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# Beyond Light: Physical, Geological, and Geochemical Parameters as Possible Submersed Aquatic Vegetation Habitat Requirements

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**ABSTRACT:** When determining the suitability of a certain area as a habitat for submersed aquatic vegetation (SAV), light and parameters that modify light (epiphytes, total suspended solids, chlorophyll concentration, nutrients) are the first factors to be taken into consideration. As a result, in the past 10 years, light has been the major focus of SAV research. Even so, we are still unable to explain why SAV often occurs in one area but is absent just a few meters away. Recent studies have shown that SAV may not occur in areas where light levels are adequate but other parameters like wave energy and sulfide concentrations are excessive. It is time to look beyond light when determining SAV habitat requirements. This paper summarizes the impact that physical (waves, currents, tides, and turbulence), geological (sediment grain size and organic matter), and geochemical (mainly sulfide) parameters may have on SAV habitat suitability. Light remains an integral part of the discussion but the focus shifts from maximum depths of distribution (determined mainly by light) to the range SAV can colonize between the maximum and minimum depths of distribution (determined mainly by physical forces). This paper establishes minimum depths of occurrence resulting from the effects of tides and waves, preferred ranges in particle size, organic content, and sulfide, as well as limits on currents and waves as related to the capacity to stay rooted at one extreme and diffusive boundary layer constrains at the other.

## Introduction

Light has been identified as the major factor controlling the distribution and abundance of marine (seagrasses), estuarine, and freshwater flowering plants, also called submersed aquatic vegetation (SAV) (Giesen et al. 1990; Dennison et al. 1993; Bach et al. 1998; Hall et al. 1999). Therefore, biological and chemical parameters that alter light availability (epiphyte biomass, dissolved inorganic nitrogen and phosphorous, suspended chlorophyll concentration) are commonly listed as SAV habitat requirements (Batiuk et al. 1992; Hosper 1994). Physical, geological, and geochemical parameters that may also affect SAV distribution are usually not considered (Demas et al. 1996; Livingston et al. 1998; Robbins and Bell 2000; Touchette and Burkholder 2000a,b; van Katwijk and Hermus 2000). For example, high wave energy may prevent SAV from becoming established (due to the drag exerted on the plants and/or the constant shifting of sediment particles) even when the light requirements for SAV growth are met (Clarke 1987; Dan et al. 1998; Robbins and Bell 2000). A literature search (Aquatic Sciences and Fisheries Abstracts—ASFA) confirms this bias towards light-related research. In the last 10 years, 62% of the published seagrass papers focused on light and epiphytes while only 18% focused on hydrodynamic parameters, 17% on sediment characteristics, and 3% on seagrass geochemistry.

The objectives of this paper are to describe parameters other than light which may also be important SAV habitat requirements, to identify physical, geological, and geochemical parameters for which insufficient information is available to assess their importance as a possible SAV habitat requirement, and to suggest thresholds for physical, geological, and geochemical parameters in SAV habitats when sufficient data are available. Light will not be excluded from the discussion as physical, geological, and geochemical parameters in SAV habitats often affect light availability. Additionally, the response of SAV to these parameters often depends on light availability. For example, a SAV habitat characterized by sediments with high sulfide levels may not be as detrimental if sufficient light is available than if light levels are relatively low.

## SAV as an Ecosystem Engineer

As we begin to discuss physical, geological, and geochemical parameters as possible SAV habitat requirements, one needs to keep in mind that SAV beds alter the habitats they colonize and that feedback mechanisms between SAV and its habitat are common. As SAV beds reduce current velocity (Fonseca et al. 1982; Fonseca and Fisher 1986; Gambi et al. 1990; Koch 1993; Sand-Jensen and Mebus 1996; Rybicki et al. 1997; Koch and Gust 1999), attenuate wave energy (Fonseca and Cahal-

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an 1992; Koch 1996; Koch and Gust 1999), alter the sediment characteristics (Scoffin 1970; Wanless 1981; Almasi et al. 1987; Wigand et al. 1997), and change the height of the water column (Powell and Schaffner 1991; Rybicki et al. 1997), they can be viewed as ecosystem engineers (Jones et al. 1994). These SAV-induced changes in habitat characteristics then affect the entire plant community, from the smallest (bacteria) to the largest organisms (plants and animals) including the SAV. Due to this complex feedback between SAV and the habitat it colonizes, it is inappropriate to attribute the distribution of SAV to only one factor (usually light).

### SAV and Current Velocity

SAV beds reduce current velocity by extracting momentum from the moving water (Madsen and Warnke 1983). The magnitude of this process depends on the density of the SAV bed (Gambi et al. 1990; Carter et al. 1991; van Keulen 1997), the hydrodynamic conditions of the area (stronger reduction in tide-dominated versus wave-dominated areas; Koch and Gust 1999), as well as the depth of the water column above the plants (Fonseca et al. 1982). Currents in SAV beds can be 2 to 10 times slower than in adjacent unvegetated areas (Ackerman 1983; Madsen and Warnke 1983; Carter et al. 1988; Gambi et al. 1990; Rybicki et al. 1997). The advantages of reduced water flow in SAV meadows include: 1) reduced self-shading due to the more vertical position of the blades in the water resulting from reduced drag on SAV leaves (Fonseca et al. 1982); 2) lower friction velocities at the sediment surface within the vegetation than in unvegetated areas (Fonseca and Fisher 1986) reducing sediment resuspension and total suspended solids concentration and, therefore, increasing light availability (Kemp et al. 1984; references in Fonseca 1996); 3) increased settlement of organic and inorganic particles (Grady 1981; Kemp et al. 1984; Newell et al. 1986), increasing light availability (Moore et al. 1994), and sediment nutrient concentration (Kenworthy et al. 1982; Ward et al. 1984; references in Fonseca 1996); 4) high water residence-time, allowing molecules of dissolved nutrients to stay in contact with SAV leaves and epiphytes for longer periods of time, therefore increasing the likelihood of being taken up; as a result, reduced currents lead to reduced nutrient concentrations in the water column (Beundorf and Puetz 1987) perhaps limiting epiphytic growth which would otherwise lead to further reduction in light availability; and 5) increased settlement of spores of algae and larvae of a variety of organisms resulting in higher species diversity of invertebrates and algae in SAV canopies than in adjacent unvegetated areas (Homziak et al. 1982).

Reduced water flow can also have detrimental effects such as increased concentration of sulfide in marine/estuarine sediments colonized by SAV due to reduced porewater advection (Koch 1999) and increased accumulation of organic matter (Robblee et al. 1991). The concentration of phytotoxins in the sediment leads to an increase in oxygen demand by the roots which, if not met due to poor light availability, has the potential to kill the plants (Robblee et al. 1991; Carlson et al. 1994). Additionally, thicker blade diffusion boundary layers will form under reduced current velocity in SAV beds (Koch 1994). The diffusive boundary layer (DBL) is a thin (10s to 100s of µm) layer of water on the surface of any submersed object (including plants) where the transport of solutes (e.g., carbon needed for photosynthesis or oxygen produced by photosynthesis) is dominated by diffusion.

