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Long-Term Trends in Submersed Aquatic Vegetation (SAV) in Chesapeake Bay, USA, Related to Water Quality

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Abstract Chesapeake Bay supports a diverse assemblage of marine and freshwater species of submersed aquatic vegetation (SAV) whose broad distributions are generally constrained by salinity. An annual aerial SAV monitoring program and a bi-monthly to monthly water quality monitoring program have been conducted throughout Chesapeake Bay since 1984. We performed an analysis of SAV abundance and up to 22 environmental variables potentially influencing SAV growth and abundance (1984–2006). Historically, SAV abundance has changed dramatically in Chesapeake Bay, and since 1984, when SAV abundance was at historic low levels, SAV has exhibited complex changes including long-term (decadal) increases and decreases, as well as some large, single-year changes. Chesapeake Bay SAV was grouped into three broad-scale community-types based on salinity regime, each with their own distinct group of species, and detailed analyses were conducted on these three community-types as well as on seven distinct case-study areas spanning the three salinity regimes. Different trends in SAV abundance were evident in the different salinity regimes. SAV abundance has (a) continually increased in the low-salinity region; (b) increased initially in the medium-salinity region, followed by fluctuating abundances; and (c) increased initially in the high-salinity region, followed by a subsequent decline. In all areas, consistent negative correlations between measures of SAV abundance and nitrogen loads or concentrations suggest that meadows are responsive to changes in inputs of nitrogen. For smaller case-study areas, different trends in SAV abundance were also noted including correlations to water clarity in high-salinity case-study areas, but nitrogen was highly correlated in all areas. Current maximum SAV coverage for almost all areas remain below restoration targets, indicating that SAV abundance and associated ecosystem services are currently limited by continued poor water quality, and specifically high nutrient concentrations, within Chesapeake Bay. The nutrient reductions noted in some tributaries, which were highly correlated to increases in SAV abundance, suggest management activities have already contributed to SAV increases in some areas, but the strong negative correlation throughout the Chesapeake Bay between nitrogen and SAV abundance also suggests that

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further nutrient reductions will be necessary for SAV to attain or exceed restoration targets throughout the bay.

Keywords Submersed aquatic vegetation · Salinity community-types · Chesapeake Bay · Abundance · Nutrients · Nitrogen · Water quality

Introduction

Populations of a number of plant and animal species in many estuaries and coastal areas throughout the world have undergone substantial alterations with the advent of human settlement (Pandolfi et al. 2003; Lotze et al. 2006; Halpern et al. 2008). These changes have been attributed to a variety of factors but most notably from increasing nutrients and sediments from the alteration of the surrounding watersheds and their subsequent effects on water quality, e.g., reduced clarity, increased phytoplankton, hypoxia, and anoxia (Kemp et al. 2005; Diaz and Rosenberg 2008). In addition, habitat alteration from dredging and filling, overfishing and its indirect effects, and invasive species have also contributed to the decline of native species (Jackson et al. 2001; Myers et al. 2007; Williams 2007).

Declining water quality, especially light penetration, influences one notable group of species, the freshwater and marine submersed angiosperms (Duarte 1991, 1995; Vermaat and De Bruyne 1993; Middlelboe and Markager 1997; Scheffer et al. 2001; Krause-Jensen et al. 2008). These species, which operate as ecological engineers (sensu Wright and Jones 2006; van der Heide et al. 2007), provide a diversity of ecosystem services to estuaries and coastal areas, e.g., nutrient sequestration, high primary and secondary productivity, provision of nursery and refuge habitat, alteration of hydrodynamics, and sediment stabilization (Heminnga and Duarte 2000; Larkum et al. 2006). Because of their relatively high light requirements, they are often considered biological sentinels (Dennison et al. 1993; Krause-Jensen et al. 2005; Orth et al. 2006). In increasingly urbanized coastal lagoons and estuaries, as well as freshwater lakes and streams, their abundances have been greatly diminished. Lotze et al. (2006) report a 65% and 48% loss of seagrasses and other submersed angiosperms, respectively, in 12 estuaries and coastal seas since colonial establishment. Pandolfi et al. (2003) reported approximately 50% of the seagrasses have been lost in coral reef ecosystems during a similar time frame. A recent worldwide quantitative assessment of seagrass abundances showed accelerated rates of decline since 1990 and that current loss rates (7% year^{-1}) are similar to reported rates of declines for mangroves, coral reefs, and tropical rainforests (Waycott et al. 2009). Although these losses were attributed to a variety of factors, most notable was declining water quality attributed to eutrophication (Lotze et al. 2006; Burkholder et al. 2007; Krause-Jensen et al. 2008; Waycott et al. 2009). Scheffer et al. (2001) highlight changes in submersed vegetation in shallow lakes subject to human-induced eutrophication and associated increased phytoplankton and turbidity as “one of the best-studied and most dramatic shifts” from clear to turbid states, and Sand-Jensen et al. (2000) reported that freshwater submersed vegetation has been virtually wiped out in Denmark over the past 100 years.

A diverse assemblage of submersed angiosperm species (subsequently referred to as SAV) is found in Chesapeake Bay (Fig. 1) and its numerous tributaries spanning a broad salinity range (0–30) over a 300-km distance (Stevenson and Confer 1978). Biostratigraphic records show the first evidence of change in these populations coinciding with periods of extensive land clearing following initial European settlements (Davis 1985; Brush and Hilgartner 2000). Some of the most notable changes in recent history (last 100 years) are the decline in freshwater species in the early 1900s in the tidal freshwater portions of the Potomac River due to declining water quality attributed to increasing wastewater contributions (Carter et al. 1985); the decline of *Zostera marina* in the 1930s in the saline portions of the lower bay from a wasting disease and hurricane and its subsequent recovery by the 1960s (Orth and Moore 1984); a bay-wide decline of all species beginning in the late 1960s and accelerating in the 1970s following the passage of Tropical Storm Agnes in June 1972 (Bayley et al. 1978; Kemp et al. 1983, 2005; Orth and Moore 1983); and changes in native species with the introduction and persistence of non-natives, e.g., *Myriophyllum spicatum* (watermilfoil; Bayley et al. 1968, 1978) and *Hydrilla verticilatta* (hydrilla; Carter and Rybicki 1986; Rybicki and Landwehr 2007). By the 1970s, abundance and diversity of SAV in Chesapeake Bay and its tidal tributaries was substantially altered from what existed in the recent history of the bay (Orth and Moore 1983, 1984; Kemp et al. 2005).

Concerns regarding the role of increasing nutrients and sediments in altering important processes fundamental to the survival of key sentinel species or communities such as SAV (light) or benthos (dissolved oxygen) in Chesapeake Bay and elsewhere (Krause-Jensen et al. 2008) resulted in management decisions to reduce nutrient inputs (e.g., Hennessey 1994; Greening and Janicki 2006). In Chesapeake Bay, requirements for light, turbidity, chlorophyll-a, and nutrients critical for the survival of SAV were developed concurrently to allow managers to gauge the response of SAV to water quality improvements (Batiuk et al. 1992; Dennison et al. 1993; Kemp et al. 2004). In addition, specific areal restoration targets had been set for both bay-wide as well as tributary specific regions by bay

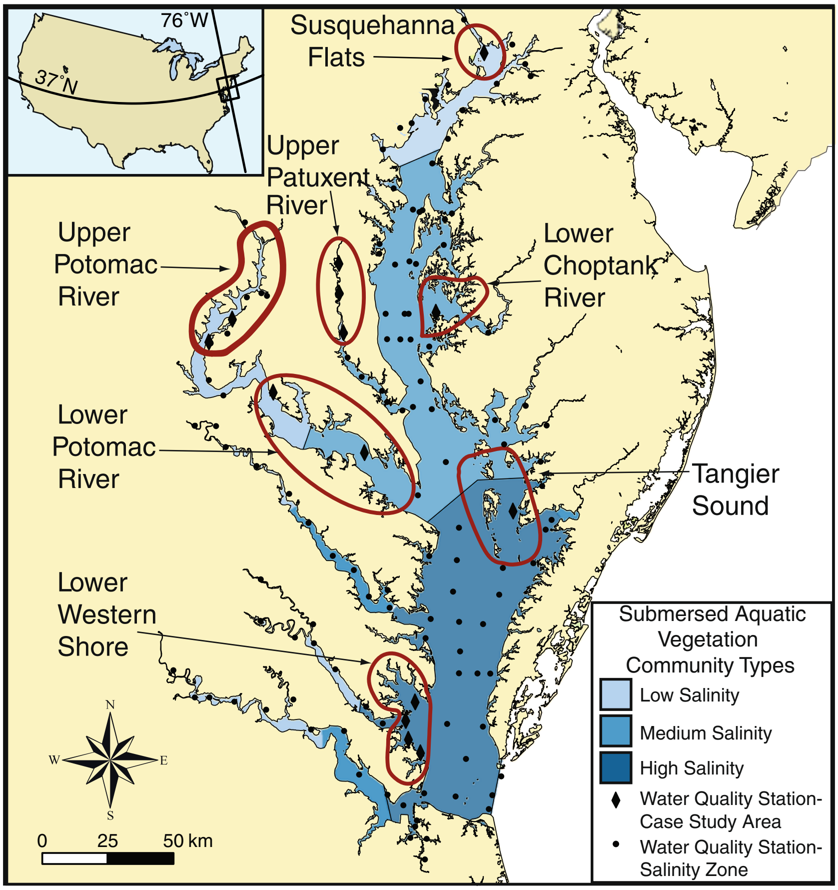

Fig. 1 Map of Chesapeake Bay showing boundaries of the three SAV community-type zones (low-, medium-, and high-salinity), location of the case-study areas where a more in-depth analysis was conducted of SAV trends, and location of water quality stations used in the analyses (*diamonds* represent stations used in the selected case studies, *solid circles* represent stations used in the community studies, which also include those stations used in the case studies)

resource managers for assessing improvements in water quality (Chesapeake Bay Program 2003, 2004a). Finally, SAV abundance has recently been included in the water quality standards of Chesapeake Bay for assessing attainment of water clarity goals that were developed for SAV growth (Orth et al. 2010). Monitoring with aerial photography was adopted as a technique to provide a quantitative measure of annual changes in these SAV communities. Monitoring a variety of water quality variables commenced at a large number of sites throughout the Chesapeake Bay and tributaries and at the Fall Lines of each tributary, providing bi-monthly to monthly and annual information on these parameters.

