), DIN (μM), and DIP (μM). PLL is calculated from Eq. 2 (Fig. 3). Calibrated numer-

ical calculations (Bartleson 1988) were used to generate a family of curves relating epiphytic algal biomass (B_e) as a function of DIN (or DIP) concentration for different light conditions (Fig. 5). With decreasing water clarity [as measured by optical depth, $OD = (Z)(K_d)$], maximum sustainable epiphyte biomass decreases. This hyperbolic-shaped relation between B_e and DIN was calibrated with data from mesocosm experiments, where the calculated curves (shaded area) correspond well to observed values (open circles). As suggested from nutrient enrichment experiments (Neundorfer and Kemp 1993), the algorithm uses DIN if the DIN/DIP ratio is <16 for growing season median concentrations; otherwise, it uses DIP.

Values for K_e ($cm^2 (\mu g\ chl\ a)^{-1}$) are calculated in two steps (Kemp et al. 2000). Total mass (B_{de} , $g\ dw$ ($g\ SAV)^{-1}$) of epiphytic material is computed from a relationship with epiphytic algal biomass (B_e , $mg\ chl\ a$ ($g\ SAV)^{-1}$) and TSS ($mg\ l^{-1}$),

$$B_{de} = 0.107TSS + 0.832B_e \quad (8)$$

K_e is then estimated from a relationship to the ratio B_e/B_{de} ($\mu g\ chl\ a$ ($mg\ dw)^{-1}$)

$$K_e = 0.07 + 0.32(B_e/B_{de})^{-0.88} \quad (9)$$

These empirical relations were derived from field (Neckles 1990; Stankelis et al. 2001; Carter and Rybicki unpublished data) and experimental (Staver 1984) observations. Units for B_e are converted between $mg\ C$ ($mg\ C\ SAV)^{-1}$ generated from Fig. 5 and $\mu g\ chl\ a$ ($cm^2\ SAV)^{-1}$ needed for Eqs. 8 and 9, assuming $C:chl\ a = 100$ for epiphytic material (Staver 1984), and $0.5\ mg\ C$ ($mg\ dw\ SAV)^{-1}$ and $0.3\ cm^2\ leaf$ ($mg\ dw\ SAV)^{-1}$ for plants (Goldsborough and Kemp 1988; Duarte 1991). Much of the data used here are from studies on three plant species (*Potamogeton perfoliatus*, *Ruppia maritima*, and *Zostera marina*) historically abundant in Chesapeake Bay (Kemp et al. 1983).

The algorithm developed here was applied to analyze submerged plant habitat suitability for 50 sites in Chesapeake Bay using water quality data collected over 14 yr (1985–1998) of monitoring (Batiuk et al. 2000). For each site at 1 m depth, values were calculated both for percent surface light available both at the SAV canopy (PLW) and light potentially available at SAV leaf surfaces (PLL). Despite considerable variation among sites throughout the Bay, a plot of PLL versus PLW revealed clear patterns (Fig. 7). Calculations suggest that light attenuation by epiphytic material is important throughout the Bay, contributing 20–60% additional attenuation (beyond PLW) in tidal freshwater and oligohaline regions, where nutrient and TSS concentrations were highest, and 10–50% in the less turbid mesohaline and polyhaline re-

gions. This range of calculated epiphyte shading is consistent with literature reports (Kemp et al. 2000) and with the values established for SAV light requirements, where the PLL_{min} requirement represents 30% additional light reduction from the PLW_{min} requirement (Table 2).

Expanded Analyses of Relations between SAV and Water Quality

WATER QUALITY VARIATIONS FROM CHANNEL TO ADJACENT SHOALS

For most coastal and estuarine ecosystems where water quality conditions are monitored, samples are routinely collected from mid-channel stations. Such monitoring data may not be representative of conditions at adjacent shallow nearshore sites within SAV habitats. In shallow areas, benthic photosynthesis and sediment resuspension can cause water quality to differ significantly from conditions in nearby deeper areas (Ward et al. 1984; Moore 1996). Comparative studies at sites throughout Chesapeake Bay revealed that parallel measurements at adjacent nearshore and mid-channel stations were statistically indistinguishable 90% of the time, when station pairs were separated by <2 km (Karrh 2000). In several cases, paired observations of key water quality variables at nearshore and channel sites compared poorly at various temporal and spatial scales (Stevenson et al. 1993). Even though water quality sampled at mid-channel Bay stations generally provided reasonable estimates of conditions at potential SAV habitats in nearby shoals, more information is needed to fully understand the consequences of using these data as indices of shallow-water conditions.

COMPARING LIGHT CONDITIONS WITH SAV DISTRIBUTION

We tested the robustness of computations with this algorithm by relating calculated values for PLL at 0.5 and 1 m water depths to SAV presence over the 14-yr record from 1978–1997 in areas near water quality monitoring stations. Patterns of calculated PLL versus observed SAV presence were then compared with the respective PLL_{min} values (Table 2). Using data from aerial surveys, five quantitative categories of SAV presence were defined (Bergstrom 2000). Listed in order of decreasing probability of plant presence, they are: always abundant, AA (minimum SAV cover > 200 ha); always some, AS (minimum SAV cover > 0 ha); sometimes none, SN (minimum cover = 0 ha, but median > 0 ha); usually none, UN (median cover = 0 ha, but maximum > 0 ha); and always none, AN (maximum = 0 ha).

We assumed that SAV should be able to grow in a Bay segment if the calculated median PLL at a

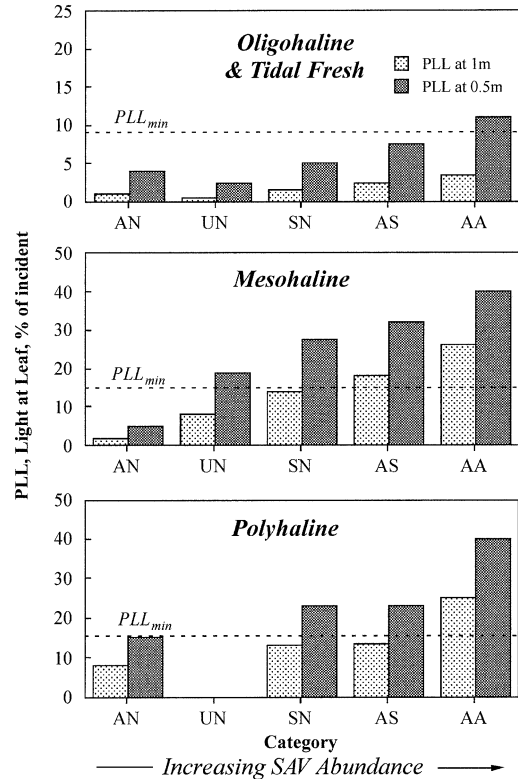


Fig. 8. Percent of surface light at SAV leaves (PLL) calculated using growing season median water quality data collected in Chesapeake Bay monitoring program at stations throughout the estuary compared to relative abundance of SAV in adjacent shallows in 1985–1996. PLL is calculated for water column depths of both 1 m (light bars) and 0.5 m (dark bars). Categories of SAV abundance (AN, always none; UN, usually none; SN, sometimes none; AS, always some; AA, always abundant) are defined in text.