The thickness of this DBL increases with decreasing current velocities (like those found in SAV beds). That leads to a longer diffusional path (thick DBL) for carbon molecules to move from the water column to the SAV leaf, where they are used for photosynthesis. As the current velocity decreases, a critical DBL thickness, where the flux of carbon to the plant does not meet the requirement to support maximum photosynthesis, can be reached (Jones et al. 2000). The critical DBL thickness was estimated to be 98 µm for *Cymodocea nodosa* and 280 µm for *Thalassia testudinum* leaves without epiphytes (Koch 1994) and 950 µm for artificial leaves with epiphytes (Jones et al. 2000). Koch (1994) also suggested that seagrasses can acclimate to water flow (i.e., DBL thickness) but further studies are needed to test this hypothesis.

If a plant is exposed to DBL thicknesses greater than the critical DBL thickness (i.e., reduced current velocity or thick epiphytic layers) for long periods of time, the plant can die due to carbon limitation (Jones et al. 2000) independent of the light levels at the site. The length of time that a plant can survive under such conditions depends on the internal carbon reserves in the plant tissue and how fast these reserves can be accessed (Koch 1993). This has not yet been determined for most SAV species and has the potential to be important in areas where marinas and other structures that cause stagnant conditions in SAV habitats are constructed.

Some estuarine and freshwater SAV species like *Potamogeton pectinatus* are capable of colonizing relatively stagnant waters (like those found in ponds) due to a physiological adaptation: the release of $H^+$ on one side of the blade (polar leaves) which re-

TABLE 1. Summary of minimum and maximum current velocities required for SAV growth and occurrence.

| | Minimum Current Velocities Required to Saturate Photosynthesis | |
|---|---|---|
| Current (cm s$^{-1}$) | Species | Source |
| >0.04 | *Potamogeton pectinatus** | Madsen and Sondergaard (1983) |
| >0.08 | *Callitriche stagnalis* | Westlake (1967) |
| >0.5 | *Ranunculus pseudofluitans* | Westlake (1967) |
| >3 | *Zostera marina* | Koehl personal communication |
| >5 | *Ranunculus pencillatus* | Werner and Wise (1982) |
| >5 | *Thalassia testudinum* | Koch (1994) |
| >13 | *Cymodocea nodosa* | Koch (1994) |
| >16 | *Zostera marina* | Fonseca and Kenworthy (1987) |
| | Maximum Currents at Which the Following Species Occur | |
| Current (cm s$^{-1}$) | Species | Source |
| <7 | *Vallisneria americana* | Merrell (1996) |
| <45 | *Ranunculus pencillatus* | Werner and Wise (1982) |
| <50 | *Zannichellia palustris* | Sculthorpe (1967) |
| <50 | *Zostera marina* | Conover (1964) |
| <120 | *Zostera marina* | Scoffin (1970) |
| <150 | *Zostera marina* | Fonseca et al. (1982) |
| <180 | *Zostera marina* | Phillips (1974) |

* Species for which leaf polarity has been confirmed.

duces the pH in the DBL (Prins et al. 1982). This decrease in pH shifts the carbon balance towards $CO_2$, increasing local DBL $CO_2$ concentration and increasing the flux of $CO_2$ into the plant. Other SAV can also incorporate $CO_2$ from the porewater where dissolved inorganic carbon concentrations are usually much higher than open-water concentrations (Sondergaard and Sand-Jensen 1979; Madsen 1987). The $CO_2$ incorporated by the roots is then transported to the photosynthetic tissue via the lacunae system (Madsen and Sand-Jensen 1991).

Although epiphytes are usually seen as organisms that are detrimental to SAV growth (shading and competition for carbon and nutrients), the very early stages of epiphytic colonization on SAV leaves have the potential to be beneficial for the plants (Koch 1994). Very low densities of epiphytes protruding through the DBL may disrupt the DBL enhancing the flux of carbon to the blade (Koch 1994). As epiphytes compete for light, nutrients, and carbon, later stages of epiphytic colonization (when the flow skims over the epiphytic layer) become detrimental to SAV growth (Jones et al. 2000). At the community level, epiphytes will probably contribute to the reduction in current velocity (due to increased leaf drag; Verduin and Backhaus 2000) which leads to the positive aspects listed above. In some aspects, epiphytes can have positive effects on SAV communities, although the overwhelming negative effects of epiphytes on SAV leaves (light attenuation, reduced carbon availability, and increased drag potentially dislodging them at high flows) also need to be kept in perspective.

SAV and their epiphytes appear to respond to water flow independently from each other. In a study using acrylic plates, maximum epiphytic biomass was observed at intermediate current velocities. Diatoms were dominant under high current velocities while a green alga was dominant at lower current velocities (Horner et al. 1990). In a mesocosm experiment, epiphyte biomass on *Vallisneria americana* leaves increased with current velocity (Merrell 1996). These data suggest that a second order of complexity (water flow) needs to be added to models evaluating the effect of epiphytes on light availability to SAV leaves.

From the positive and negative effects of the reduced current velocities found in SAV beds, it can be concluded that these plants could benefit from intermediate current velocities (Boeger 1992; Merrell 1996; Koch 1999). A literature review (Table 1) revealed that the range of current velocities tolerated by marine angiosperms (seagrasses) lies between approximately 5 and 180 cm s$^{-1}$ (physiological and mechanical limits, respectively); the range of current velocities tolerated by freshwater angiosperms seems to be generally lower than that for the marine species; and some freshwater species can tolerate extremely low current velocities due to alternative mechanisms of carbon acquisition (polar leaves).

Survival of SAV in high current velocity environments may be possible if the development of seedlings occurred under conditions of slow current velocity in space (e.g., protected cove) or time (e.g., low water discharge period). Once a bed is established under such conditions it can expand into adjacent areas with higher currents (due to the reduced currents at the edge of the bed) or persist during times of higher water flow. Therefore, the life stage of the plants (seeds, seedlings,

TABLE 2. Attenuation of wave energy in seagrass beds (meadow formers).

| Attenuation | Wave Period (s) | Site | Seagrass | Comments | Source |
|---|---|---|---|---|---|
| 1.6% | 2.9 | field | *Thalassia* | within bed | Koch (1996) |
| 7.7% | 2.9 | field | *Thalassia* | edge | Koch (1996) |
| 43% | 0.4 and 0.7 | flume* | *Zostera* | 1 m bed | Fonseca and Cahalan (1992) |
| 43% | 0.4 and 0.7 | flume* | *Syringodium* | 1 m bed | Fonseca and Cahalan (1992) |
| 41% | 0.4 and 0.7 | flume* | *Halodule* | 1 m bed | Fonseca and Cahalan (1992) |
| 44% | 0.4 and 0.7 | flume* | *Thalassia* | 1 m bed | Fonseca and Cahalan (1992) |
| $6.25\ J\ m^{-2}$ | 15 | field | *Amphibolis* | $100\ m^2$ bed | Verduin and Backhaus (2000) |

* Plants occupied the entire water column.

vegetative shoots, reproductive shoots) needs to be taken into account when determining current velocity requirements for SAV. No data are available on the current velocity requirements of plants other than those found in well-established beds.