This paper documents changes in the annual distributions of these plant communities between 1984 and 2006 following a period what was referred to as an unprecedented decline of all SAV species bay-wide (Orth and Moore 1983) and broadly explores SAV trends at different spatial scales in relationship to water quality conditions to identify the most informative scale for synthesizing monitoring data to assess system changes. The three spatial scales considered are the whole bay, three salinity-based SAV community-types (low-, medium-, and high-salinity), and finally a series of case-study areas of smaller sections of the bay and tributaries.

Materials and Methods

Regional Analyses: Community-Type Zones and Case-Study Areas

The freshwater and marine SAV species that inhabit Chesapeake Bay and its tributaries are spread across multiple regions with potentially independent factors affecting both water quality and SAV populations. To describe and analyze changes in SAV in ecologically distinct areas of the Chesapeake Bay, we subdivided the bay and its tributaries into three zones reflecting different SAV community-types (Fig. 1), each characterized by a particular mix of species (Table 1) whose broad distributions are generally constrained by salinity. Species information for each zone was derived from thousands of ground observations made over the 23-year survey period by a diverse array of private, public, and scientific groups and annotated onto maps showing the distribution of SAV each year (http://vims.edu/bio/sav). The three zones approximate the three salinity regions typically used to divide estuaries (polyhaline, mesohaline, and oligohaline-tidal freshwater; Carriker 1967), but are not directly based on salinity data. The highest SAV diversity (up to 13 co-occurring species) can be found in the low-salinity

Table 1 Species present in the three community-type zones

Low-salinity	Medium-salinity	High-salinity
V. americana	*R. maritima*	*Z. marina*
H. verticillata	*P. perfoliatus*	*R. maritima*
M. spicatum	*Z. marina*	
E. canadensis	*S. pectinata*	
S. pectinata	*Z. palustris*	
H. dubia		
N. guadalupensis		
N. minor		
P. crispus		
P. perfoliatus		
P. pusillus		
C. demersum		
Z. palustris		

community-type, which is spread across the upper sections of the bay's many tributaries as well as the head of the bay, and includes four invasive species, *Najas minor*, *Potamogeton crispus*, *M. spicatum*, and *H. verticillata*. One species often identified as *Elodea canadensis*, may actually be two separate species, with *Elodea nuttalli*, possibly being misidentified. The medium-salinity community-type supports up to five or six species, although recently, *Ruppia maritima* has been the only dominant species in most field surveys of SAV beds throughout this zone. The lowest SAV species diversity (two co-occurring species, *Z. marina* and *R. maritima*, generally considered to be true seagrasses, based on genetic evidence: Les et al. 1997) is found in the high-salinity community-type, a single contiguous region of the lower mainstem bay and tributaries. These three community-types differ slightly from the four communities identified by Moore et al. (2000), primarily in that their *Potamogeton* and *Ruppia* communities are both incorporated in our medium-salinity community-type zone, allowing the use of a single geographic delineation of the zone across the study period.

In addition to the community-type zones, we selected seven specific areas of the bay (Fig. 1) as case studies for more in-depth analysis of changes in SAV abundance. Although the community-type zones incorporate broad geographic regions and multiple tributaries (and consequently a wide range of environmental influences), we selected case-study areas to be large, relatively contiguous areas that had shown significant changes in SAV over the study period, suggesting responsiveness to local conditions. The boundaries of selected case-study areas were defined by geographic "segments" of the estuary employed by the Chesapeake Bay Program (Chesapeake Bay Program 2004b). Specific case-study areas were: (1) Susquehanna Flats, (2) the Upper Patuxent River, (3) the Upper Potomac River, (4) the Lower Potomac River, (5) the Lower Choptank River, (6) Tangier Sound, and (7) the Lower Western Shore (Fig. 1).

SAV Abundance Data

Annual peak SAV abundance is presented as bed area, defined as the area within SAV bed boundaries regardless of their density or patchiness (and is therefore unresponsive to changes in bed structure, i.e., density or patchiness). In addition, percent change in bed area from the previous year was used as a response variable in analyses to detect relationships sensitive to annual-scale perturbations, rather than long-term condition changes.

Bed area was derived from aerial photography acquired on an annual basis from 1984 through 2006, except for 1988 (Orth et al. 2007; Moore et al. 2009). Black and white photography was acquired at a scale of 1:24,000 with a standard mapping camera, following acquisition timing guidelines that optimize visibility of SAV beds. Acquisition timing rules specified tidal stage (±90 min of low tide), plant growth season (peak biomass), sun angle (between 20–40°), atmospheric transparency (cloud cover less than 10%), water turbidity, and wind (less than 10 knots; Dobson et al. 1995). Images incorporated 60% flight-line overlap and 20% side lap. Approximately 170 flight lines were flown each year covering all shorelines and adjacent shoal areas of Chesapeake Bay and its tributaries, yielding over 2,000 photographs. Acquisition commenced in the late spring (mid-May) to capture the higher-salinity regions at peak plant biomass and continued through late summer and early fall (August through October) to capture the dominant freshwater species at their peak biomass. The timing of the aerial photography in the low-salinity and freshwater areas did not capture the presence of *Zannichelia palustris*, a highly dynamic annual species that is locally abundant during the winter and early spring period but dies out in June or early July. The contribution of *Z. palustris* to the SAV population dynamics, its ecosystem services, and its response to water quality are currently unknown. Poor atmospheric conditions (clouds, wind) or water conditions (high turbidity or higher tides than predicted), at times compromised data acquisition during these optimal periods, as did security issues following Sept. 11, 2001, which resulted in additional airspace restrictions over several areas of the bay (e.g., Washington, DC). Daily coordination with the contractor and approvals from federal security personnel allowed acquisition of the photography with only a few exceptions (e.g., tidal freshwater areas of Potomac River) even with these additional challenges. Missing SAV data for salinity zones is estimated to represent less than 10% of the total area for each of the years except for the low-salinity community-type zone in 1984 (14%), 1999 (20%), and 2001 (27%). Three of the case-study areas are estimated to be missing more than 10% of the total area for a single year (Lower Potomac River, 1984, 66%; Upper Patuxent River, 1999, no data; Upper Potomac River, 2001, 34%). SAV in the low-salinity and freshwater areas of the James, York, and Rappahannock rivers were not mapped prior to 1998, but their annual abundances are estimated to have represented less than 5% of the total low-salinity community-type SAV area. Mapping of SAV beds was initially accomplished by manually tracing bed outlines onto translucent US Geological Survey 7.5-min quadrangle maps directly from the photographs and then digitizing these bed boundaries into a geographic information system (GIS) dataset for analysis. Since 2001, the aerial photography was scanned from negatives and ortho-rectified using (ERDAS LPS) image-processing software (ERDAS, Atlanta, GA). SAV bed boundaries were then directly photo-interpreted on-screen while maintaining a fixed scale using ESRI ArcMap GIS software (ESRI, Redlands, CA; Orth et al. 2007).

Water Quality Data

Year-to-year variations in annual peak SAV abundance were analyzed relative to changes in up to 22 environmental variables that are related to key factors shown in past studies to influence SAV growth and abundance (e.g., Dennison et al. 1993; Kemp et al. 2004). These include eight variables calculated at the Fall Line of major rivers by the US Geological Survey (www.usgs.gov): total nitrogen, total phosphorus, total suspended sediment, and nitrate (NO_3) loads and flow-weighted concentrations of these four variables (i.e., riverine loads divided by flow each month). Twelve variables (period-of-interest mean and median of six variables) were derived from the Chesapeake Bay Program's mainstem and tidal tributary water quality monitoring program (http://www.chesapeakebay.net/data_waterquality.aspx): surface-dissolved inorganic nitrogen, total suspended solids, chlorophyll-a, Secchi depth, salinity, and water temperature. The mean and median values of each parameter were calculated over the period-of-interest indicated in Table 2, and measurements were collected at tidal water sampling stations two times per month, except during the months of November to February where only one sampling was conducted. Below-Fall-Line point-source total nitrogen and total phosphorus loads were obtained from the same source (http://www.chesapeakebay.net/data_pointsource.aspx). Total suspended-sediment data from the lower bay mainstem stations were excluded from the analysis due to currently unresolved data-quality issues. Case-study area boundaries and sampling periods analyzed are given in Table 2.