prescribed depth (MTL) for the SAV growing season was near or above the minimum light requirement (PLL_{min}). For the mesohaline and polyhaline regions of the Bay, we found (Fig. 8) that the median PLL value (at 1 m depth) calculated for sites categorized as SN (14% and 13%, respectively) compared well with our estimated PLL_{min} (15%). The situation appears to be more complex for the combined tidal fresh and oligohaline regions of the Bay. SAV growing in these fresh and brackish reaches of the upper Bay and its tributaries are predominantly canopy-forming species (Moore et al. 2000). Although these waters tend to be very turbid (Schubel and Biggs 1969), there are extensive shallow (0.5 m) subtidal flats available as potential SAV habitat (Batiuk et al. 1992; Kemp et al. 2000). We inferred that, for these estuarine regions, use of a shallower application depth (0.5 m MTL) would be more appropriate for comparing PLL to SAV presence. In this case, median values for PLL in tidal fresh-oligohaline regions ranged

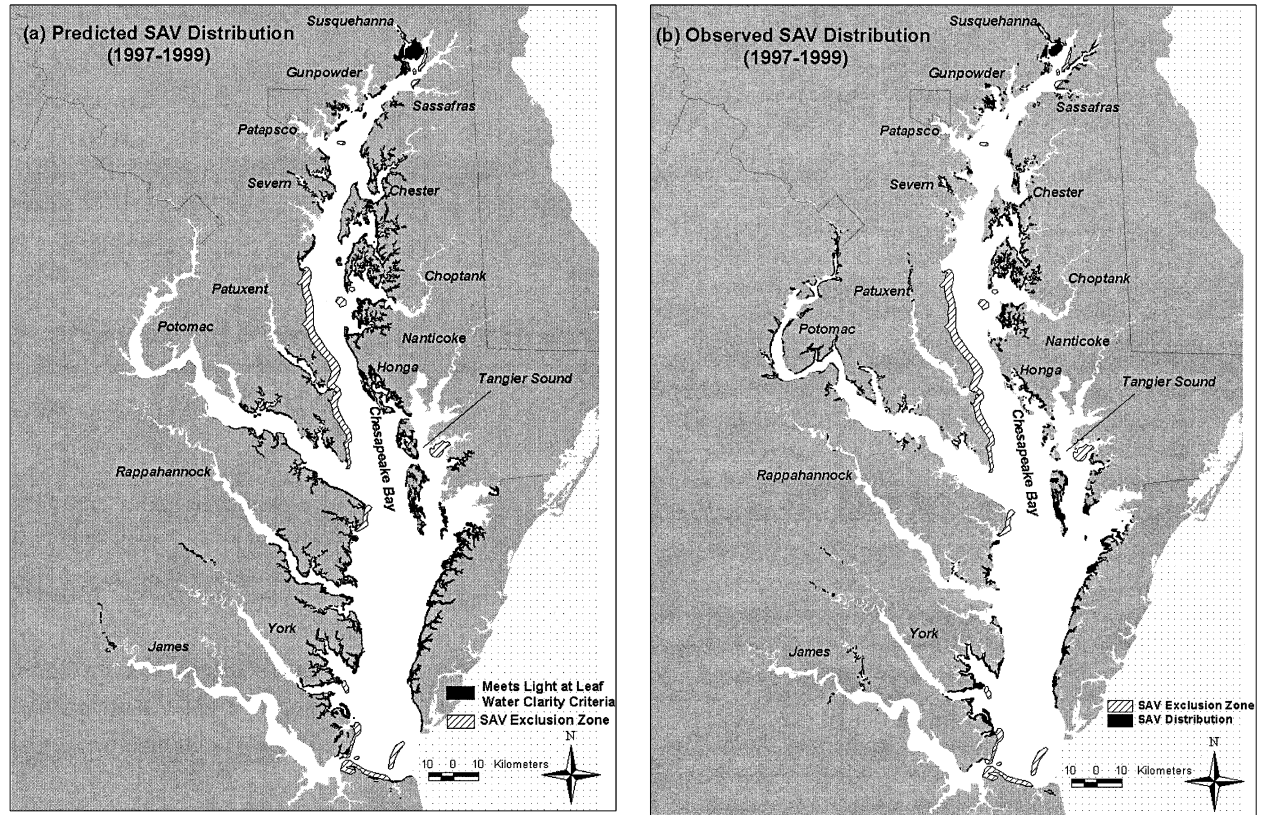


Fig. 9. Maps of Chesapeake Bay and its tidal tributaries showing predicted areas where there is sufficient light to support sustained SAV growth at 1 m depth based on algorithm described in this paper ($PLL > PLL_{min}$) using 1997–1999 water quality data, and composite figure of actual SAV distributions observed in aerial photographic monitoring program in 1997–1999.

from 5% to 8% to 12% at sites categorized as SN, AS, and AA, respectively (Fig. 8). These values are close to the PLL_{min} of 9% computed for tidal fresh and oligohaline regions. Although agreement between PLL_{min} values and predictions of SAV presence were weakest in tidal fresh and oligohaline reaches of the Bay, these areas represent only 20–25% of the whole estuary's potential SAV habitat area (Table 1).

We also defined the spatial distribution of shoal areas where PLL values calculated from water quality variables exceeded PLL_{min} for respective salinity regions (Fig. 9). PLL values were estimated as medians over three growing seasons (1997–1999). For simplicity, PLL was computed for a depth of 1 m throughout the Bay. These maps predict potential SAV distribution where computed PLL exceeds PLL_{min} (Fig. 9). We also provide a composite map of actual plant distribution based on 1997–1999 aerial surveys. Both maps also include designated exclusion zones, where strong wave action and coarse-grain sediments appear to preclude growth of SAV (Batiuk et al. 1992; Koch 2001).