In summary, intermediate current velocities (possibly between 5 and 100 $cm\ s^{-1}$) are needed to support the growth and distribution of healthy seagrass beds. These requirements are lower for freshwater/estuarine species (possibly between 0 and 50 $cm\ s^{-1}$), especially for those with polar leaves. If currents are above or below these critical levels, the feedback mechanisms in the system may become imbalanced and possibly lead to the decline or even complete loss of the vegetation. Although some of the feedback mechanisms between SAV beds and current velocity involve light availability (resuspension of sediments, self-shading, and epiphytic growth), extreme currents alone can limit the growth of SAV (Dan et al. 1998; van Katwijk and Hermus 2000). Current velocity should be evaluated as a possible SAV habitat requirement but extensive work is still needed.

## SAV and Waves

As waves propagate over SAV beds, wave energy is lost (Fonseca and Cahalan 1992; Koch 1996; Verduin and Backhaus 2000). This is due to the same mechanism that causes SAV beds to reduce current velocities: loss of momentum (Kobayashi et al. 1993). The efficiency with which waves are attenuated by SAV beds depends on the water depth (Ward et al. 1984; Mork 1996), the current velocity (Stewart et al. 1997), the leaf length (Fonseca and Cahalan 1992), and the type of vegetation (canopy or meadow; Elwany et al. 1995; Mork 1996; Stewart et al. 1997; Verduin and Backhaus 2000).

Wave attenuation is strongest in dense SAV meadows (where most of the biomass is found close to the sediment surface; like *Zostera, Thalassia, Halodule,* and *Vallisneria*) colonizing shallow waters, where plant biomass takes up a large portion of the water column. Canopies which have long stems and concentrate most of their biomass, and consequently drag, near the water surface (like *Hydrilla, Myriophyllum,* and *Potamogeton perfoliatus*), have the tendency to oscillate with the waves. Acting as though imbedded in the water column, the canopy-forming species probably impose less drag on the waves than meadows and, therefore, have less impact on wave attenuation, especially when waves are relatively long (low frequency). Further studies are needed to determine if this process observed in kelp beds (Seymour 1996) also applies to SAV canopies.

Table 2 summarizes the capacity of seagrasses to attenuate waves under a variety of field and laboratory conditions. The values obtained in the lab are much higher than those obtained in the field, probably because the meadow-forming plants used in the lab experiments occupied the entire water column, and wave attenuation is positively correlated with the percentage of the water column occupied by the vegetation.

SAV growth and distribution seem to be limited by high (but not low) wave energy (Dan et al. 1998; Robbins and Bell 2000; van Katwijk and Hermus 2000; Table 3), although high wave exposure can

TABLE 3. Quantitative and qualitative wave tolerance of some SAV species.

| | | |
|---|---|---|
| Canopy formers | | |
| *Myriophyllum spicatum* | wave limited | Rawls (1975); Stewart et al. (1997) |
| *Zannichellia palustris* | wave limited | Stevenson and Confer (1978) |
| Flowering structures of *Ruppia maritima* | wave sensitive | Joanen and Glasgow (1965) |
| Meadow formers | | |
| *Zostera marina* | 2 m waves | Dan et al. (1998) |
| *Potamogeton pectinatus* | wave tolerant | Hannan (1967) |
| *Vallisneria americana* | more wave tolerant than *Myriophyllum* | Stewart et al. (1997) |

also be beneficial to the plants by reducing the epiphytic biomass (Strand and Weisner 1996; Kendrick and Burt 1997; Weisner et al. 1997) and reducing self-shading through blade flapping. The mechanism that allows for reduced epiphytic biomass on plants exposed to high wave energy is not well understood. It could be due to the rubbing of the blades against each other.

The impact of waves on SAV can be direct or indirect. The direct impact of waves on SAV can be seen when waves (in combination with currents) erode the edges of an SAV bed (Clarke 1987), when the landscape heterogeneity of seagrass beds is altered due to wave action (Robbins and Bell 2000), or when portions of the plants are removed by storm-generated (Thomas et al. 1961; Eleuterius and Miller 1976; Rodriguez et al. 1994; Dan et al. 1998) or boat-generated waves (Stewart et al. 1997). The aboveground biomass of *P. pectinatus* was observed to depend directly on wave exposure; shoots were shorter in areas with high wave exposure than in areas with low wave exposure (Idestam-Almquist and Kautsky 1995). Wave exposure may not only affect plant morphology (acclimation to drag) but may also lead to the breakage of the plants (Idestam-Almquist and Kautsky 1995; Stewart et al. 1997). This effect has been observed to be more severe for a canopy-forming species (*Myriophyllum* spp.) than for a meadow-forming species (*Vallisneria* spp.; Stewart et al. 1997). Breakage of underwater plants exposed to waves is inversely related to current velocity. As current velocity increases, the plants lie closer to the sediment surface and are less affected by the orbital motion of the waves (Stewart et al. 1997). In areas of high wave exposure, sediments are coarser which leads to lower nutrient concentration in the sediment. Belowground biomass has been found to be reduced (makes the plants more vulnerable to waves; Idestam-Almquist and Kautsky 1995) as well as increased (allows plants to obtain more nutrients; Short 1983; Onuf 1996) in areas with coarse sediments. The reason for this inconsistency is not clear.

Indirect impacts of waves on SAV beds include sediment resuspension, changes in sediment grain size, mixing of the water column, and epiphytic growth. If the capacity of an SAV bed to attenuate waves is reduced due to a reduction of shoot density or an increase in water depth (tides, storm surges), the underlying sediment will become more vulnerable to erosion and higher concentrations of suspended sediment particles (and lower light availability) can be expected in the water. This is especially true for SAV beds in which fine particles have accumulated over time. These sediments may be resuspended at lower wave energy than the coarser sediments outside the SAV bed (Posey et al. 1993).

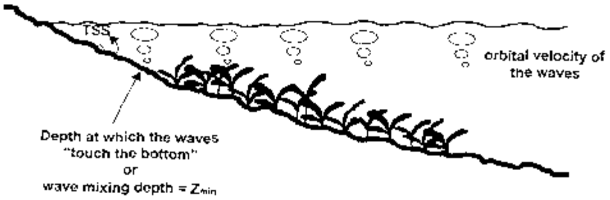

Fig. 1. SAV beds can be forced into deeper waters due to wave exposure. Waves reaching the shoreline (and "touching the bottom") can constantly shift sediments not allowing for the establishment of SAV. Waves also continuously resuspend sediments increasing the concentration of total suspended solids which leads to reduced light availability. According to Chambers (1987), the zone where waves do not allow SAV colonization is defined as the depth equivalent to half the wavelength and is represented as the minimum depth of distribution ($Z_{min}$).