To match the appropriate period of water quality data with each year's SAV abundance, we divided the water quality data set into 12-month periods incorporating the SAV growing seasons between subsequent SAV data acquisition dates (in summer or fall depending on community-type). Growing seasons were defined for each community-type to best match seasonal growth cycles (e.g., high-salinity community growing season includes March and November). For each community-type, we calculated the average date on which aerial surveys were flown to determine the applicable period of water quality and set the yearly cut-off date as the first day of the month containing the average date flown (Table 2).

Statistical Analysis

Relationships between SAV and water quality variables were examined by SAV community-type zone and by case-study area independently. For the three SAV salinity community-type zones and the seven case-study areas, separate univariate linear regressions were performed using each of the 22 water quality variables (total suspended solids and point-source inputs were not used the southern bay areas, and the latter was not used for Susquehanna Flats) as the independent variable and bed area and percent change in bed area as the response variable. The sample size (*n*) for most analyses was 22 (i.e., years) because no SAV data are available for 1988. Moreover, in instances where tidal water quality variables are used, $n=21$ or 20 because available data are incomplete for 1984 and, in some cases, 2006. Missing bed area data further reduced sample site in the Upper Patuxent River, Upper Potomac River, and the low-salinity community-type zone. Quadratic curve fits were done on total SAV area between 1984 and 2006, for the whole bay, low-, medium-, and high-salinity zones. The SAV community-type zones are spread across multiple tributaries (especially the low-salinity community-type, which incorporates dozens of independent watersheds), potentially obscuring important relationships existing at smaller scales. Consequently, we focused more effort on case-study area analyses by exploring univariate linear and multiple linear regressions and did not conduct any analyses with the independent variables at the bay-wide scale. For case-study areas, multiple linear regression models were developed for each of the response variables using a stepwise variable selection procedure. Possible artifacts associated with the effects of collinearity were determined by assessing whether variance inflations were larger than ten, condition indices were well above 100, and variance proportions were greater than 0.50 (Thielbar et al. 2005). Other than the mean and median of the same variable, there was no collinearity. Where both median and mean water quality values were selected in the final multiple regression model (or found to be significant in univariate analyses), the variable with less explanatory power was excluded from the model (or for univariate analyses, not reported). All regressions and curve fits were

Table 2 Dates of submersed aquatic vegetation (SAV) data acquisition for each region (Chesapeake Bay Program segments), and sources (CBP sampling stations) and date ranges for independent variables

Region	SAV boundary (CBP segment[a])	Photography acquired	Water quality data (CBP station[a])	Water quality data source period	
				Prior year	Same year
Community-type zones					
Low-salinity	See Fig. 1	Mid-Sep	See Fig. 1	9/1–10/31	4/1–8/31
Mid-salinity	See Fig. 1	Mid-Aug	See Fig. 1	8/1–10/31	4/1–7/31
High-salinity	See Fig. 1	Mid-Jun	See Fig. 1	6/1–11/31	3/1–5/31
Case-study areas					
Susquehanna Flats	CB1TF	Mid-Sep	CB1.1	9/1–10/31	4/1–8/31
Upper Patuxent River	PAXTF, PAXOH	Mid-Sep	TF1.5–1.7	9/1–10/31	4/1–8/31
Upper Potomac River	POTTF	Mid-Sep	TF2.3–2.4	9/1–10/31	4/1–8/31
Lower Potomac River	POTMH	Mid-Aug	RET2.4–LE2.2	8/1–10/31	4/1–7/31
Lower Choptank River	CHOMH1	Mid-Aug	EE2.1	8/1–10/31	4/1–7/31
Tangier Sound	TANMH	Mid-Jun	EE3.2	6/1–11/30	3/1–5/31
Lower Western Shore	MOBPH	Mid-Jun	WE4.1–4.4	6/1–11/30	3/1–5/31

For example, analyses compared Tangier Sound SAV data acquired around 15 Jun 1995 with WQ data aggregated for the combined period 1 Jun 1994–30 Nov 1994 and 1 Mar 1995–31 May 1995

[a] These notations of segment names and stations are formal names given to these entities and a reference to these designations can be found at http://www.chesapeakebay.net/content/publications/cbp_13272.pdf

determined using SAS statistical software (v9.2). SAV abundance data for the low-salinity community-type zone for 1984, 1999, and 2001 were excluded from the analysis, as was SAV data for the Lower Potomac River, Upper Patuxent River, and Upper Potomac River case-study areas in 1984, 1999, and 2001, respectively. Statistical results are reported for all analyses with the slope (positive or negative), coefficient of determination (r^2), and significance indicated by * ($0.05 \geq p > 0.01$), or ** ($p \leq 0.01$). Because we consider these water quality analyses exploratory in nature, we have only shown the significance range within which each p-value lies as an indication of the relative strength of inferences among all results.

Results

SAV Patterns at Bay-Wide and Community-Type Scales

Total SAV abundance at the bay-wide scale (the sum of SAV area in the three salinity-based community-types) generally increased by ~1–28% per year from 1984 (15,470 ha) until 1993 (29,587 ha), after which total bed area leveled off, generally fluctuating under 30,000 ha, reaching a bay-wide maximum of 36,283 ha in 2002, and declining to 23,941 ha at the end of our study period (Figs. 2 and 3). Yearly SAV abundance at the bay-wide scale significantly increased over the 23-year study period, whereas abundance in the three major salinity zones exhibited distinctly different patterns (Fig. 2; Table 3).

For the low-salinity community-type (Fig. 1), SAV abundance had a significant overall increase (Table 3) from its initial low point of 4,229 ha in 1985 (Figs. 2 and 3). The region was characterized by high year-to-year variability, with large single-year gains (over 1,500 ha y^{-1}) in 1998, 2004, and 2006 increasing the total bed area to a maximum of 12,981 ha in 2005. The full 23-year period had a 166% increase in bed area. Nitrogen, phosphorus, and Secchi depth (the latter in a counterintuitive inverse relationship) showed a significant relationship with SAV bed area (Table 4). Total suspended solids (counterintuitive, but positive relationship) and Secchi depth (again counterintuitive) showed a significant relationship with percent change in SAV bed area (Table 4). The strongest associations for SAV bed area were for below-Fall-Line total nitrogen point-source load, contributing 70% of the variation explained by the model and median Secchi, contributing 42% of the variation explained by the model (Table 4).

For the medium-salinity community-type (Fig. 1), SAV abundance demonstrated a significant overall increase (Table 3) from its initial low point of 1,069 ha in 1984. However, since 2000, the area has become more variable with total area showing no trend (Figs. 2 and 3). The region was also characterized by high year-to-year variability, with large gains in both 2001 and 2002, resulting in a total bed area of 12,270 ha in 2002. A large loss in 2003 resulted in bed area similar to 2000 (Fig. 2). The full 23-year period had a 261% increase in bed area. SAV bed area was related to below-Fall-Line total nitrogen point-source load contributing 36% of the variance