With a few notable exceptions, there was very

good agreement between observed SAV distribution and potential habitat based on PLL calculations. PLL calculations predicted the observed widespread distribution of SAV all along the Bay's southeastern shore, around the islands west of Tangier Sound, and at the mouths of the eastern tributaries from the Honga to Chester Rivers (Fig. 9). Calculated PLL exceeds PLL_{min} at sites that generally coincided with observed SAV presence in large areas near the York River mouth, along the Bay's western shore between the York, Rappahannock, and Potomac Rivers, and in isolated western shore tributaries between the Severn, Patapsco, and Susquehanna Rivers. Aerial surveys confirmed PLL-predicted SAV absence from upper tidal reaches of large and small tributaries throughout the eastern shore and on the western shore below Potomac River, as well as the Patapsco River and small upper western shore tributaries (Fig. 9).

In contrast, PLL predictions of SAV distribution were consistently incorrect for the upper Potomac, Patuxent, and Sassafras Rivers and for other small tributaries on the upper eastern shore (Fig. 9). The oligohaline and tidal freshwater regions of

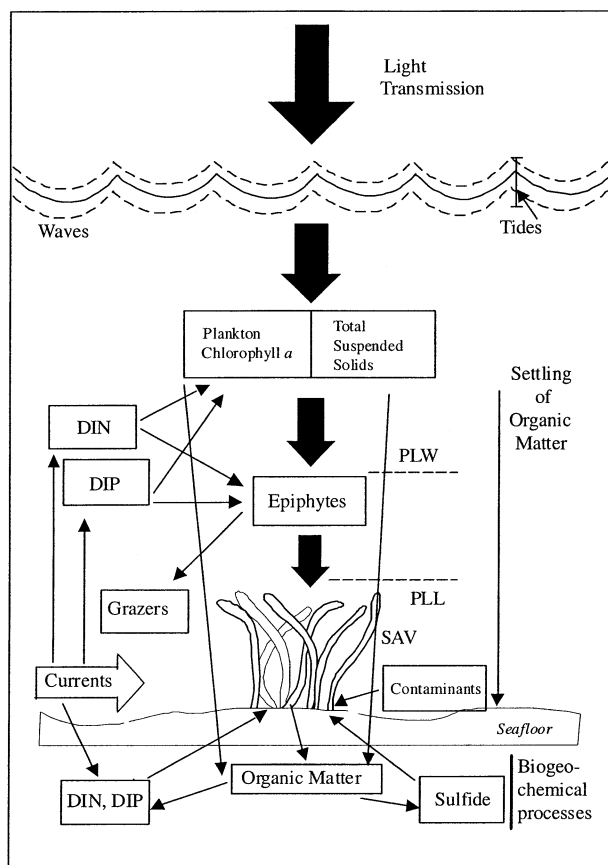


Fig. 10. Conceptual representation illustrating how availability of light to support photosynthesis of seagrasses and other SAV (as influenced by dissolved and particulate material in the water column and by epiphytic material accumulating on plant leaves) interacts with other physical, geological, and chemical factors. These physical-chemical factors include waves, tides, currents, sediment organic matter and biogeochemical processes. See Fig. 1 for further explanation.

these and other tributaries contain extensive shallows that are potential habitat for canopy-forming SAV species. It might be appropriate to compare observed SAV distributions with PLL calculations for 0.5 m rather than 1 m depth. Although PLL predictions for SAV presence at the mouths of the Patuxent and Potomac did not correspond with observations in 1997–1999, more recent observations (see <http://www.vims.edu/bio/sav/sav01/quadindex.html>) reveal extensive beds now in these areas, suggesting delayed re-vegetation after water quality improvements.

Physical, Chemical, and Geological Factors Influencing SAV

The focus of this paper involves defining SAV habitat requirements in terms of light availability to support plant photosynthesis, growth, and survival, even though physical, geological, and chem-

ical factors may preclude SAV from particular sites even when light requirements are met (Koch 2001). Some of these effects operate directly on SAV, and others involve inhibition of SAV-light interactions. Tides and waves alter the light climate by changing water column height over which light is attenuated and by increasing TSS and associated light attenuation by resuspending bottom sediments. Particle sinking rate, coastal erosion, and other sedimentological processes alter texture, grain-size distribution, and organic content of bottom sediments. Increased deposition of fine-grain organic particles can affect SAV growth either by increasing porewater nutrients (Barko and Smart 1986) and by producing phytotoxic reduced sulfur compounds (Carlson et al. 1994; Goodman et al. 1995).

An extensive review of the literature revealed that certain SAV species and functional groups appear to have a limited range in their ability to tolerate selected physical, sedimentological and chemical variables (Table 3 adapted from Koch 2001). Freshwater plants, particularly canopy-forming species, tend to be relatively tolerant of quiescent habitats with little water movement, whereas meadow-forming seagrasses require substantially higher minimum velocities ($0.04\text{--}5\text{ cm s}^{-1}$ versus $3\text{--}16\text{ cm s}^{-1}$). Seagrasses seem to tolerate rapid water movement better (maximum velocities of $50\text{--}180\text{ cm s}^{-1}$) than do freshwater plants ($7\text{--}50\text{ cm s}^{-1}$), indicating a tendency for meadow-forming species to have less drag and to be better anchored to the sediments. This is consistent with the observation that the more fragile canopy-forming species tend to be less tolerant of wave energy (Table 3). Although sediment grain-size distribution appears to have little effect on freshwater plants, seagrasses are generally more abundant in sediments in which silts and clays constitute less than 20–30% (by weight). For both marine and freshwater SAV, sediments with >5% organic content or 2 mM of porewater sulfide are usually devoid of submerged plants (Table 3). SAV are sensitive to many contaminants such as herbicides, with significant stress evident for some compounds at low concentrations (e.g., <10 ppb), which are periodically encountered in estuaries (Kemp et al. 1985).

Concluding Comments

Our algorithm for assessing SAV habitat conditions represents a scientifically-based approach with broad management applicability. This algorithm complements use of water quality models (Madden and Kemp 1996; Cerco and Moore 2001) for managing SAV resources. Simulation models can be used to predict how SAV habitat conditions respond to scenarios for changing nutrient and

TABLE 3. Summary of physical, geological, and chemical factors possibly defining habitat constraints for submerged aquatic vegetation (SAV) (modified from Koch 2001).