Due to their capacity to attenuate waves, the worldwide decline of SAV (Dennison et al. 1993; Fletcher and Fletcher 1995; Short and Wyllie-Echeverria 1996; Short and Neckles 1999) may be leading to higher wave energy reaching the shorelines (Christiansen et al. 1981). As a result, an increase in shoreline erosion is expected. In Chesapeake Bay, before the major loss of SAV in the 1970s, shore erosion (caused by wave action) was estimated to contribute 13% of the total suspended matter in the upper bay and 52% in the mid bay (Biggs 1970). After the massive loss of SAV (Orth 1976), shoreline erosion probably increased even further but no revised estimates are available for comparison.

The distribution of SAV in lakes with good water quality has been correlated with the wave-resuspended sediments (Fig. 1). As wind intensifies, wave period and wave length increase, and wave mixing becomes deeper. Chambers (1987) suggested that the minimum depth of distribution ($Z_{min}$) of lake plants can be determined by the wave mixing depth ($Z_{wave}$) which extends to a depth equal to half the wavelength (L).

$$Z_{min} = Z_{wave} = \frac{L}{2} \qquad (1)$$

where L can be calculated from the wave period (T) using Eq. 2:

$$L = \frac{gT^2}{2\pi} \qquad (2)$$

where g is acceleration of gravity ($9.805 \text{ m s}^{-2}$). This is a standard equation for waves propagating over depths larger than half the wavelength (i.e., before waves "feel the bottom" and define $Z_{min}$). The wave period (T) for these deep-water waves can be predicted according to Eq. 3:

$$T = \left[\frac{0.46W}{g}\right]\left[\frac{gF}{W^2}\right]^{0.28} \tag{3}$$

where W is the wind velocity (m $s^{-1}$) and F is the fetch (m).

The above equations are appropriate for lakes and other SAV habitats with relatively deep waters (depth > L/2) and/or with steep slopes. It becomes much more difficult to predict $Z_{wave}$ and $Z_{min}$ when the SAV habitat is shallow and/or has extensive gentle slopes. Under such conditions waves are being generated (wind) at the same time they are being dissipated (bottom and vegetation) (Young and Verhagen 1996). No model exists that can predict the wave climate in shallow (< 1 m) vegetated areas.

The minimum depth of distribution of aquatic plants is also a function of light availability and tidal amplitude. As eutrophication increases and light availability decreases, SAV populations are forced into shallower waters (Arnold et al. 2000) where they are more susceptible to desiccation and wave exposure. Due to the lack of resistance of most SAV species to desiccation, tides tend to force SAV to colonize deeper waters (where exposure to the air is less likely). If waves also force the SAV to inhabit deeper waters (due to sediment resuspension in areas shallower than the wave mixing depth; see Fig. 1), then the minimum depth of distribution of SAV beds should be determined by the mean low water (tide) plus the wave mixing depth. This can be visualized by imagining the water level in Fig. 1 fluctuating up and down with the tides as the waves continue to propagate onshore. No data are available to verify this hypothesis.

Although waves have the potential to force SAV to colonize deeper areas (Fig. 1) and tides may further restrict this minimum depth of colonization, it may be difficult to establish a wave exposure habitat requirement especially in shallow vegetated areas with gentle slopes. Wave exposure indexes (based on fetch and wind intensity) have been successfully used to predict SAV distribution in lakes (i.e., habitat with steep slopes; Keddy 1982; Chambers 1987) as well as in an estuarine area (Murphey and Fonseca 1995; Fonseca and Bell 1998). A similar attempt failed in the Chesapeake Bay possibly due to the extensive shallow areas with gentle slopes (waves are being generated and dissipated at the same time), local bathymetry (shoals, sandbars), wave refraction, and different sampling and modeling scales (Chiscano 2000). Further research is needed to better understand waves in shallow SAV habitats as well as the effect of waves on the ecology and distribution of SAV beds.

## SAV and Turbulence

Turbulence consists of temporally and spatially irregular water motion superimposed on the larger flow pattern. It forms at boundaries like the sediment surface or the surface of SAV leaves. Production of turbulence within the vegetation is dominated by the plant wake rather than by the bottom-boundary shear, as in open channel flows (Nepf et al. 1997). Turbulence is then transferred from larger to smaller scales (eddy sizes). The distance between plant structures (shoots, leaves, flowers) determines the size of the turbulence scale/eddies (Anderson and Charters 1982; Nowel and Jumars 1984; Ackerman and Okubo 1993; Nepf 1999). Epiphytes colonizing seagrass blades can also affect turbulence by decreasing the distance between obstructions to the flow (like blades and shoots) (Koch 1994, 1996). Turbulence in these plant communities is not only generated but also rescaled (shifting the scale of the eddies formed in a seagrass bed; Anderson and Charters 1982; Gambi et al. 1990; Ackerman and Okubo 1993; Koch 1996; Nepf 1999) perhaps creating mixing lengths of biological importance. Since mass transfer of nutrients and carbon in turbulent flows takes place by eddy diffusion (Sanford 1997), turbulence has the potential to be of extreme ecological importance in SAV beds (Nepf et al. 1997; Nepf 1999). Turbulence also has the potential to affect the dispersion of particles such as pollen, larvae, seeds, and spores in the SAV beds (Ackerman 1997), but the effect of turbulence on these plants is poorly understood.

Although the observations of turbulence in SAV beds may seem contradictory, there is consensus that a region of high turbulence levels can be observed at the canopy-water interface (Gambi et al. 1990; Dunn et al. 1996; Koch and Gust 1999). The contradictions come from measurements made within the vegetation. Decreased as well as increased turbulence within the vegetation have been reported (Ackerman and Okubo 1993; Worcester 1995; Dunn et al. 1996; Grizzle et al. 1996). This difference in results may be linked to the flow characteristics (wave × tide-dominated flows) and the structure of the SAV bed (Koch and Gust 1999). Turbulence is strongly related to the product of water depth and plant density (Dunn et al. 1996), as well as current velocities. As the current velocity increases, turbulence levels also increase until the point where the vegetation begins to bend over due to the current velocity. Under these conditions, water flow is redirected over the vegetation (skimming flows) and turbulence levels among the plants may decrease again (Nepf 1999).

Since mass transport of nutrients and carbon in

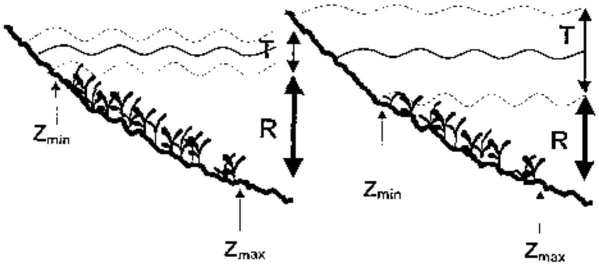

Fig. 2. The minimum depth of distribution of SAV can be shifted into deeper waters due to the tidal range (T). The minimum depth of distribution ($Z_{\min}$) is limited by the low tide while the maximum depth of distribution ($Z_{\max}$) is limited by light availability. As a result, the SAV range (R) between the maximum and minimum depths of distribution decreases as tidal range increases (assuming equal light availability).