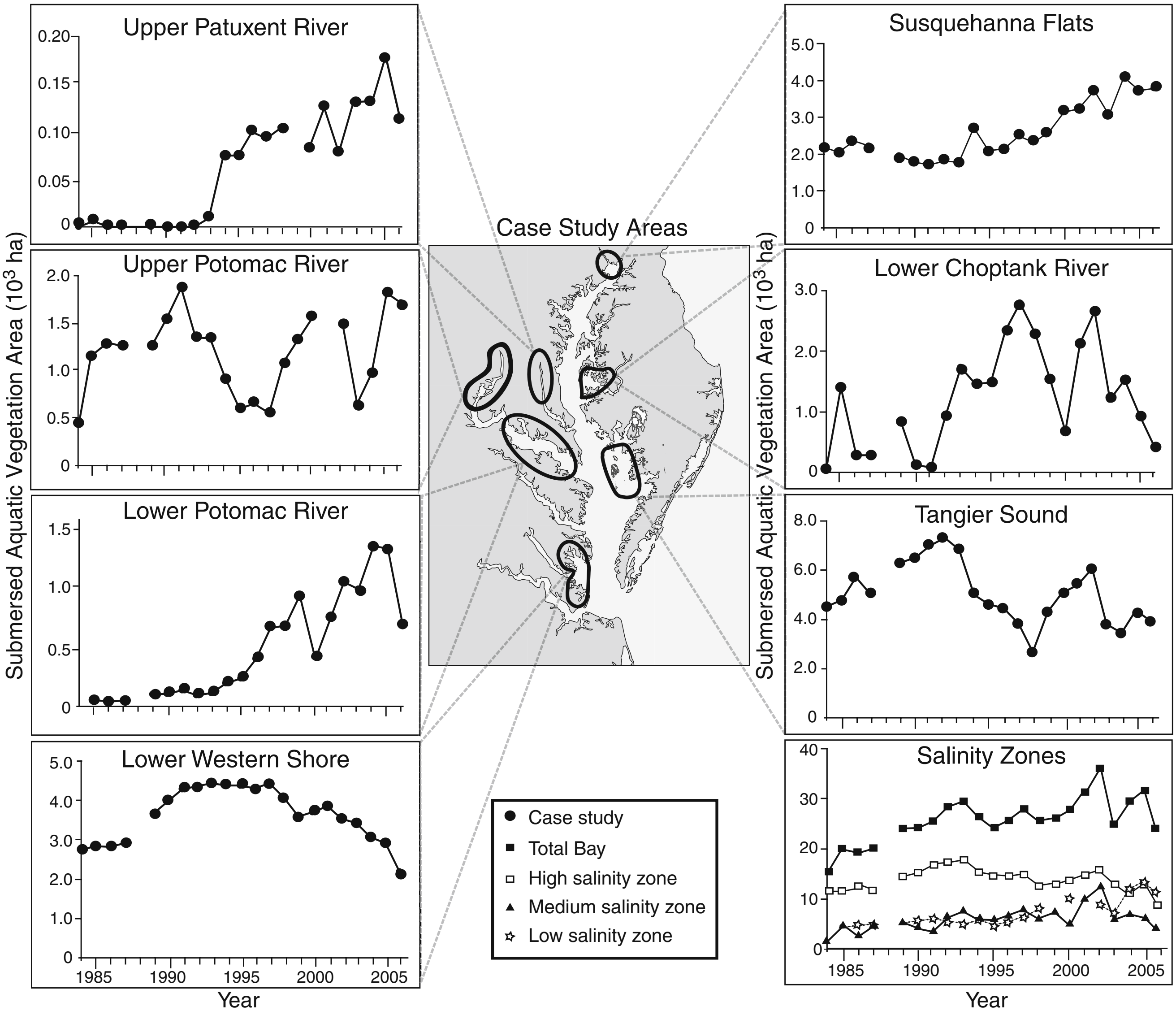

Fig. 2 SAV bed area from 1984 through 2006 for the entire Chesapeake Bay, the three salinity community-types (high, medium, and low), and the seven case-study areas: Susquehanna Flats, Upper Patuxent River, Upper Potomac River, Lower Potomac River, Lower Choptank River, Tangier Sound, and Lower Western Shore (note: no data for all sites in 1988. Some small portions of the Chesapeake Bay were not flown in several years resulting in partial data for the salinity community-types and case-study areas. Refer to the Methods section for details of sites with partial SAV data)

explained by the model (Table 4), with no other significant variables. For percent change, below-Fall-Line total phosphorus point-source load contributed 39% of the variance captured in the model (Table 4), with no other significant variables.

In the high-salinity community-type (Fig. 1), SAV abundance generally increased between 1984 (11,283 ha) and the early 1990s, reaching a peak bed area of 17,608 ha in 1993, followed by a subsequent decline in area (Figs. 2 and 3). Losses in 2003 and 2006 resulted in a study period minimum in 2006 of 22% less bed area than in 1984. SAV bed area was related to median dissolved inorganic nitrogen, the only variable to show a significant relationship with SAV, contributing 25% of the variance explained by the model (Table 4).

Regional SAV Patterns: Case-Study Areas

Annual SAV abundance is presented for the seven case-study areas (Fig. 2). At the smaller spatial scale of the case-study areas, significant relationships among dependent SAV variables and independent water quality variables emerged in every case-study area. In all case studies, nitrogen was among the predictors that were negatively related to SAV abundance. Univariate linear and multiple linear regressions are presented in Tables 5 and 6, respectively.

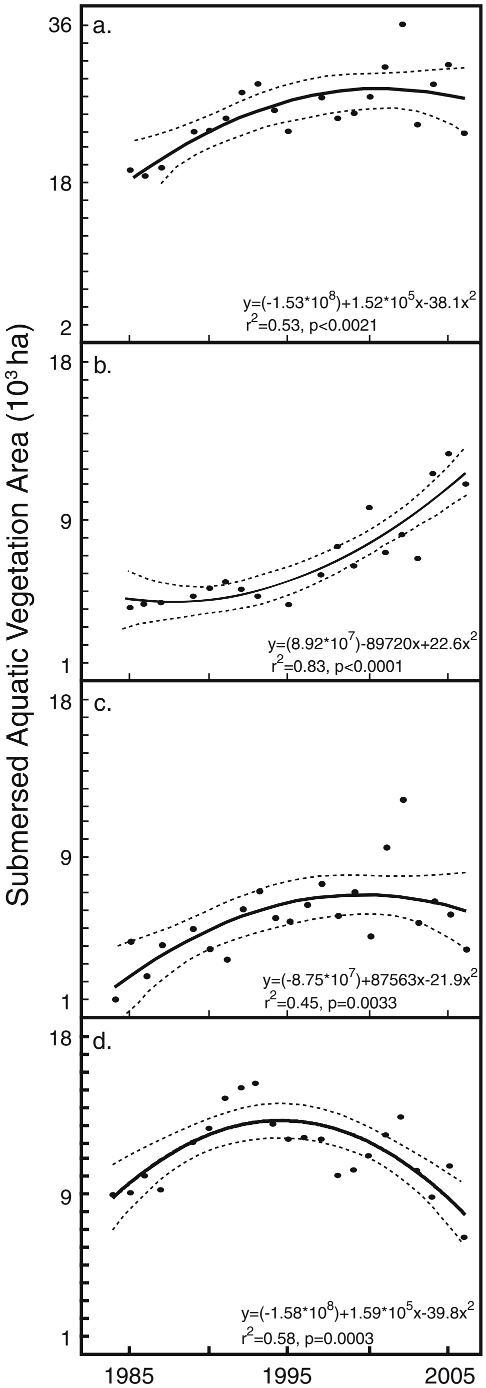

Fig. 3 Quadratic curve fits for 1984–2006 SAV area for **a** total bay, **b** low-salinity community type zone, **c** medium-salinity community type zone, and **d** high-salinity community type zone. Dotted lines show a 95% confidence interval

Susquehanna Flats

A diverse array of species has consistently been reported in Susquehanna Flats case-study area, with up to 13 species found in any single year (one site had 12 species in a small area). Over the 23-year study period, species reported most commonly were *M. spicatum*, *Heteranthera dubia*, *H. verticillata*, *Vallisneria americana*, *Ceratophyllum demersum*, and *N. minor*. In the late 1990s, SAV began a steady increase and reached maximum abundance over the 23-year period in 2004 when 4,089 ha of bed area were recorded (Fig. 2), representing 34% of the total SAV bed area in the low-salinity zone and a significant increase over the entire study period (Table 3).

Univariate regressions of bed area and median Secchi depth (again counterintuitive in direction) and flow-weighted concentrations of total nitrogen were significant as was the univariate regression of annual percent change in SAV bed area and median chlorophyll-a (Table 5). The best-fit multiple regression model for SAV bed area included median Secchi depth, mean temperature, total suspended solids, and flow-weighted concentrations of total nitrogen (Table 6). Median chlorophyll-a was the only significant variable in the relationship with annual percent change in SAV bed area (Table 5) and was the only variable selected in the best-fit multivariate model (Table 6).

Upper Patuxent River

Dominant species in this area were *H. verticillata*, *Najas guadalupensis*, *N. minor*, *E. canadensis,* and *C. demersum*. SAV was essentially absent in the Upper Patuxent River case-study area until 1993 when 9 ha were reported following 7 of 8 years with zero plant cover (Fig. 2). SAV (principally *N. guadalupensis*, and *H. verticillata*) rapidly spread within this section increasing to 75 ha in 1994 and steadily increasing to 182 ha in 2005, with a significantly positive overall trend for the 23-year study period (Table 3).

Initial water quality analyses were conducted separately for the freshwater and oligohaline sections of this case-study area, but we found no substantial differences in the results and subsequently combined the sections for all analyses. All highly significant univariate regression relationships were related to nitrogen (Table 5), and a combination of below-Fall-Line total phosphorus point-source load, mean Secchi depth, and below-Fall-Line total nitrogen point-source load (Fig. 4a) gave the best multiple linear regression (Table 6). No significant relationships were found between water quality variables and annual percent change in SAV bed area (Tables 5 and 6).

Upper Potomac River

Dominant species were *H. verticillata*, *M. spicatum*, *H. dubia*, *V. americana*, *C. demersum*, and *N. minor.* SAV abundance in the Upper Potomac River case-study area exhibited repeated large fluctuations, with high points near 1,800 ha of SAV bed area in 1991, 2005, and 2006, and low

Table 3 Linear regression statistics, areal coverage range (1984–2006), SAV restoration targets (hectares), and the potential habitat <2m available for SAV growth for Chesapeake Bay the three salinity zones, and seven case-study areas

Location	Regression			Coverage		Restoration target	Area <2m
	Slope	r^2	sig	Min	Max		
Total bay	+	0.41	**	15,470	36,283	74,854	260,412
Low-salinity	+	0.73	**	4,229	12,981	14,183	69,014
Medium-salinity	+	0.31	**	1,069	12,270	31,072	124,361
High-salinity	−	0.02	ns	8,848	17,608	29,598	67,037
Susquehanna Flats	+	0.66	**	1,709	4,089	5,224	8,461
Upper Patuxent River	+	0.81	**	0	182	30	860
Upper Potomac River	−	0.00	ns	475	1,870	1,768	7,083
Lower Potomac River	+	0.77	**	43	1,376	4,117	18,536
Lower Choptank River	+	0.18	*	58	2793	3,255	8,440
Tangier Sound	−	0.19	*	2,676	7,330	15,364	28,289
Lower Western Shore	−	0.00	ns	2,183	4,442	6,109	13,755

See methods for years that were removed from the analysis due to partial data

*$0.05 > p \geq 0.01$; **$p < 0.01$

points in 1984 and 1997 (Fig. 2), with no significant trend over the 22-year study period (Table 3).