Factor	Description	Constraint	Submerged Plants
Water Movement ^a	Minimum velocities (cm s ⁻¹)	0.04–5	Freshwater plants
	Maximum velocities (cm s ⁻¹)	3–16 7–50 50–180	Seagrasses Freshwater plants Seagrasses
Wave Tolerance ^b	Height < 0.5 m	Limited growth	Canopy-formers (e.g., <i>M. spicatum</i> , <i>R. maritima</i> reproductive)
	Height < 2 m	Tolerant growth	Meadow formers (e.g., <i>Z. marina</i>)
Sediments ^c	Grain size (% silts and clays)	2–62 0.4–72	Freshwater plants Seagrasses
	Organic matter (%)	0.4–16	Mixed species
Porewater Sulfide ^d	(mM)	<1	Healthy plants
		>1	Reduced growth
		>2	Death

^a Conover 1964; Westlake 1967; Sculthorpe 1967; Scoffin 1970; Phillips 1974; Fonseca et al. 1982; Madsen and Sondergaard 1983; Werner and Wise 1982; Fonseca and Kenworthy 1987; Koch 1994; Merrell 1996.

^b Joanan and Glasgow 1965; Hannan 1967; Rawls 1975; Stevenson and Confer 1978; Stewart et al. 1997; Dan et al. 1998.

^c Burrell and Schubel 1977; Carter et al. 1985; Posey et al. 1993; Short et al. 1993; Edgar and Shaw 1995; Dan et al. 1998.

^d Pulich 1983; Carlson et al. 1994; Kuhn 1992; Goodman et al. 1995; Holmer and Bondgaard 2001; Koch and Erskine 2001.

sediment loads to the estuary. This algorithm uses monitoring data to assess quantitatively recent trends and changes in suitability of sites as habitats for supporting SAV growth. This approach has formed the basis for developing water clarity criteria for adoption as state water quality standards and for setting caps on nutrient and sediment loads to estuaries (Chesapeake Executive Council unpublished material; National Research Council 2001).

Although the approach described here tends to predict SAV presence effectively on broad time and space scales, it is less suitable for habitat assessment at smaller scales, such as a specific hectare of estuarine bottom. There is considerable room for the algorithm to be improved and generalized with additional research. Any future improvements on this approach should strive to maintain the flexibility needed for a science-based management tool that assesses SAV habitat conditions using readily available monitoring data. Although the algorithm presented here was developed and calibrated for Chesapeake Bay, its structure is sufficiently general for it to be calibrated and used for other coastal ecosystems where SAV distribution is limited by light availability and where nutrient-stimulated epiphyte shading is important.

ACKNOWLEDGMENTS

We are indebted to numerous colleagues who contributed useful comments and discussions during the development of this project. This long list includes: J. Barko, R. Davis, K. Dixon, K. Dunton, M. Durako, M. Fonseca, J. Fourqurean, B. Glazer, H. Greening, D. Hammerschlag, J. Kenworthy, H. Neckles, R. Orth, H. Phelps, K. Price, F. Short, M. Smart, J. Titus, D. Tomasko, B. Virnstein, L. Valdes, D. Wetzel, and D. Zimmerman. We also thank M. Teichberg, R. Herbst, D. Jasinski, and T. Caruthers who provided essential technical and editorial assis-

tance. In addition, the paper has benefited from the useful comments of two anonymous reviewers.

LITERATURE CITED

- ABAL, E. AND W. C. DENNISON. 1996. Seagrass depth range and water quality in southern Moreton Bay, Queensland. *Australian Journal of Marine and Freshwater Research* 47:763–771.
- BARKO, J. W. AND M. SMART. 1986. Sediment-related mechanisms of growth limitation in submersed macrophytes. *Ecology* 67:1382–1340.
- BARTLESON, R. D. 1988. The relative influence of current reduction by seagrasses on sediment nutrients and seagrass growth in high and low nutrient waters: A simulation model and field observations. M.S. Thesis, University of Florida, Gainesville, Florida.
- BATIUK, R., P. BERGSTROM, M. KEMP, E. KOCH, L. MURRAY, C. STEVENSON, R. BARTLESON, V. CARTER, N. RYBICKI, J. LANDWEHR, C. GALLEGOS, L. KARRH, M. NAYLOR, D. WILCOX, K. MOORE, S. AILSTOCK, AND M. TEICHBERG. 2000. Chesapeake Bay submerged aquatic vegetation water quality and habitat-based requirements and restoration targets: A second technical synthesis. CBP/TRS 245/00. EPA 903-R-00-014. U.S. EPA, Chesapeake Bay Program, Annapolis, Maryland.
- BATIUK, R., R. ORTH, K. MOORE, J. C. STEVENSON, W. DENNISON, L. STAYER, V. CARTER, N. RYBICKI, R. HICKMAN, S. KOLLAR, AND S. BIEBER. 1992. Submerged aquatic vegetation habitat requirements and restoration targets: A technical synthesis. U.S. EPA, Chesapeake Bay Program, Annapolis, Maryland.
- BERGSTROM, P. 2000. Setting, applying and evaluating minimum light requirements for Chesapeake Bay SAV, p. 95–120. *In* R. Batiuk, R. Orth, K. Moore, J. C. Stevenson, W. Dennison, L. Stayer, V. Carter, N. Rybicki, R. Hickman, S. Kollar, and S. Bieber (eds.), Chesapeake Bay Submerged Aquatic Vegetation Water Quality and Habitat-Based Requirements and Restoration Targets: A Second Technical Synthesis. CBP/TRS 245/00. EPA 903-R-00-014. U.S. EPA, Chesapeake Bay Program, Annapolis, Maryland.
- BORUM, J. 1985. Development of epiphytic communities on eelgrass (*Zostera marina*) along a nutrient gradient in a Danish estuary. *Marine Biology* 87:211–218.
- BULTHUIS, D. A. AND W. J. WOELKERLING. 1983. Biomass accumulation and shading effects of epiphytes on leaves of the seagrass, *Heterozostera tasmanica*, in Victoria, Australia. *Aquatic Botany* 16:137–148.