SAV beds depends on turbulence levels, it can be predicted that SAV can benefit from turbulence in the water. The optimal turbulence levels for SAV is yet unknown but it is interesting to note that most SAV beds tend to occur in areas where flow is characterized by the laminar-turbulent transition (Ackerman 1998). Although advances have been made in our understanding of turbulence in vegetated areas, until the significance of turbulence in SAV beds is better understood, few predictions regarding the importance of turbulence for the health and distribution of SAV can be made.

### SAV and Tides

Most SAV species are not tolerant of desiccation and can not grow in the intertidal zone. Only small seagrass species in intertidal pools (like plants from the genus *Halophila*) and beds that retain water between their leaves when exposed at low tide, can colonize the intertidal area. These are the exceptions. Most species of SAV are found in subtidal areas. Plants colonizing the intertidal area in temperate zones may not only dry out but are also often removed by shifting ice during the winter. The minimum depth of distribution of most SAV species is limited to the mean low water level (Fig. 2). Since waves may also limit the minimum depth of SAV, tides and waves need to be considered as confounding factors when analyzing the vertical distribution of SAV. As waves and tides co-occur in many SAV habitats, the wave mixing depth will constantly change. Theoretically, the minimum depth of distribution should be at a depth below the mean low water (MLW) line: the MLW level plus the wave mixing depth.

Based on tides alone, the minimum depth of distribution can be defined as half the tidal amplitude (A in m) below mean tidal level (MTL). In areas with diurnal tidal cycles, this will be [MHW-MLW]/2 while in areas with semi-diurnal tides it will be [MHHW-MLLW]/2 (MHW = mean high water, MHHW = mean high high water, MLLW = mean low low water). The calculations of Chambers (1987) to predict the minimum depth of SAV distribution ($Z_{\min}$) in lakes (based on the wave mixing depth) could be altered to also include the effect of tides:

$$Z_{\min} = \frac{A}{2} + \frac{\frac{gT^2}{2\pi}}{2} \tag{4}$$

where the first term of Eq. 4 refers to the tidal amplitude and the second term to the wave mixing depth. This equation suggests that in areas of high tidal amplitude and high wave exposure, SAV will be forced to colonize relatively deep waters. Their success in colonizing such areas will depend on their maximum depth of distribution.

The maximum depth of distribution ($Z_{\max}$) of SAV depends on the light attenuation in the water column ($K_d$) as well as on the water depth (which is a function of tides). Tides and $Z_{\max}$ are confounding factors (Carter and Rybicki 1990; Koch and Beer 1996). In areas with high tidal amplitude, the $Z_{\min}$ is forced into deeper areas due to desiccation and freezing (Fig. 2) and the $Z_{\max}$ is forced into shallower areas due to lower light availability (i.e., at high tide there is more water to attenuate light). The vertical distribution of the SAV bed is limited by the upper (determined by tides and waves) and lower (determined by light penetration) depths of distribution (Fig. 2).

The maximum depth of distribution ($Z_{\max}$) can be calculated based on the Lambert-Beer equation:

$$Z_{\max} = \frac{-\ln\left(\frac{I_z}{I_o}\right)}{K_d} \tag{5}$$

where $I_z/I_o$ is the percentage light required by the species under consideration or the percentage light at the maximum depth of distribution of the plants and $K_d$ is the light attenuation coefficient. From Eq. 5, it is evident that, as $K_d$ increases, the maximum depth of distribution becomes shallower further restricting the vertical distribution of the plants. No SAV species can survive if $Z_{\max} \leq Z_{\min}$. This shifts the focus from considering how deep SAV can grow ($Z_{\max}$) to how narrow their depth of distribution ($Z_{\max} - Z_{\min}$) or vertical range can be in order to sustain healthy beds. For *Zostera marina* to successfully colonize an area in Long Island Sound, Koch and Beer (1996) found that: $Z_{\max} \geq Z_{\min} + 1$ m was a necessary condition for the existence of this seagrass. This 1 m vertical range below $Z_{min}$ seems to be necessary as a buffer when, during storm events, the shallower portion of the SAV bed is exposed to air, rain, or ice. The deeper portions of this bed can provide the necessary energy (via translocation in the rhizomes) to allow the shallower portion of the bed to recover from the stress of exposure (Koch and Beer 1996).

The management implication of not only considering the maximum depth of distribution for SAV but the vertical depth range that they can colonize is that, in areas with high tidal ranges, light requirements need to be more stringent than in areas with small tidal ranges. If the tidal range is large (i.e., $Z_{min}$ is relatively deep) and the light availability is low (i.e., $Z_{max}$ is relatively shallow), SAV may be restricted to such a narrow vertical range that their long-term survival is not viable (Koch and Beer 1996). Sea-level rise also has the potential to affect $Z_{min}$ (Arnold et al. 2000).

When SAV light requirements are calculated based on the Lambert-Beer equation the water level is assumed to be at MTL or MLW (Batiuk et al. 1992). When MLW is used, $Z_{max}$ is over-estimated and water quality necessary to allow SAV to grow to a certain depth is underestimated. By including half the tidal amplitude (A/2) in the Lambert-Beer equation, this error can be minimized:

$$K_d = \frac{-\ln\left(\frac{I_z}{I_o}\right)}{Z + \frac{A}{2}} \qquad (6)$$

Based on Eq. 6, Fig. 3 shows how $K_d$ in combination with tidal range and depth can be used to predict the potential vertical distribution of SAV in an area. For example, in Fig. 3, a tidal range of 0.8 m (see x-axis), a light requirement of 14% ($I_z/I_o$), and a $K_d = 1.5\ m^{-1}$ are assumed. A line is drawn vertically from the 0.8-m tidal range. The depth at which it intersects the diagonal line determines $Z_{min}$ (half the tidal range) while $Z_{max}$ is calculated based on the selected $K_d$ value. In this case, SAV has the potential to grow in a 0.9-m range between 0.4 and 1.3 m in depth (vertical bar in Fig. 3). For simplicity, no waves were included in this example.

In summary, tidal amplitude and $K_d$ have a strong confounding effect on the distribution of SAV. This has been conclusively demonstrated in the literature and simple equations exist to predict the SAV distribution based on the interaction of tides and $K_d$ (Koch and Beer 1996). In order to incorporate tidal amplitude as an SAV habitat requirement, it is necessary to determine $Z_{min}$ as well as the minimum vertical range of distribution for the species in question.