The best correlations with bed area in univariate regressions (out of seven significant variables, Table 5) were median total suspended solids and median temperature. Similar to Susquehanna Flats and the Upper Patuxent River case-study areas, nitrogen (TN load) was negatively related to SAV abundance. The best-fit multiple regression models included only temperature (Table 6). No significant relationships were found between water quality variables and annual percent change in SAV bed area (Tables 5 and 6).

Lower Potomac River

Dominant species in this area were *R. maritima*, *M. spicatum*, *Potamogeton perfoliatus*, *Stuckenia pectinata*, *E. canadensis*, and *C. demersum*. SAV remained at very low abundance until a gradual increase began in the mid-1990s (Fig. 2), reaching maximum bed area of 1,376 ha in 2004, with a significant positive increase over the 23-year study period (Table 3).

There was a strong and significant relationship of SAV bed area and below-Fall-Line total nitrogen point-source load (Fig. 4b; Table 5). Additional significant relationships were found with flow-weighted concentrations of NO_3, median total suspended solids, and total phosphorus load, although the relationship with total phosphorus load was positive rather than negative (Table 5). The best-fit multiple linear regression models for SAV bed area did not include any variables other than below-Fall-Line total nitrogen point-source load (Table 6). No significant relationships were found with annual percent change in SAV bed area (Tables 5 and 6).

Lower Choptank River

One species, *R. maritima*, dominated beds in this case-study area. SAV bed area underwent dramatic fluctuations

Table 4 Linear regression results for the three community-type zones (1984–2006)

Dependent variable	Independent variable	Slope	r^2	p
Low-salinity				
SAV bed area	BFL total nitrogen PS load	−	0.70	**
	Median Secchi	−	0.42[a]	**
	BFL total phosphorus PS load	−	0.30	*
	Total phosphorus load	+	0.27[a]	*
	Total phosphorus concentration	+	0.23[a]	*
Percent change	Mean Secchi	−	0.28[a]	*
	Median total suspended solids	+	0.27[a]	*
Medium-salinity				
SAV bed area	BFL total nitrogen PS load	−	0.36	**
Percent change	BFL total phosphorus PS load	−	0.39	**
High-salinity				
SAV bed area	Median dissolved inorganic nitrogen concentration	−	0.25	*

Only analyses with $p \leq 0.05$ are shown

See methods for years that were removed from the analysis due to partial data

BFL below-Fall-Line, *PS* point-source, *concentrations* flow-weighted

[a] Indicates counterintuitive result (increased stressor linked to increased submersed aquatic vegetation)

*$0.05 \geq p > 0.01$; **$p \leq 0.01$

Table 5 Linear regression results for the seven case-study areas (1984–2006)

Case-study area	Dependent variable: SAV bed area				Dependent variable: percent change			
	Independent variable	Slope	r^2	p	Independent variable	Slope	r^2	p
Susquehanna Flats	Median Secchi	−	0.46[a]	**	Median chlorophyll-*a*	−	0.28	*
	Total nitrogen concentration	−	0.25	*				
Upper Patuxent River	BFL total nitrogen PS load	−	0.60	**	No models fit			
	Total nitrogen concentration	−	0.56	**				
	Nitrate concentration	−	0.51	**				
	Total phosphorus concentration	−	0.23	*				
	Mean salinity	−	0.22	*				
Upper Potomac River	Median total suspended solids	−	0.45	**	No models fit			
	Median temperature	−	0.40	**				
	Total phosphorus load	−	0.30	*				
	Total nitrogen load	−	0.29	*				
	Total nitrate load	−	0.27	*				
	Mean chlorophyll-*a*	−	0.24	*				
	Total phosphorus concentration	−	0.21	*				
Lower Potomac River	BFL total nitrogen PS load	−	0.71	**	No models fit			
	Nitrate concentration	−	0.28	*				
	Median total suspended solids	−	0.21	*				
	Total phosphorus load	+	0.19[a]	*				
Lower Choptank River					Total nitrogen concentration	−	0.41	**
					BFL total phosphorus PS load	+	0.40	**
Tangier Sound	Mean Secchi	+	0.41	**	Total nitrogen load	−	0.24	*
	Median chlorophyll-*a*	−	0.33	**	Mean salinity	+	0.24	*
	Median salinity	+	0.24	*				
Lower Western Shore	Median dissolved inorganic nitrogen concentration	−	0.43	**	Median temperature	−	0.24	*
	BFL total phosphorus PS load	−	0.34	*	Total nitrogen concentration	+	0.23	*
					Mean Secchi	+	0.20	*

Only analyses with $p \leq 0.05$ are shown

See methods for years that were removed from the analysis due to partial data

BFL below-Fall-Line, *PS* point-source, *concentrations* flow-weighted

[a] Indicates counterintuitive result (increased stressor linked to increased submersed aquatic vegetation)

*$0.05 \geq p > 0.01$; **$p \leq 0.01$

in abundance, with gains and losses of 1,000–2,000 ha over the span of just a few years (Fig. 2). Abundance peaked in 1997 with 2,793 ha and again in 2002 (2,665 ha), with an overall positive increase over the 23-year study period (Table 3).

Flow-weighted concentrations of total nitrogen and below-Fall-Line total phosphorus point-source load were significant variables for the annual percent change in SAV bed area (Table 5). There were no other significant univariate regressions (Table 5), but a significant multiple linear regression model for the annual percent change in SAV bed area included flow-weighted concentrations of total nitrogen, median Secchi depth, and mean chlorophyll-a (Table 5); no variables were significantly related to bed area in multiple linear regressions (Table 6).

Tangier Sound

Two species, *Z. marina* and *R. maritima*, were the dominant SAV species in the Tangier Sound case-study area. Between 1984 and 1992, SAV abundance increased to its peak bed area of 7,330 ha, then declined for six consecutive years to the study period minimum in 1998 (Fig. 2). SAV area rebounded for 4 years, but ended the study period in 2006

Table 6 Multiple linear regression results for the seven case-study areas

Case-study area	Dependent variable: SAV bed area				Dependent variable: percent change			
	Model	Slope	r^2	p	Model	Slope	r^2	p
Susquehanna Flats	Median Secchi+mean temperature+ mean total suspended solids+total nitrogen concentration	−	0.91	**	Median chlorophyll-*a*	−	0.28	*
Upper Patuxent River	BFL total phosphorus PS load+mean Secchi+BFL total nitrogen PS load	−	0.80	**	No models fit			
Upper Potomac River	Median temperature	+	0.53	**	No models fit			
Lower Potomac River	BFL total nitrogen PS load	−	0.71	**	No models fit			
Lower Choptank River	No models fit				Total nitrogen concentration+median Secchi+mean chlorophyll-*a*	−	0.76	**
Tangier Sound	Mean Secchi	+	0.41	**	Mean salinity	+	0.24	*
Lower Western Shore	Median dissolved inorganic nitrogen concentration+total nitrogen concentration	+	0.76	**	Total nitrogen concentration	+	0.23	*

Only analyses with $p<0.05$ are shown

See methods for years that were removed from the analysis due to partial data

BFL below-Fall-Line, *PS* point-source, *concentrations* flow-weighted

*$0.05>p\geq0.01$; **$p<0.01$

with 13% less bed area than in 1984, with an overall significant decline for the 23-year study period (Table 3).

Univariate linear regression showed a significant relationship between SAV bed area and mean Secchi depth (Fig. 4c; Table 5), as with median chlorophyll-a and median salinity (Table 4). There were also significant regressions of annual percent change in SAV bed area on total nitrogen load and mean salinity (Table 5). The best-fit multiple regression models did not include any variables other than mean Secchi depth for bed area and mean salinity for annual percent change in SAV bed area (Table 6).

Lower Western Shore

Two species, *Z. marina* and *R. maritima*, were present in the Lower Western Shore case-study area. SAV abundance increased after 1984 and leveled off in the 1990s near 4,400 ha (Fig. 2). From 1998 to 2006, SAV abundance slowly declined to 2,183 ha, 20% below the 1984 abundance. Although the overall trend for this area was not significant (Table 3), SAV had a significant negative trend ($r^2=0.86$, $p\leq0.01$) from 1997 through 2006.

Univariate regressions were significant for median dissolved inorganic nitrogen and below-Fall-Line total phosphorus point-source load (Table 5) with SAV bed area, but median temperature, flow-weighted concentrations of total nitrogen, and mean Secchi depth were significant variables for annual percent change in SAV bed area (Table 5). The best-fit multiple linear regression models included median dissolved inorganic nitrogen and flow-weighted concentrations of total nitrogen as variables for bed area (Table 6). Flow-weighted concentration of total nitrogen was the only significant variable for annual percent change in SAV area in the multiple regressions (Table 6).