- BURD, A. B. AND K. H. DUNTON. 2001. Field verification of a light-driven model of biomass changes in the seagrass *Halodule wrightii*. *Marine Ecology Progress Series* 209:85–98.
- BURRELL, D. C. AND J. R. SCHUBEL. 1977. Seagrass ecosystem oceanography, p. 196–232. In C. P. McRoy and C. Helfferich (eds.), *Seagrass Ecosystems: A Scientific Perspective*. Marcel Dekker, Inc., New York.
- BUZZELLI, C. P., R. L. WETZEL, AND M. B. MEYERS. 1998. Dynamic simulation of littoral zone habitats in lower Chesapeake Bay. II. Seagrass habitat primary production and water quality relationships. *Estuaries* 21:673–689.
- CAFFREY, J. AND W. M. KEMP. 1990. Nitrogen cycling in sediments with estuarine populations of *Potamogeton perfoliatus* and *Zostera marina*. *Marine Ecology Progress Series* 66:147–160.
- CAMBRIDGE, M. L. AND A. J. MCCOMB. 1984. The loss of seagrasses in Cockburn Sound, Western Australia. I. The time course and magnitude of seagrass decline in relation to industrial development. *Aquatic Botany* 20:229–243.
- CANFIELD, JR., E. D., K. A. LANGELAND, S. B. LINDA, AND W. T. HALLER. 1985. Relations between water transparency and maximum depth of macrophyte colonization in lakes. *Journal of Aquatic Plant Management* 23:25–28.
- CARLSON, P. R., L. YARBRO, AND T. BARBER. 1994. Relationship of sediment sulfide to mortality of *Thalassia testudinum* in Florida Bay. *Bulletin of Marine Science* 54:733–746.
- CARTER, V., J. E. PASCHAL, AND N. BARTOW. 1985. Distribution and abundance of submerged aquatic vegetation in the tidal Potomac River and estuary, Maryland and Virginia, May 1978 to November 1981—A water quality study of the tidal Potomac River and estuary. Water Supply Pap 223A. U.S. Geological Survey, Reston, Virginia.
- CARTER, V., N. RYBICKI, J. LANDWEHR, AND M. NAYLOR. 2000. Light requirements for SAV survival and growth, p. 11–34. In R. Batiuk, R. Orth, K. Moore, J. C. Stevenson, W. Dennison, L. Staver, V. Carter, N. Rybicki, R. Hickman, S. Kollar, and S. Bieber (eds.), *Chesapeake Bay Submerged Aquatic Vegetation Water Quality and Habitat-Based Requirements and Restoration Targets: A Second Technical Synthesis*. CBP/TRS 245/00. EPA 903-R-00-014. U.S. EPA, Chesapeake Bay Program, Annapolis, Maryland.
- CERCO, C. F. AND K. A. MOORE. 2001. System-wide submerged aquatic vegetation model for Chesapeake Bay. *Estuaries* 24:522–534.
- CHAMBERS, P. A. AND J. KALFF. 1985. Depth distribution and biomass of submersed aquatic macrophyte communities in relation to secchi depth. *Canadian Journal of Fisheries and Aquatic Science* 42:701–709.
- CONGDON, R. A. AND A. J. MCCOMB. 1979. Productivity of *Ruppia*: Seasonal changes and dependence on light in an Australian estuary. *Aquatic Botany* 6:121–132.
- CZERNY, A. B. AND K. H. DUNTON. 1995. The effects of in situ light reduction on the growth of two subtropical seagrasses, *Thalassia testudinum* and *Halodule wrightii*. *Estuaries* 18:418–427.
- DAN, A., A. MORIGUCHI, K. MITSUHASHI, AND T. TERAWAKI. 1998. Relationship between *Zostera marina* and bottom sediments, wave action offshore in Naruto, Southern Japan. *Fisheries Engineering* 34:229–204.
- DE JONGE, V. N. AND D. J. DE JONG. 1992. Role of tide, light and fisheries in the decline of *Zostera marina* L. in the Dutch Wadden Sea. *Netherlands Institute for Sea Research Publication* 20:161–176.
- DENNISON, W. C., R. J. ORTH, K. A. MOORE, J. C. STEVENSON, V. CARTER, S. KOLLAR, P. BERGSTROM, AND R. BATIUK. 1993. Assessing water quality with submersed aquatic vegetation. Habitat requirements as barometers of Chesapeake Bay health. *Bioscience* 43:86–94.
- DIXON, L. K. 2000. Establishing light requirements for the seagrass *Thalassia testudinum*: An example from Tampa Bay, Florida, p. 9–32. In S. A. Bortone (ed.), *Seagrasses Monitoring, Ecology, Physiology and Management*. CRC Press, Boca Raton, Florida.
- DUARTE, C. M. 1991. Seagrass depth limits. *Aquatic Botany* 40:363–377.
- DUARTE, C. M. AND J. KALFF. 1987. Latitudinal influences on the depths of maximum colonization and maximum biomass of submerged angiosperms in lakes. *Canadian Journal Fisheries and Aquatic Sciences* 44:1759–1764.
- DUNTON, K. H. 1996. Photosynthetic production and biomass of the subtropical seagrass *Halodule wrightii* along an estuarine gradient. *Estuaries* 19:436–447.
- EDGAR, G. J. AND C. SHAW. 1995. The production and trophic ecology of shallow-water fish assemblages in southern Australia. III. General relationships between sediments, seagrasses, invertebrates and fishes. *Journal of Experimental Marine Biology and Ecology* 194:107–131.
- FONG, P., M. E. JACOBSEN, M. MESCHER, D. LIRMAN, AND M. C. HARWELL. 1997. Investigating the management potential of a seagrass model through sensitivity analysis and experiments. *Ecological Applications* 7:300–315.
- FONSECA, M. S., J. S. FISHER, J. C. ZIEMAN, AND G. W. THAYER. 1982. Influence of the seagrass *Zostera marina* on current flow. *Estuarine, Coastal and Shelf Science* 15:351–364.
- FONSECA, M. S. AND W. J. KENWORTHY. 1987. Effects of current on photosynthesis and distribution of seagrasses. *Aquatic Botany* 27:59–78.
- GALLEGOS, C. L. 1994. Refining habitat requirements of submersed aquatic vegetation: Role of optical models. *Estuaries* 17:198–219.
- GALLEGOS, C. L. 2001. Calculating optical water quality targets to restore and protect submersed aquatic vegetation: Overcoming problems in partitioning the diffuse attenuation coefficient for photosynthetically active radiation. *Estuaries* 24:381–397.
- GLAZER, B. T. 1999. Analysis of physical, chemical, and biological factors inhibiting growth and restoration of submerged vascular plants in Delaware's Indian River and Rehoboth Bays. M.S. Thesis, University of Delaware, Newark, Delaware.
- GOLDSBOROUGH, W. G. AND W. M. KEMP. 1988. Light response and adaptation for the submersed macrophyte, *Potamogeton perfoliatus*: Implications for survival in turbid tidal waters. *Ecology* 69:1775–1786.
- GOODMAN, J., K. MOORE, AND W. DENNISON. 1995. Photosynthetic responses of eelgrass (*Zostera marina*) to light and sediment sulfide in shallow barrier lagoon. *Aquatic Botany* 50:37–48.
- GORDON, D. M., K. A. GREY, S. C. CHASE, AND C. J. SIMPSON. 1994. Changes to the structure and productivity of a *Posidonia sinuosa* meadow during and after imposed shading. *Aquatic Botany* 47:265–275.
- GUARRACI, M. 1999. Interaction between epiphyte organic mass and resuspended inorganic materials on leaves of natural and artificial SAV. M.S. Thesis, University of Maryland, College Park, Maryland.
- HANNAN, H. H. 1967. Macrophyte standing crop and metabolism in a constant temperature river. Ph.D. Dissertation, Oklahoma State University, Stillwater, Oklahoma.
- HECK, K. L., K. ABLE, C. ROMAN, AND M. FAHAY. 1995. Composition, abundance, biomass and production of macrofauna in a New England estuary: Comparisons among eelgrass meadows and other nursery habitats. *Estuaries* 18:379–389.
- HICKS, S. D. 1964. Tidal wave characteristics of Chesapeake Bay. *Chesapeake Science* 5:103–113.
- HOLMER, M. AND E. J. BONDGAARD. 2001. Photosynthetic and growth response of eelgrass to low oxygen and high sulfide concentrations during hypoxic events. *Aquatic Botany* 70:29–38.
- JOANEN, T. AND L. L. GLASGOW. 1965. Factors influencing the