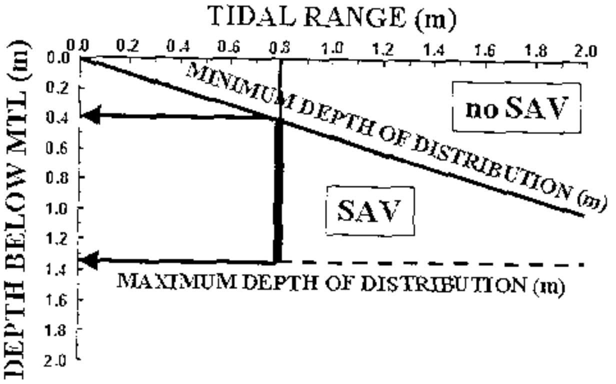

Fig. 3. An example of how the vertical distribution of SAV ($Z_{max}$—$Z_{min}$) can be predicted. A tidal amplitude of 0.8 m (see x-axis), a light requirement of 14% and a $K_d = 1.5\ m^{-1}$ are assumed. $Z_{max}$ is determined by using the Lambert-Beer equation (depth is the only unknown). $Z_{min}$ is determined by plotting a diagonal line passing through the origin and half the tidal range. A line is then drawn vertically from the 0.8-m tidal range. The depth at which it intersects the diagonal line determines $Z_{min}$. In this case, SAV has the potential to grow in a 0.9-m fringe between 0.4 and 1.3 m depth.

## SAV and the Sediment They Colonize

Sediments are important in determining the growth, morphology, and distribution of SAV (Short 1987; Demas et al. 1996; Livingston et al. 1998; Touchette and Burkholder 2000a) due to erosional/depositional processes as well as the availability of nutrients and phytotoxins (Marba and Duarte 1994; Dan et al. 1998; Koch 1999; Robbins and Bell 2000). Extreme events causing massive erosion/deposition of sediments can form gaps in the vegetation (Bell et al. 1999) or cause the death of entire SAV populations. For example, the sediment underlying an SAV bed in Florida was completely eroded away and redeposited elsewhere (Hine et al. 1987). The massive destabilization of this population may have been caused by heavy grazing of the plants. At the other extreme, high sedimentation rates can also be responsible for the decline of SAV populations. Moderate depositional rates can stimulate the growth of *T. testudinum* (Gallegos et al. 1993) and *C. nodosa* (Marba and Duarte 1994), but high depositional rates can lead to the disappearance of these plants. Since seedlings are more susceptible to high burial rates than established SAV beds (Marba and Duarte 1994), the season of depositional events is important in determining the chances of survival of SAV beds. The deposition of more than 10 cm of sediment on top of *Vallisneria* tubers reduced their chances of becoming mature plants and establishing a meadow (Rybicki and Carter 1986). Such high depositional rates can occur during severe storms. In contrast, *Z. marina* seeds need to be buried at least 0.5 cm, where conditions are anoxic, to promote germination (Moore et al. 1993).

During less extreme conditions, SAV can modify the characteristics of the sediment it colonizes by reducing current velocity and attenuating waves within their beds (see the review by Fonseca 1996). This leads to the deposition of small inorganic and light organic particles. The suitability of fine sediments and sediments with high organic content for SAV growth are addressed below.

### GRAIN SIZE DISTRIBUTION

Sediments within SAV beds are finer than those in adjacent unvegetated areas (Scoffin 1970; Wanless 1981; Almasi et al. 1987). As grain size distribution becomes skewed towards silt and clay, the porewater exchange with the overlaying water column decreases (Huettel and Gust 1992; Huettel and Rusch 2000). This may result in increased nutrient concentrations (Kenworthy et al. 1982) and phytotoxins such as sulfide in marine sediments (Holmer and Nielsen 1997). At the other extreme, if SAV colonizes coarse sand, the exchange of porewater with the overlaying water column will be higher than in finer sediments (Huettel and Gust 1992; Huettel and Rusch 2000) and nutrient availability in the sediment may be lower than that in finer sediments (Idestam-Almquist and Kautsky 1995).

In an experiment using different grain sizes of glass particles (to avoid adsorbed nutrients), *Ruppia maritima* was found capable of colonizing noncohesive sediments from a silt/clay mixture to coarse sand. Maximum growth was observed in fine and medium sand particles (Seeliger and Koch unpublished data).

Table 4 lists quantitative and qualitative data on silt and clay found in healthy SAV beds. The values range from 0.4% to 72%. The highest values seem to be associated with beds in lower salinity environments with the exception of a *Zostera muelleri* bed. Perhaps, in such environments, the plants are able to colonize sediment with reduced porewater exchange with the water column because sulfide does not occur at the same levels as in marine/estuarine systems. In higher salinity environments, it appears that plants need sediments which are more oxygenated (coarser) and in which sulfide levels can be reduced via higher porewater advection rates. SAV growth may be limited by the physical and geochemical processes associated with a certain sediment type (Barko and Smart 1986) and not by the grain size per se.

### SEDIMENT ORGANIC CONTENT

Due to the reduction in current velocity and wave energy, SAV beds tend to accumulate organic particles. Organic matter can also be accumulated in SAV-colonized sediments through the burial of rhizomes and roots produced over time. The age of the organic deposits beneath a *Posidonia oceanica* bed was found to be up to 3,370 years old (Mateo et al. 1997). High burial rates and/or low decomposition rates may account for the accumulation of organic matter over such long periods.

Barko and Smart (1983) suggested that the growth of SAV is limited to sediments containing less than 5% organic matter. This is also supported by the data summarized in Table 5 where the majority of the values were lower than 5%. The mechanism behind this limitation of high organic content on SAV growth is not well understood. It may be due to nutrient limitation in very fine sediments associated with high organic deposits (Barko and Smart 1986) or due to high sulfide concentrations in marine sediments, known to be toxic to seagrasses (Carlson et al. 1994; Goodman et al. 1995).

The data in Table 5 lists organic contents of less than 16.4% for SAV colonized sediments. The higher values (6.5% to 16.4%) are mostly associated with seagrasses that have large leaves. Perhaps these plants can colonize sediments with high organic content due to large oxygen production in the leaves and, consequently, also higher transport of oxygen to the roots. If the rhizosphere is well oxygenated, the detrimental effects associated with high organic content in the sediments may be neutralized (Lee and Dunton 2000). The distribution of *Potamogeton* spp. in English Lakes (Pearsall 1920; summarized in Hutchinson 1975) was directly correlated with sediment organic content (X) and minimum light requirement (Y) where $Y = 0.70 + 0.65\ X$ ($r^2 = 0.90$). Plants growing in more organic sediments with higher concentrations of phytotoxic metabolites seem to require more light to support greater release of oxygen from their roots to the rhizosphere. This mechanism has been used to explain the decline in abundance of SAV populations in eutrophic regions which have experienced an increase in sediment organic content (Nienhus 1983).

Due to the large number of studies that observe the percent organic matter in healthy SAV beds to be below 5%, it is recommended that caution should be taken when transplanting SAV into areas where the sediment organic content is higher than that value. Additional studies are needed to fine-tune the SAV habitat requirement for organic matter for different SAV species.