Discussion

Previous research has demonstrated the link between water quality conditions and growth of SAV in experimental and observational studies in numerous locations worldwide. These studies include marine [Cambridge and McComb 1984 (Australia); Lapointe and Clark 1992 (USA); Komatsu 1996 (Japan); Moore et al. 1996, 1997 (USA); Short and Burdick 1996 (USA); Rask et al. 1999 (Denmark); Hauxwell et al. 2001 (USA); Boström et al. 2002 (Finland); Kendrick et al. 2002; Baden et al. 2003 (Sweden); Cardoso et al. 2004 (Portugal); Moore 2004 (USA); Tomasko et al. 2005 (USA); Greening and Janicki 2006 (USA)] and freshwater species [Twilley et al. 1985 (USA); Rybicki and Carter 1986 (USA); Stevenson et al. 1993 (USA); Vermaat and De Bruyne 1993 (The Netherlands); Brush and Hilgartner 2000 (USA); Sand-Jensen et al. 2000 (Denmark); Brodersen et al. 2001 (Denmark); Körner 2002 (Germany); Morris et al. 2003 (Australia): Rybicki and Landwehr 2007 (USA); Moss 2008 (England)]. The mechanisms most often cited as causal links for declines in SAV were high levels of suspended solids

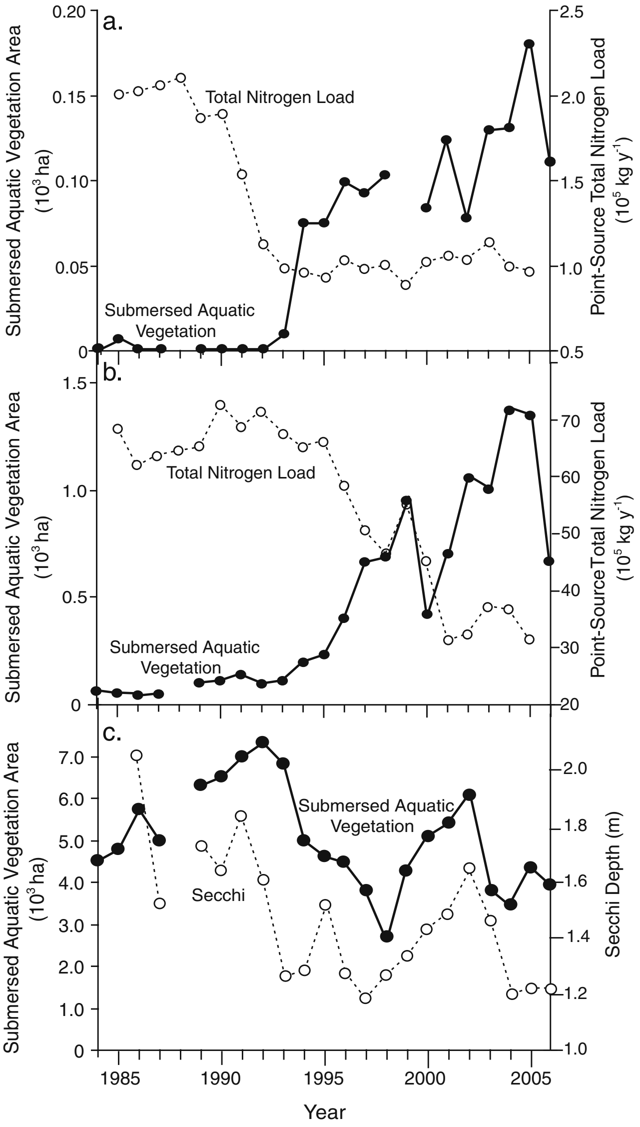

Fig. 4 **a** Time series of SAV bed area and below-Fall-Line point-source total nitrogen loads for the Upper Patuxent River case-study area; **b** time series of SAV bed area and below-Fall-Line point-source total nitrogen loads for the Lower Potomac River case-study area; **c** time series of SAV bed area and mean Secchi depth for the Tangier Sound case-study area

or increased levels of nitrogen and/or phosphorus that would result in reduced light to the leaf surface (Scheffer et al. 2001; Burkholder et al. 2007; Krause-Jensen et al. 2008). The current analysis supports these factors being relevant to the dynamics of SAV populations in Chesapeake Bay at various spatial scales.

The mean percent area contributed by the high-salinity SAV community was 52% of the total Chesapeake SAV between 1984 and 2006, while the mean percent area contributed by the medium- and low-salinity communities was 22% and 26% of the total SAV area respectively, during the same time period (Table 7). Although it contributes more than half the total SAV area, the area of the high-salinity community had a relatively weak correlation to the total Chesapeake SAV abundance compared with the low-, and particularly the medium-salinity SAV communities (Table 7). This can be explained by the increase followed by decline in the high-salinity zone, as well as the high year-to-year variability in SAV area within the low- and medium-salinity communities (CV 0.41 and 0.42 versus 0.16 in the high-salinity community), which reflects the very different life-history strategies of SAV communities in the three salinity zones within the bay (Stevenson and Confer 1978; Moore et al. 2000).

Even though Chesapeake Bay has some system-wide and long-term stressors, such as high nutrient inputs (Kemp et al. 2005), patterns in bay-wide SAV occur at multiple spatial scales. There are two spatial scales that provide insight into the analyses of SAV and water quality: (1) SAV community-types as defined by salinity regimes (high-, medium-, and low-salinity community-types), which in Chesapeake Bay occur over hundreds of kilometers and (2) case-study areas (Susquehanna Flats, Upper Patuxent River, Upper Potomac River, Lower Potomac River, Lower Choptank River, Tangier Sound, and Lower Western Shore) which in Chesapeake Bay occur over tens of kilometers. The SAV community-types are relevant to water quality analyses due to the morphological and physiological responses of the dominant genera. The case-study areas are relevant to water quality analyses due to localized watershed land-use patterns (Li et al. 2007).

Broad-scale patterns in SAV abundance were found, with an increase in SAV area in the low-salinity zone, increase followed by leveling off in the medium-salinity zone, and increase followed by decline in the high-salinity zone. For all case-study areas and salinity zones, measures of nitrogen load and concentration were highly negatively correlated with year-to-year variability in SAV abundance. Within these regions, more regionally specific relationships between SAV area and water quality metrics, including nutrients in tidal tributaries and water clarity in the high-salinity Tangier Sound and Lower Western Shore case-study areas, were demonstrated.

Low-Salinity Zone and Case-Study Areas

SAV in the low-salinity zone with its diverse assemblage of freshwater species showed modest gains in the first decade but underwent a large increase in the last decade. This pattern was also reflected in the Susquehanna Flats and upper Patuxent River case-study areas within the zone. Nitrogen and phosphorus were significant independent variables at the scales of both the salinity community zone and the localized case-study areas. The influence of nitrogen and phosphorus on SAV was, however, apparent in different measured forms for different regions: (1) below-

Table 7 Comparison of total bay and submersed aquatic vegetation community areas and trends

	Submersed aquatic vegetation community-type zone			Total bay
Salinity	Low	Medium	High	
Area (ha)	6,812 (635)	5,591 (505)	13,620 (466)	26,100 (955)
Area (%)	26 (1.8)	22 (1.3)	52 (2.0)	
Coeff Var	0.41	0.42	0.16	0.16
r^2	0.33**	0.74***	0.23*	

Data 1984–2006, measures of central tendency are mean (±standard error; see methods for years that were removed from the analysis due to partial data)

*$p<0.05$; **$p<0.01$; ***$p<0.001$

Fall-Line total nitrogen point-source load, below-Fall-Line total phosphorus point-source load, total phosphorus load, and flow-weighted concentrations of total phosphorus for the whole low-salinity zone; (2) flow-weighted concentrations total nitrogen for the Susquehanna Flats case-study area; and (3) below-Fall-Line total nitrogen point-source load and flow-weighted concentrations of total nitrogen for the Upper Patuxent River case-study area. Whereas nitrogen loading from the Susquehanna River to the mainstem bay increased by 2.5-fold between 1945 and 1990, input rates during the last 10–15 years have shown signs of a declining trend (Hagy et al. 2004; Kemp et al. 2005). This decline in nitrogen loadings coincides with the recent SAV increase in Susquehanna Flats case-study area and other low-salinity regions, presumably related to decreases in epiphytes, phytoplankton, and associated shading of SAV (Kemp et al. 2004). Phosphorus was banned in detergents in the 1980s (Kemp et al. 2005; http://www.chesapeakebay.net/content/publications/cbp_13049.pdf), which may have been a contributing factor, in part, to this resurgence.

Additional water quality parameters that were significantly linked to SAV in the case-study areas included median Secchi depth, mean surface-water temperature, mean total suspended solids, and median chlorophyll-a for the Susquehanna Flats case-study area, mean Secchi depth and salinity for the Upper Patuxent River case-study area, median total suspended solids, mean chlorophyll-a, and median surface-water temperature in the Upper Potomac River case-study area. Each of these factors, except temperature and salinity, have been identified as key habitat requirements for SAV survival in Chesapeake Bay (Dennison et al. 1993). Because the various freshwater species in this zone have distinct salinity tolerances, salinity patterns driven by drought or rain could influence species distribution patterns at the lower ends of their distribution.

Significant negative correlations were determined between light availability (measured as Secchi and TSS) and SAV bed area, in the low-salinity region of the bay, a trend which was confirmed in the Susquehanna Flats case-study area. The most likely cause for these counterintuitive results was the specific location of water quality sampling stations in deeper channels, around the edges of shallow flats supporting SAV beds. As a result, the SAV can locally improve water clarity within the meadow by increasing sediment deposition, even when turbidity is high or increasing in the more open sections of the upper Chesapeake Bay (e.g., Moore 2004; van der Heide et al. 2007). Visual inspection of the aerial photographs acquired for SAV monitoring in many areas showed clear conditions over the SAV beds as noted by the distinct SAV signature on the photographs, while the adjacent, unvegetated deeper areas were distinctly more turbid.