- establishment of widgeon grass stands in Louisiana. *Southeastern Association Game Fish Commission Conference* 19:78–92.
- KARRH, L. 2000. Comparing nearshore and midchannel water quality conditions, p. 131–158. In R. Batiuk, R. Orth, K. Moore, J. C. Stevenson, W. Dennison, L. Staver, V. Carter, N. Rybicki, R. Hickman, S. Kollar, and S. Bieber (eds.), Chesapeake Bay Submerged Aquatic Vegetation Water Quality and Habitat-Based Requirements and Restoration Targets: A Second Technical Synthesis. CBP/TRS 245/00. EPA 903-R-00-014. U.S. EPA, Chesapeake Bay Program, Annapolis, Maryland.
- KEMP, W. M., R. BARTLESON, AND L. MURRAY. 2000. Epiphyte contributions to light attenuation at the leaf surface, p. 55–70. In R. Batiuk, R. Orth, K. Moore, J. C. Stevenson, W. Dennison, L. Staver, V. Carter, N. Rybicki, R. Hickman, S. Kollar, and S. Bieber (eds.), Chesapeake Bay Submerged Aquatic Vegetation Water Quality and Habitat-Based Requirements and Restoration Targets: A Second Technical Synthesis. CBP/TRS 245/00. EPA 903-R-00-014. U.S. EPA, Chesapeake Bay Program, Annapolis, Maryland.
- KEMP, W. M., W. R. BOYNTON, J. J. CUNNINGHAM, J. C. STEVENSON, T. W. JONES, AND J. C. MEANS. 1985. Effects of atrazine and linuron on photosynthesis and growth of macrophytes, *Potamogeton perfoliatus* L. and *Myriophyllum spicatum* L., in an estuarine environment. *Marine Environmental Research* 16:255–280.
- KEMP, W. M., W. R. BOYNTON, J. C. STEVENSON, R. R. TWILLEY, AND J. C. MEANS. 1983. The decline of submerged vascular plants in upper Chesapeake Bay: Summary of results concerning possible causes. *Marine Technology Society Journal* 17:78–89.
- KEMP, W. M., S. PUSKARIC, A. FAGANELI, E. SMITH, AND W. BOYNTON. 1999. Pelagic-benthic coupling and nutrient cycling, p. 295–339. In T. Malone, A. Malej, L. Harding, N. Smoldlaka, and R. Turner (eds.), Ecosystems at the Land-Sea Margin: Drainage Basin to Coastal Sea. American Geophysical Union Publication, Washington, D.C.
- KIRK, J. T. O. 1994. Light and Photosynthesis in Aquatic Ecosystems. Cambridge University Press, Cambridge, U.K.
- KOCH, E. W. 1994. Hydrodynamics, diffusion-boundary layers and photosynthesis of the seagrasses *Thalassia testudinum* and *Cymodocea nodosa*. *Marine Biology* 118:767–776.
- KOCH, E. W. 2001. Beyond light: Physical, geological and geochemical parameters as possible submersed aquatic vegetation habitat requirements. *Estuaries* 24:1–17.
- KOCH, E. W. AND S. BEER. 1996. Tides, light and the distribution of *Zostera marina* in Long Island Sound, USA. *Aquatic Botany* 53:97–107.
- KOCH, E. W. AND G. GUST. 1999. Water flow in tide- and wave-dominated beds of the seagrass *Thalassia testudinum*. *Marine Ecology Progress Series* 184:63–72.
- KOCH, M. S. AND J. M. ERSKINE. 2001. Sulfide as a phytotoxin to the tropical seagrass *Thalassia testudinum*: Interactions with light, salinity and temperature. *Journal of Experimental Marine Biology and Ecology* 266:81–95.
- KUHN, W. A. 1992. Interacting effects of light and sediment sulfide on eelgrass (*Zostera marina*) growth. M.S. Thesis, University of Maryland, College Park, Maryland.
- LANDWEHR, J. M., J. T. REEL, N. B. RYBICKI, H. A. RUHL, AND V. CARTER. 1999. Chesapeake Bay habitat criteria scores and the distribution of submersed aquatic vegetation in the tidal Potomac River and estuary. Open File Report 99-219. U.S. Geological Survey, Reston, Virginia. (<http://water.usgs.gov/pubs/ofr/ofr99-219/>)
- LEE, K. AND K. H. DUNTON. 1997. Effects of in situ light reduction on the maintenance, growth and partitioning of carbon resources in *Thalassia testudinum* Banks ex. König. *Journal of Experimental Marine Biology and Ecology* 210:53–73.
- LOSEE, R. F. AND R. G. WETZEL. 1983. Selective light attenuation by the periphyton complex, p. 89–96. In R. G. Wetzel (ed.), Periphyton of Freshwater Ecosystems. Dr. W. Junk Publishers, The Hague, Netherlands.
- LUBBERS, L., W. R. BOYNTON, AND W. M. KEMP. 1990. Variations in structure of estuarine fish communities in relation to abundance of submersed vascular plants. *Marine Ecology Progress Series* 65:1–14.
- MABERLY, S. C. 1993. Morphological and photosynthetic characteristics of *Potamogeton obtusifolius* from different depths. *Journal of Aquatic Plant Management* 31:34–39.
- MADDEN, C. AND W. KEMP. 1996. Ecosystem model of an estuarine submersed plant community: Calibration and simulation of eutrophication responses. *Estuaries* 19:457–474.
- MADSEN, T. V. AND M. SØNDERGAARD. 1983. The effects of current velocity on photosynthesis of *Callitriche stagnalis*. *Aquatic Botany* 15:187–193.
- MCGLATHERY, K. J. 1995. Nutrient and grazing influences on a subtropical seagrass community. *Marine Ecology Progress Series* 122:239–252.
- MERRELL, K. C. 1996. The effects of flow and mixing on *Vallisneria americana* and its associated community in experimental mesocosms. M.S. Thesis, University of Maryland, College Park, Maryland.
- MIDDELBOE, A. L. AND S. MARKAGER. 1997. Depth Limits and minimum light requirements of freshwater macrophytes. *Freshwater Biology* 37:553–568.
- MOORE, K. A. 1996. Relationships between seagrass growth and survival and environmental conditions in a lower Chesapeake Bay tributary. Ph.D. Dissertation, University of Maryland, College Park, Maryland.
- MOORE, K. A., H. A. NECKLES, AND R. J. ORTH. 1996. *Zostera marina* (eelgrass) growth and survival along a gradient of nutrients and turbidity in the lower Chesapeake Bay. *Marine Ecology Progress Series* 142:247–259.
- MOORE, K. A., D. J. WILCOX, AND R. J. ORTH. 2000. Analysis of the abundance of submersed aquatic vegetation communities in the Chesapeake Bay. *Estuaries* 23:115–127.
- NECKLES, H. A. 1990. Relative effects of nutrient enrichment and grazing on epiphyton-macrophyte (*Zostera marina* L.) dynamics. Ph.D. Dissertation, College of William and Mary, Williamsburg, Virginia.
- NEUNDORFER, J. V. AND W. M. KEMP. 1993. Nitrogen versus phosphorus enrichment of brackish waters: Response of *Potamogeton perfoliatus* and its associated algal communities. *Marine Ecology Progress Series* 94:71–82.
- NIELSEN, S. L., K. SAND-JENSEN, J. BORUM, AND OLE GEERTZ-HANSEN. 2002. Depth colonization of eelgrass (*Zostera marina*) and macroalgae as determined by water transparency in Danish coastal waters. *Estuaries* 25:1025–1032.
- NATIONAL RESEARCH COUNCIL. 2001. Assessing the TMDL approach to water quality management. National Academy Press, Washington, D.C.
- OLESEN, B. 1996. Regulation of light attenuation and eelgrass *Zostera marina* depth distribution in a Danish embayment. *Marine Ecology Progress Series* 134:187–194.
- ORTH, R. J. AND K. A. MOORE. 1983. Chesapeake Bay: An unprecedented decline in submerged aquatic vegetation. *Science* 222:51–53.
- PHILLIPS, R. C. 1974. Temperate grass flats, p. 244–299. In H. T. Odum, B. J. Copeland, and E. A. McMahan (eds.), Coastal Ecological Systems of the United States, Volume 2. Conservation Foundation, Washington, D.C.
- POSEY, M. H., C. WIGAND, AND J. C. STEVENSON. 1993. Effects of an introduced aquatic plant, *Hydrilla verticillata*, on benthic communities in the upper Chesapeake Bay. *Estuarine, Coastal and Shelf Science* 37:539–555.
- PULICH, W. M. 1983. Growth response of *Halophila engelmannii* to sulfide, copper and organic nitrogen in marine sediments. *Plant Physiology* 71:975–978.