## SAV and Sediment Geochemistry

Nutrients in the sediment can be limiting to the growth of SAV (Short 1987; Rattray et al. 1991; Agawin et al. 1996; Touchette and Burkholder

TABLE 4. Percent silt + clay (<63 μm) or sediment type found in healthy seagrass/SAV beds (arranged in ascending order of maximum percentage of fine sediments).

| % Fines/Sediment Type | Species | Source |
|---|---|---|
| 1.9 | *S. filiforme* | Wood et al. (1969) |
| 4.8 | *T. testudinum* | Wood et al. (1969) |
| 0.4–9.0 | *P. oceanica* | Edgar and Shaw (1995) |
| 1.8–9.2 | *T. testudinum, S. filiforme, H. wrightii* | Livingston et al. (1998) |
| 7.3–9.9 | *S. filiforme* | Hoskin (1983) |
| 6–10 | Chesapeake Bay SAV | Batiuk et al. (1992) |
| 10.2–12.4 | *H. wrightii* | Hoskin (1983) |
| 14 | *Z. marina* | Marshall and Lukas (1970) |
| 11–14 | *R. maritima* | Dunton (1990) |
| 14 | *H. wrightii* | Dunton (1994) |
| 14.6 | *T. testudinum* | Scoffin (1970) |
| 0.8–14.7 | *Thalassia* and *Halodule* | Grady (1981) |
| 15 | *Z. marina* | Orth (1977) |
| 2.2–17.1 | *T. testudinum* | this study |
| 22 | *H. wrightii* | Dunton (1990) |
| 22 | *T. testudinum* | Lee and Dunton (1996) |
| 8.1–28.8 | *Halodule* and *Zostera* | Murphey and Fonseca (1995) |
| 2.8–30.9 | *H. tasmanica* | Edgar and Shaw (1995) |
| 1–34 | *T. testudinum* | Burrell and Schubel (1977) |
| 12.2–34.1 | *T. testudinum* | Hoskin (1983) |
| 23–35 | *T. testudinum* | Kaldy and Dunton (2000) |
| 2–39% clay | Tidal Potomac River SAV | Carter et al. (1985) |
| 40 | *Hydrilla* and *Vallisneria* | Posey et al. (1993) |
| 2.3–56.3 | *Z. marina* | this study |
| 58 | *H. verticillata* | Posey et al. (1993) |
| 4–62% silt | Tidal Potomac River SAV | Carter et al. (1985) |
| 48% silt and 14% clay | *V. americana* | Hutchinson (1975) |
| 0.5–72 | *Z. muelleri* | Edgar and Shaw (1995) |
| silt loving | *P. pectinatus* | Sculthrope (1967), Haslam (1978) |
| silty substrate | *P. perfoliatus* | Haslam (1978) |
| silty substrate | *S. sagittifolia* | Haslam (1978) |
| mud | *C. demersus* | Hutchinson (1975) |
| organic ooze | *M. spicatum* | Patten (1956) |
| soft or sandy mud | *M. spicatum* | Springer (1959) |
| muds or sand | *R. maritima* | Anderson (1972) |
| clay and sand | *Z. palustris* | Stevenson and Confer (1978) |
| medium grained substrate | *M. spicatum* | Haslam (1978) |
| medium grained substrate | *Ranunculus* | Haslam (1978) |
| sandy | *N. guadalupenses* | Martin and Uhler (1939) |

2000a) but do not seem to prevent the plants from colonizing certain areas. In marine siliceous sediments, nitrogen may be limiting to seagrass growth (Short 1987; Alcoverro et al. 1997) while in freshwater sediments, as well as in marine carbonate sediments, phosphorus may be limiting to SAV growth (Rattray et al. 1991; Wigand and Stevenson 1994). Potassium has also been suggested to be limiting to freshwater macrophytes (Anderson and Kalf 1988). Mycorrhizae can facilitate the phosphorus assimilation in the freshwater angiosperm, *V. americana* (Wigand and Stevenson 1994) although no mycorrhizae have been found associated with two seagrasses, *Z. marina* and *T. testudinum* (Nielsen et al. 1999). The lack of mycorrhizae on seagrasses may be due to the low oxygen levels in marine sediments as well as the high salinities.

Although light seems to be more limiting to SAV growth than sediment nutrient concentrations, exceptions can be found. In tropical seagrass beds, light and temperature were found to be limiting in the winter while nutrients were limiting in the summer (Alcoverro et al. 1997). Ammonium concentrations as low as 25 μM (in the seawater) can be toxic to *Z. marina* and ultimately lead to its decimation (van Katwijk et al. 1997). See Touchette and Burkholder (2000a) for an extensive review of nitrogen and phosphorous metabolism in seagrasses.

A wide variety of potentially phytotoxic substances are produced by bacterial metabolism in anaerobic sediments, including phenols and organic acids, reduced iron and manganese, and hydrogen sulfide (Yoshida 1975; Gambrell and Patrick 1978). In many aquatic environments, sulfide probably constitutes the most important of these toxic bac-

TABLE 5. Sediment organic matter (% of dry weight) in healthy seagrass/SAV beds (arranged in ascending order of maximum percentage of organic matter).

| Percent Organics | Species | Source |
|---|---|---|
| 1.25 | *Z. marina* | Marshall and Lucas (1970) |
| 1.25 | *Z. marina* | Orth (1977) |
| 0.41–1.38 | *Z. marina* | Dan et al. (1998) |
| 1.7 | *Z. marina* | this study |
| 0.5–2.3 | *T. testudinum* | this study |
| <2 | *R. maritima* | Ward et al. (1984) |
| 2.5 | *S. filiforme* | Wood et al. (1969) |
| 3.25 | *R. maritima* | Kemp et al. (1984) |
| 0.77–3.62 | *Halodule* and *Zostera* | Murphey and Fonseca (1995) |
| 3.5–4.9 | *T. testudinum* | Wood et al. (1969) |
| 0.4–5.3 | *Z. marina* | this study |
| <5 | *Hydrilla* and *P. nodosus* | Barko and Smart (1983) |
| 1–5.3 | Chesapeake Bay SAV | Batiuk et al. (1992) |
| 2.6–5.3 | *H. tasmanica* | Edgar and Shaw (1995) |
| 6.37 | *Z. marina* | Short et al. (1993) |
| <6.5 | *V. americana* | Hutchinson (1975) |
| 6.8 | *Z. marina* | Short et al. (1993) |
| 0.8–7.3 | *Z. muelleri* | Edgar and Shaw (1995) |
| 7.57 | *Z. marina* | Short et al. (1993) |
| 1.6–12 | *Posidonia* spp. | Edgar and Shaw (1995) |
| 11.6 | *Z. marina* | this study |
| 16.41 | *Z. marina* | Short et al. (1993) |
| <26 mg C g$^{-1}$ | *P. pectinatus* | van Wijck et al. (1992) |

terial metabolites and has been shown to be toxic to estuarine and marine SAV species (van Wijck et al. 1992; Carlson et al. 1994).