The resurgence of SAV in the Susquehanna Flats and Upper Patuxent River case-study areas provides insight into the dynamics of these SAV populations and how rapidly they can recover. The Susquehanna Flats were recognized in the first part of the twentieth century for the abundant waterfowl that was attracted to the vast stands of native SAV species, but in the late 1950s these species were replaced by the invasive *M. spicatum* (Bayley et al. 1968). Although SAV populations were gradually decreasing in abundance during the 1960s, they underwent a dramatic decline in 1972 when massive amounts of sediments and nutrients were driven into the bay by the intense rainfall associated with Tropical Storm Agnes (Bayley et al. 1978; Kemp et al. 1983). The Susquehanna Flats remained very sparsely vegetated until the late 1990s, with only sporadic patches of several species recorded, notably *M. spicatum*, *C. demersum*, *and H. verticilatta* (Orth et al. 2007).

The rapid expansion from the late 1990s through 2006, likely from both seed production and vegetative fragmentation from these meadows as they have increased in area (Rybicki et al. 2001), has resulted in the largest and most diverse SAV beds (13 species) in the Chesapeake Bay, including meadow and canopy-forming natives (e.g., *V. americana* and *H. dubia*) and exotics (*M. spicatum and H. verticillata*) and may be approaching abundances not recorded here since the 1950s (Bayley et al. 1968; Kemp et al. 2005; Orth et al. 2007).

In the Upper Patuxent River case-study area, improvements in sewage-treatment plants in the late 1980s and 1990s led to the initial removal of phosphorus and then nitrogen (Boynton et al. 2008). Fisher et al. (2006) suggested nitrogen as the key nutrient controlling SAV populations, as it was only when nitrogen was reduced that SAV populations rebounded, and although phosphorus was also a significant water quality variable in our analysis, nitrogen was most commonly negatively related to SAV abundance at multiple spatial scales. Many small SAV beds, consisting of a variety of freshwater species, were initially reported from field surveys in the late 1980s and early 1990s (http://vims.edu/bio/sav) in the small creeks entering the upper Patuxent. In 1993, SAV was first reported outside these small creeks in the mainstem upper Patuxent River and subsequently rapidly established in the fringing shoals of this case-study area, most likely from propagules exported from these small creeks. These beds, which now consist primarily of *H. verticillata*, *C. demersum*, and *N. guadalupensis*, have persisted through 2006. A major limitation to their widespread expansion is the absence of extensive shoal areas with potential SAV habitat; in contrast, the broad shallow areas of Susquehanna Flats offered ideal habitat for large SAV beds once environmental conditions improved.

SAV trends in the Upper Potomac River case-study area exhibited an almost threefold change over the period of this study, with dramatic fluctuations in the last 15 years. This case-study area is dominated by the invasive *H. verticillata*, which first appeared near Washington, DC around 1982 (Carter and Rybicki 1986; Rybicki and Landwehr 2007). Prior to 1982, this study area was completely unvegetated (Carter and Rybicki 1986). *H. verticillata* spread rapidly downriver and has become a permanent member of the SAV community along with numerous other native SAV species (Rybicki and Landwehr 2007). In an earlier analysis of SAV resurgence from 1980–1989, prior to the fluctuations observed in the 1990s, Carter et al. (1994) reported that Secchi depth, chlorophyll-a, and particularly total suspended solids, were strongly correlated with SAV cover, thus underscoring the importance of water clarity in regulating SAV abundance. In a subsequent study of this region that spanned the 1985–2001 period, Rybicki and Landwehr (2007) found SAV diversity was negatively related to nitrogen concentration. They noted that point-source loadings of total nitrogen were reduced by one half to this tidal freshwater portion of the Potomac River between 1985 and 1998 by improvements to the sewage-treatment plant serving metropolitan Washington, DC (Butt and Brown 2000), supporting data from this study on the role of nitrogen influencing SAV abundance.

Medium-Salinity Zone and Case-Study Areas

SAV in the medium-salinity zone increased initially followed by fluctuating abundances. This pattern was also reflected in the Lower Choptank River case-study area within this zone. The medium-salinity zone is currently dominated by one species, *R. maritima.* Prior to the 1972 bay-wide dieback of all SAV species (Orth and Moore 1983), this zone often supported several co-dominant species (*Z. marina*, *P. perfoliatus*, *S. pectinata*, and *Z. palustris*) (Stevenson and Confer 1978). Those species are generally rare in this zone today, except in localized areas with lower salinity for the latter two species (Orth et al. 2007).

R. maritima is an opportunistic species that has a worldwide distribution with well-known “boom or bust” cycles (Kandrud 1991) similar to what we have noted in this section. Cho and Poirrier (2005) and Johnson et al. (2003) reported increases in *R. maritima* populations in Lake Pontchartrain, Louisiana, and in San Diego, CA, respectively, with the onset on ENSO events (El Nino Southern Oscillation), but for different reasons. Cho and Poirrier (2005) suggested drought conditions associated with the ENSO increased salinities and improved water clarity, allowing *R. maritima* to increase and replace several freshwater species. In our study, the strong 2001 medium-salinity SAV expansion coincided with a drought, and the subsequent dramatic decline in 2003 occurred during one of the wettest years on record. Johnson et al. (2003) suggested that warming seawater (1.5°C to 2.5°C) conditions favored increased growth of *R. maritima* over *Z. marina*. In Chesapeake Bay, winters have been warmer in recent years (Pyke et al. 2008), but SAV abundance was not correlated with yearly mean water temperature.

Overall, the medium-salinity zone SAV abundance exhibited significant relationships with nitrogen and phosphorus loading from watersheds. Point-source nitrogen (bed area) and phosphorus (percent change) were related to SAV abundance for the case-study areas. Point-source nitrogen load, flow-weighted concentrations of nitrate, total phosphorus load, and median total suspended solids were related to SAV bed area for the Lower Potomac River case-study area. In addition, annual percent change in SAV bed area was correlated with flow-weighted concentrations of total nitrogen, and below-Fall-Line total phosphorus point-source load, and the multiple linear regression included flow-weighted concentrations of total nitrogen, median Secchi, and mean chlorophyll-a in the Lower Choptank River case-study area. Previous studies have emphasized the importance of interannual variations in river flow as controls on SAV abundance in the Choptank River Estuary (e.g., Stevenson et al. 1993). Recent analyses have shown that from 1996 through 2005, year-to-year variations in

SAV abundance in a portion of the Lower Choptank River were significantly related to Secchi depths, which were, in turn, related to spring river flow (Kemp and Murray 2008; Najjar et al. 2010). Together, these results emphasize the dominant control on SAV abundance in this region of the bay exerted by nutrients and suspended solids, and the implied importance of water clarity (e.g., Kemp et al. 2004).

Although a counterintuitive positive correlation was determined between total phosphorus load and SAV bed area in the Lower Potomac River case-study area, there was a much stronger and negative relationship to measures of nitrogen, suggesting that phosphorus was less of a significant variable than nitrogen at this location. These results suggest that nitrogen may be more important as a limiting nutrient to phytoplankton and or epiphytic macroalgae growing upon the SAV (Neundorfer and Kemp 1993; Fisher et al. 1999).

High-Salinity Zone and Case-Study Areas

SAV in the high-salinity zone showed an initial increase, but then, an overall decline, with bed area being less in 2006 than what was first recorded in 1984. For the whole high-salinity zone, only dissolved inorganic nitrogen showed a significant correlation to SAV bed area, making measures of water column nitrogen significant correlates to SAV abundance throughout the entire bay. The results for the Tangier Sound case-study area, which spans the northern (medium-salinity) border of the high-salinity zone, indicate strong correlation with mean Secchi depth, median chlorophyll-a, and median salinity. In contrast, for the Lower Western Shore case-study area, SAV abundance was related to median dissolved inorganic nitrogen and below-Fall-Line total phosphorus point-source load, but annual percent change in SAV bed area was related to median temperature, flow-weighted concentrations of total nitrogen, and mean Secchi depth.

The particular growth characteristics and dynamics of the two SAV species in this zone and related case-study areas may be related to their light requirements and thus the relative greater importance of Secchi depth. *Z. marina* forms more stable meadows with a higher below-ground biomass ratio and higher light requirements than either *R. maritima* or the other low-salinity species. Additionally, *R. maritima* and the freshwater species often grow very rapidly to the surface to form very dense canopies at the surface, even at high tide (Kemp et al. 2004). Thus, *Z. marina* may be much more sensitive to relatively small changes in light availability, explaining the relationship of Secchi depth and SAV for both the Tangier (total area) and Lower Western Shore (percent change) case-study areas.

The overall SAV trend in this zone and the two case-study areas is likely to be tied to anthropogenic factors. Continued long-term stresses associated with declining water clarity combined with other shorter-term stressors could limit the ability of SAV populations to recover from natural perturbations (e.g., pulsed events such as storms that could alter salinity and turbidity as well as scour newly established plants or unusual temperature events). In the summer of 2005, *Z. marina* died back in much of the lower bay as a result of higher-than-usual summertime water temperatures (Moore and Jarvis 2008). A natural recovery started in 2006 from seeds produced by plants in 2005 prior to the dieback and surviving adult plants (Moore and Jarvis, 2008; Orth and Marion 2008) with some areas approaching abundance levels noted in 2005. However, many areas had very sparse beds that were undetectable or noted as less dense in the 2006 SAV survey (Orth et al., 2007). This one perturbation, which had not been observed previously during this survey, contributed to the declining populations already being shown here prior to 2005. Potential increases in the frequency of abnormally high summertime temperatures associated with climate (see Pyke et al. 2008; Najjar et al. 2010) could present a challenge for *Z. marina*. Because light requirements for this species increase with temperature (Moore 2004) any increase in the frequency of high water temperatures combined with reduced light levels due to increased turbidity (Duarte et al. 2007) places an even greater stress on the plants during the summer months (Moore and Jarvis 2008). This is a period when eutrophication impacts on water clarity are typically at their seasonal worst (Moore et al. 1996, 1997).