- PULICH, W. M. AND W. A. WHITE. 1991. Decline of submerged vegetation in the Galveston Bay system: Chronology and relationships to physical processes. *Journal of Coastal Research* 7: 1125–1138.
- QUAMMEN, M. L. AND C. P. ONUF. 1993. Laguna Madre: Seagrass changes continue decades after salinity reduction. *Estuaries* 16:302–310.
- RAWLS, C. K. 1975. Mechanical control of Eurasian watermilfoil in Maryland with and without 2,3-D application. *Chesapeake Science* 16:266–281.
- RØRSLETT, B. 1987. A generalized spatial niche model for aquatic macrophytes. *Aquatic Botany* 29:63–81.
- RYBICKI, N. B., H. L. JENTER, V. CARTER, R. A. BALTZER, AND M. TURTORA. 1997. Observations of tidal flux between a submersed aquatic plant stand and the adjacent channel in the Potomac River near Washington, D.C. *Limnology and Oceanography* 42:307–317.
- SAND-JENSEN, K. 1990. Epiphyte shading: Its role in resulting depth distribution of submersed aquatic macrophytes. *Folia Geobotanica et Phytotaxonomica* 25:315–320.
- SAND-JENSEN, K. AND J. BORUM. 1983. Regulation of growth of eelgrass (*Zostera marina* L.) in Danish coastal waters. *Marine Technology Society Journal* 17:15–21.
- SCHUBEL, J. R. AND R. B. BIGGS. 1969. Distribution of seagrass in upper Chesapeake Bay. *Chesapeake Science* 10:18–23.
- SCOFFIN, T. P. 1970. The trapping and binding of subtidal carbonate sediments by marine vegetation in Bimini Lagoon, Bahamas. *Journal of Sediment Petrology* 40:249–273.
- SCULTHORPE, C. D. 1967. *The Biology of Aquatic Vascular Plants*. Edward Arnold, Ltd., London, U.K.
- SHORT, F., D. BURDICK, J. WOLF, AND G. JONES. 1993. Eelgrass in estuarine research reserves along the East Coast, USA, Part I: Declines from pollution and disease, Part II: Management of eelgrass meadows. National Oceanic and Atmospheric Administration Coastal Ocean Program Publication, Durham, New Hampshire.
- SHORT, F. T. AND S. WYLLIE-EICHEVERRIA. 1996. Natural and human-induced disturbance of seagrasses. *Environmental Conservation* 23:17–27.
- STANKELIS, R., M. NAYLOR, AND W. R. BOYNTON. 2003. Submersed aquatic vegetation in the Patuxent River estuary past, present and future status. *Estuaries* 26:186–195.
- STAVER, K. 1984. Responses of epiphytic algae to nitrogen and phosphorus enrichment and effects on productivity of the host plant, *Potamogeton perfoliatus* L., in estuarine waters. M.S. Thesis, University of Maryland, College Park, Maryland.
- STEVENSON, J. C., L. W. STAVER, AND K. W. STAVER. 1993. Water quality associated with survival of submersed aquatic vegetation along an estuarine gradient. *Estuaries* 16:346–361.
- STEWART, R., D. MCFARLAND, D. WARD, S. MARTIN, AND J. W. BARKO. 1997. Flume study investigation of the direct impacts of navigation-generated waves on submersed aquatic macrophytes in the upper Mississippi River. ENV Report 1. U.S. Army Corps of Engineers, St. Paul, Minnesota.
- TOMASKO, D. A., C. J. DAWES, AND M. O. HALL. 1996. The effects of anthropogenic nutrient enrichment on turtle grass (*Thalassia testudinum*) in Sarasota Bay, Florida. *Estuaries* 19:448–456.
- TWILLEY, R. R., W. M. KEMP, K. W. STAVER, J. C. STEVENSON, AND W. R. BOYNTON. 1985. Nutrient enrichment of estuarine submersed vascular plant communities: I. Algal growth and effects on production of plants and associated communities. *Marine Ecology Progress Series* 23:179–191.
- VALDES-MURTHA, L. M. 1997. Analysis of critical habitat requirements for growth and restoration of submersed vascular plants in Delaware and Maryland coastal bays. M.S. Thesis, University of Delaware, Newark, Delaware.
- VAN DIJK, G. M. 1993. Dynamics and attenuation characteristics of periphyton upon artificial substratum under various light conditions and some additional observations on periphyton upon *Potamogeton pectinatus* L. *Hydrobiologia* 252:143–161.
- VANT, W. N., R. J. DAVIES-COLLEY, J. S. CLAYTON, AND B. J. COFFEY. 1986. Macrophyte depth limits in North Island (New Zealand) lakes of differing clarity. *Hydrobiologia* 137:55–60.
- VERMAAT, J. E., N. AGAWAN, M. FORTES, J. URI, C. DUARTE, N. MARBA, S. ENRIQUEZ, AND W. VAN VIERSSEN. 1996. The capacity of seagrasses to survive increased turbidity and siltation: The significance of growth form and light use. *Ambio* 25:499–504.
- VERMAAT, J. E. AND R. J. DE BRUYNE. 1993. Factors limiting the distribution of submersed waterplants in a lowland River Vecht (The Netherlands). *Freshwater Biology* 30:147–157.
- VERMAAT, J. E. AND M. J. M. HOOTSMANS. 1994. Periphyton dynamics in a temperature-light gradient, p. 193–212. In W. van Vierssen, M. Hootsmans, and J. Vermaat (eds.), *Lake Veluwe, A Macrophyte-Dominated System Under Eutrophication Stress*. Kluwer Academic Press, Dordrecht, The Netherlands.
- WALKER, D. I. AND A. J. MCCOMB. 1992. Seagrass degradation in Australian coastal waters. *Marine Pollution Bulletin* 25:5–8.
- WARD, L. G., W. M. KEMP, AND W. R. BOYNTON. 1984. The influence of water depth and submersed vascular plants on suspended particulates in a shallow estuarine embayment. *Marine Geology* 59:85–103.
- WERNER, I. AND G. WISE. 1982. Biomass production of submersed macrophytes in a selected stretch of the River Zschopau (South GDR) with special regard to orthophosphate incorporation. *Internationale Revue gestamen Hydrobiologie* 67:45–62.
- WESTLAKE, D. F. 1967. Some effects of low-velocity currents on the metabolism of aquatic macrophytes. *Journal of Experimental Botany* 18:187–205.
- WILCOX, D. J., M. C. HARWELL, AND R. J. ORTH. 2000. Modeling dynamic polygon objects in space and time: A new graph-based technique. *Cartography and Geographic Information Science* 27:153–164.
- ZIMMERMAN, R. C., J. REGUZZONI, S. WYLLIE-EICHEVERRIA, M. JOSSELYN, AND R. ALBERTE. 1991. Assessment of environmental suitability for growth of *Zostera marina* L. (eelgrass) in San Francisco Bay. *Aquatic Botany* 39:353–366.