Sulfide is generated by sulfate reducing bacteria during organic carbon oxidation and nutrient remineralization in anoxic sediments (Howarth 1984; Pollard and Moriarty 1991). A high remineralization rate leads to high nutrient availability and favors plant growth but can also lead to the accumulation of sulfide which is detrimental to plant growth. Sulfate remineralization depends on the temperature and amount of organic matter in the sediment. In freshwater sediments, sulfate reduction is less important than methanogenesis due to the lower sulfate availability. As SAV tend to accumulate more organic and inorganic particles than unvegetated areas, sulfate reduction rates can be expected to be higher within the vegetation than outside it (Isaksen and Finster 1996; Holmer and Nielsen 1997; Lee and Dunton 2000). This difference could also be due to the excretion of organic compounds through the roots (Blackburn et al. 1994).

The toxicity of sulfide to plants can be further enhanced by eutrophication. Oxygen released from seagrass roots is needed to oxidize the sulfide and reduce its toxic effects (Armstrong 1978). The release of oxygen by the roots depends on the photosynthetic rates of the plant (Lee and Dunton 2000). If eutrophication leads to a reduction in light availability, photosynthetic rates will be lower, the amount of oxygen released from the roots will be reduced, and sulfide toxicity may be enhanced (Goodman et al. 1995; Lee and Dunton 2000).

Sulfide in the sediment is an important SAV habitat determinant, especially in marine/estuarine sediments (Table 6). Correlations between porewater sulfide concentrations and growth of several seagrass species have indicated that concentrations above 1 mM may be toxic (Pregnall et al. 1984; Smith et al. 1988; Pulich 1989; Carlson et al. 1994). Direct manipulations of sulfide concentrations revealed a negative effect on photosynthesis (Goodman et al. 1995) and growth (Kuhn 1992) when levels were higher than 1 to 2 mM. Sulfide thresholds for different SAV species (in combination with different light levels) still need to be determined. Until such data are available, maximum tolerated sulfide concentrations can not be specified as SAV habitat requirements.

## Summary of Physical, Geological, and Geochemical SAV Habitat Requirements

In those areas where light attenuation remains the key factor defining SAV habitats, the plants are largely restricted to shallow waters (Arnold et al. 2000). Unfortunately, it is in these same areas that the highest levels of wave energy and sediment resuspension are most likely to occur. The aquatic environments presently most favorable to SAV growth from the perspective of light are also the least favorable from the perspective of waves and tides (Ailstock personal communication). In order to fully define SAV habitat requirements, parame-

TABLE 6. Sulfide levels in the sediments of healthy and dying SAV beds. Note the different units.

| Sulfide Concentration | Species | Plant Status | Source |
|---|---|---|---|
| 0.10 to 0.16 mM | *T. testudinum* | healthy | Lee and Dunton (2000) |
| 0.35 to 1 mM | *T. testudinum* | healthy | Carlson et al. (1998) |
| 88 m mol $m^{-2}$ AVS | *H. beaudetti* | healthy | Blackburn et al. (1998) |
| <0.2 mM $H_2S$ | *H. engelmanii* | growth | Pulich (1983) |
| <0.2 mM | *T. testudinum*<br>*S. filiforme* | non-toxic | Eldridge and Morse (2000) |
| 0.48 to 1.27 mg $g^{-1}$ | *P. pectinatus* | declining growth | Van Wijck et al. (1992) |
| >0.4 mM | *Z. marina* | reduced photosynthesis | Goodman et al. (1995) |
| ≥2 mM | *Z. marina* | root carbon drain | Pregnall et al. (1984), Smith et al. (1988) |
| >2 mM | *T. testudinum* | dead | Carlson et al. (1998) |
| <10 mM | *T. testudinum* | short-term exposure (48 h) resulted in metabolic stress but no mortality | Erskine and Koch (2000) |

ters other than light and its modifiers need to be taken into consideration. A summary of the state of our knowledge (Table 7) reveals that extensive research is still needed, especially regarding hydrodynamic requirements (currents, waves, and turbulence) for canopy-forming (most biomass near the water surface) and meadow-forming (most biomass near the sediment surface) SAV species. The vertical range over which SAV occurs ($Z_{max} - Z_{min}$) deserves further attention as eutrophication of coastal waters is forcing this fringe into shallower waters (Arnold et al. 2000). When identifying SAV

TABLE 7. Summary of suggested physical and geological SAV habitat requirements.

| Parameter | SAV Habitat Requirements | Observations |
|---|---|---|
| Current velocity | | |
| Freshwater habitat | 0 to ? cm $s^{-1}$ | More data are needed (specially for canopies and meadows, plants with polar/non-polar leaves) to truly define this SAV habitat requirement |
| Marine/estuarine | >5 and <100 cm $s^{-1}$? | |
| Wave exposure and/or fetch | ? | Intensive studies are needed (measurements and models) to define this habitat requirement. |
| Minimum depth of SAV distribution | can be defined by $Z_{min} = \frac{A}{2} + \frac{\frac{gT^2}{2\pi}}{2}$ | A is the tidal amplitude ([MHW-MLW]/2 for diurnal tides and [MHHW-MLLW]/2 for semi-diurnal tides)<br>g is the acceleration of gravity (9.805 m $s^{-2}$)<br>T is the wave period |
| Maximum depth of SAV distribution | can be defined by $Z_{max} = \frac{-\ln\left(\frac{I_z}{I_o}\right)}{K_d}$ | $I_z/I_o$ is the percent light required by the species under consideration<br>$K_d$ is the light attenuation coefficient<br>This calculation should use MTL (mean tidal level) as a reference. Using MHW (mean high water) may underestimate $Z_{max}$ and using MLW (mean low water) may overestimate $Z_{max}$. |
| Tides | SAV can be expected to successfully colonize areas where $Z_{max} \geq X + Z_{min}$ | X is the smallest vertical depth of colonization required for the long-term survival of SAV species. This value was found to be 1 m for eelgrass in Long Island Sound and needs to be defined for other species and sites.<br>$Z_{min}$ is the minimum depth of distribution and depends on the tidal range and wave missing depth. |
| Sediment grain size | | These suggestions are based on compilations of data from the literature (Table 4). Specific studies are needed to confirm these suggestions. |
| Freshwater habitat | no restrictions? | |
| Marine/estuarine | <20% silt and clay | |
| Sediment organic content | <5% | This suggestion is based on a compilation of data from the literature (Table 5). Although all values converge to the suggested value, specific studies are still needed. |
| Sediment sulfide concn. | | These suggestions are based on the few sulfide threshold data presently available in the literature. Further species-specific research is necessary to define sediment sulfide seagrass habitat requirements. |
| Freshwater habitats | does not apply ? | |
| *Zostera* | <400 μM ? | |
| *Thalassia* | <2,000 μM ? | |

habitat requirements, we need to keep in mind that SAV are rooted plants and that geological and geochemical processes are of extreme importance to SAV growth and survival.

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## Sources of Unpublished Materials

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