Challenges to Identifying the Controls on SAV Abundance

Our analyses and understanding of SAV changes over the time period of this study from both long-term monitoring and research show that SAV abundance in each community-type and case-study area is likely influenced by a variety of factors that can vary in both space and time with nitrogen playing an important role in all regions. Chesapeake Bay is a complex ecosystem that has changed measurably over the course of human settlement (Brush and Hilgartner 2000). Landscape alterations from rapid population growth in bay watersheds have resulted in the increasing nutrient and sediment inputs that are now influencing the dynamics of SAV populations bay-wide (Kemp et al. 2005). SAV populations had undergone major changes beginning in the 1960s and accelerating in the 1970s, resulting in an overall diversity and distribution that is different than what was reported at the start of this period for most areas. For example, the medium-salinity communities are now dominated by only a single species (*R. maritima*) compared to a historically diverse assemblage of several co-dominant species. Given this changing, complex system, our work has shown consistent relationships with nutrients in all areas and declining water clarity in the high-salinity areas. Interestingly, though shorter-term stressors likely had strong influences in particular regions and years, as exemplified by the temperature-driven dieback of *Z. marina* in 2005 (Moore and Jarvis 2008) and the wet-year/dry-year dynamics in the Choptank River (Kemp and Murray 2008), they did not emerge as strong individual predictors of SAV abundance across the entire time series.

There are several reasons that these analyses of Chesapeake Bay SAV and water quality did not detect consistent thresholds or "tipping points" for SAV declines and recoveries. The combination of multiple coexisting species with differing physiological constraints and the highly variable nature of environmental conditions in Chesapeake Bay SAV reduce the likelihood of observing clear threshold responses to gradual monotonic changes in water quality or even onetime pulsed events. For example, in mixed stands of *R. maritima* and *Z. marina* that are common in the high-salinity community zone (Orth and Moore 1988), *R. maritima* did not diminish when *Z. marina* declined in the summer of 2005. Furthermore, monthly water quality data from widely spaced stations and annual SAV surveys may not detect short-term temporal events (e.g., unusually high water temperatures in 2005) that would require an analysis of finer temporal or spatial scale data. Yet, the lack of linear cause–effect responses suggests that changes may be related to the exceedance or non-exceedance of threshold conditions where the SAV response may greatly exceed the absolute change in the conditions (Duarte 1995; Krause-Jensen et al. 2008). For example, if reduced water clarity attenuates available light below the compensating irradiance (where photosynthesis meets metabolic demands), SAV will continue to decline even with no subsequent reductions in water clarity. Short-term periods of water quality stress during critical growth periods such as high turbidity during spring and summer can cause significant declines during some years, while mean conditions appear unchanged (Moore et al. 1997). In addition, the effects of high turbidity could be reduced by lower-than-average temperatures during this critical time period (Moore et al. 1997; Moore and Jarvis 2008). Thresholds for controlling seagrasses have also been suggested for silt–clay content (Terrados et al. 1998) and light regimes under both clear and turbid conditions (Kenworthy and Fonseca 1996; Duarte et al. 2007).

Feedback dynamics (both positive and negative) may also influence SAV communities in ways that are not directly correlated with changes in regional water quality. Positive feedbacks may be locally important during expansion of SAV beds, such as the rapid SAV increase in the Susquehanna Flats case-study area. Resurging SAV reduces sediment resuspension and therefore improves water clarity (Ward et al. 1984; Moore 2004), and local propagule availability can further accelerate recovery. The continued increase in SAV coverage in the Susquehanna Flats case-study area, which now supports the largest and densest SAV bed in the Chesapeake Bay, may reflect the ability of this bed to strongly influence its immediate environment. Beds of freshwater species that form extremely dense canopies such as *H. verticillata* and *M. spicatum* may be less susceptible to poor water clarity and can actually improve clarity so that it is suitable to support other SAV species within the bed. Rybicki and Landwehr (2007) noted this phenomenon occurring within dense beds of *H. verticillata.* Negative feedback occurs when sediment resuspension in areas that have lost SAV prevents recolonization (Scheffer et al. 2001), either because wave and currents prevent propagule establishment (Koch 2001) or light requirements for recolonizing SAV are greater (Duarte et al. 2007).

Additional localized and/or episodic stressors that may alter patterns of SAV directly or indirectly may also have reduced correlations with water quality variables using annual time steps. Biotic factors such as the digging activities of cownose rays (*Rhinoptera bonasus*) and mute swans, an invasive species, can have serious deleterious consequences on SAV beds (Orth 1975; Hovel and Lipcius 2001). Heck and Valentine (2007) highlight the often overlooked potential top-down effects of grazing on SAV populations, something not directly measured in our study. Episodic events such as algal blooms (Gallegos and Bergstrom 2005) and hurricanes can also influence local populations of SAV. Storm effects from Hurricane Isabel in September 2003 (class 1 hurricane, Sellner 2005) had localized affects on SAV populations (Orth et al. 2005) that were directly exposed to hurricane-force winds in the lower bay. However, even though these significant events have been observed to have large impacts at the bed scale (Williams 1988), they were not found to be strong drivers of bay-wide or even region-wide patterns in SAV abundance within Chesapeake Bay.

Alternatively, localized reductions of stressors could lead to SAV increases. Water clarity improvements from dense concentrations of the filter-feeding dark false mussel (*Mytilopsis leucophaeata*) have been correlated with improvements of SAV in a medium-salinity zone of Chesapeake Bay (Bergstrom, unpublished data).

Data applicability may also be an issue. Water quality measurements used in these analyses were all made at mid-channel locations, several of which are fairly far from the shallow shoals that SAV beds inhabit and thus may not adequately reflect conditions experienced by SAV since comparisons of water quality parameters have consistently shown differences between mid-channel and shoal areas (Kemp et al. 2004; Moore 2004). Many rivers have only one water quality monitoring station often located far from existing SAV. In addition, the spatial and temporal coverage of the water quality sampling regime may not be sufficient to capture local-scale or transient processes affecting SAV. For example, in low-to-medium-salinity regions of the bay, "mahogany-tide" phytoplankton blooms over the course of several weeks were sufficient to cause localized losses of SAV in 2000 (Gallegos and Bergstrom 2005). Similar brief (2–4 weeks) periods of hydrologically driven high turbidity were associated with summertime eelgrass declines (Moore et al. 1996, 1997).

Implications

Chesapeake Bay has a long, extended salinity regime of approximately 300 km (Kemp et al. 2005), allowing the elucidation of different SAV responses to water quality in different salinities. The different SAV responses have resulted in SAV resurgence in low-salinity regions, moderate increases and then a leveling off in medium-salinity areas, and increases followed by declines in high-salinity areas. However, in all areas, consistent negative correlations to measures of SAV abundance to nitrogen loads or concentrations suggest that meadows are responsive to reduced input of nitrogen. In estuaries with more compressed salinity gradients, interpreting SAV responses to various environmental parameters is confounded by the juxtaposition of high- and low-salinity SAV and water quality gradients. Thus, the unique opportunity to differentiate between the different SAV responses in different salinity zones in Chesapeake Bay may provide an opportunity for a more targeted management strategy to protect and restore SAV. Analysis of two decades of SAV abundance data suggests that nutrient reduction strategies are still the priority in all salinity zones of Chesapeake Bay. Correlations to other metrics such as water clarity measures suggest that these are also important, especially in the higher-salinity areas of the bay.

Chesapeake Bay has historically supported large, contiguous and species-rich SAV meadows that were likely more resilient to environmental variability (Stevenson and Confer 1978; Orth and Moore 1983; Brush and Hilgartner 2000; Scheffer et al. 2001; Kemp et al. 2005). Even though many areas have shown increases in SAV abundance during this study, these SAV distributions are still below historical distributions and are more fragmented. Chesapeake Bay resource managers have developed SAV restoration targets for all areas of the bay. These targets were based on a combination of both recent historical photography obtained for the period 1937 through 1976 (when available and SAV was visible) and current abundance levels (1984 through 2001) (Chesapeake Bay Program 2003, 2004a). These targets will be used as an indicator of improving water quality (Dennison et al. 1993). Resource managers have also developed bottom area estimates of shallow water to the 2-m-depth contour as an estimate of how much area is potentially available for SAV growth to this specific depth (Table 3). Current maximum SAV coverage reported here in this time period (1984–2006) for almost all areas remain below restoration targets established for the Chesapeake Bay, salinity zones, and case-study areas (Table 3), indicating that SAV abundance and associated ecosystem services may currently be limited by continued poor water quality, and specifically high nutrient concentrations, within Chesapeake Bay. Some case-study areas have achieved or are approaching their target (e.g., Upper Patuxent River, Upper Potomac River, Susquehanna Flats) yet do have available habitat to colonize if water quality conditions continue to improve. The nutrient reductions we noted in some tributaries, which were highly correlated to increases in SAV abundance, suggest management options have already contributed to SAV increases, but the consistent negative correlation throughout the Chesapeake Bay between nitrogen and SAV abundance also suggests that further nutrient reductions may be necessary for SAV to attain or exceed restoration targets throughout the Bay.

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