SOURCES OF UNPUBLISHED MATERIALS

- BOYNTON, W., R. STANKELIS, F. ROHLAND, J. FRANK, L. MATTESON, N. BURGER, M. WEIR, AND J. HAGY. 1999. Ecosystem processes component of Chesapeake Bay water quality monitoring program. Report, University of Maryland, Chesapeake Biological Laboratory, Solomons, Maryland.
- CHESAPEAKE BAY PROGRAM. 1993. Guide to Using Chesapeake Bay Water Quality Monitoring Data. CBP/TRS 78/92. Chesapeake Bay Program Office, Annapolis, Maryland. (<http://www.chesapeakebay.net/data/index.htm>)
- CHESAPEAKE EXECUTIVE COUNCIL. 2000. Chesapeake 2000 Agreement. Chesapeake Executive Council, Annapolis, Maryland. ([website, http://www.chesapeakebay.net/pubs/](http://www.chesapeakebay.net/pubs/))
- CONOVER, J. T. 1964. Environmental relationships of benthos in salt ponds (plant relationships). Technical Report No. 3. University of Rhode Island, Graduate School of Oceanography, Narragansett, Rhode Island.
- STEVENSON, J. C. AND N. M. CONFER. 1978. Summary of available information on Chesapeake Bay submersed vegetation. OBS 78/66. U.S. Fish Wildlife Service/National Technical Information Service, Springfield, Virginia.

Received, September 17, 2002

Revised, July 14, 2003

Accepted, August 4, 2003