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Effects of Watershed and Estuarine Characteristics on the Abundance of Submerged Aquatic Vegetation in Chesapeake Bay Subestuaries

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ABSTRACT: Watershed land use can affect submerged aquatic vegetation (SAV) by elevating nutrient and sediment loading to estuaries. We analyzed the effects of watershed use and estuarine characteristics on the spatial variation of SAV abundance among 101 shallow subestuaries of Chesapeake Bay during 1984–2003. Areas of these subestuaries range from 0.1 to 101 km^2, and their associated local watershed areas range from 6 to 1664 km^2. Watershed land cover ranges from 6% to 81% forest, 1% to 64% cropland, 2% to 38% grassland, and 0.3% to 89% developed land. Landscape analyses were applied to develop a number of subestuary metrics (such as subestuary area, mouth width, elongation ratio, fractal dimension of shoreline, and the ratio of local watershed area to subestuary area) and watershed metrics (such as watershed area). Using mapped data from aerial SAV surveys, we calculated SAV coverage for each subestuary in each year during 1984–2003 as a proportion of potential SAV habitat (the area $<$ 2 m deep). The variation in SAV abundance among subestuaries was strongly linked with subestuary and watershed characteristics. A regression tree model indicated that 60% of the variance in SAV abundance could be explained by subestuary fractal dimension, mean tidal range, local watershed dominant land cover, watershed to subestuary area ratio, and mean wave height. Similar explanatory powers were found in wet and dry years, but different independent variables were used. Repeated measures ANOVA with multiple-mean comparison showed that SAV abundance declined with the dominant watershed land cover in the order: forested, mixed-undisturbed, or mixed-developed $>$ mixed-agricultural $>$ agricultural $>$ developed. Change-point analyses indicated strong threshold responses of SAV abundance to point source total nitrogen and phosphorus inputs, the ratio of local watershed area to subestuary area, and septic system density in the local watershed.

Introduction

Submerged aquatic vegetation (SAV) is an integral part of the Chesapeake Bay ecosystem. SAV provides habitat for shellfish and fish, supplies food for waterfowl and marsh mammals, absorbs excess nutrients, and helps control shoreline erosion (Lubbers et al. 1990). In the late 1960s and early 1970s, there was a dramatic Bay-wide decline in SAV abundance (Orth and Moore 1983) that was closely related to the deterioration of water quality (Kemp et al. 2004). Since then, SAV coverage has remained consistently low relative to pre-decline levels.

Human activities can harm SAV by degrading estuarine water quality and by promoting physical disturbances and algal blooms (e.g., Stevenson et al. 1993; Cerco and Moore 2001; Cerco et al. 2002; Kemp et al. 2004; Gallegos and Bergstorm 2005). Reductions in light availability associated with increased inputs of nutrients and suspended sediments are especially damaging to SAV (Cerco and Moore 2001; Kemp et al. 2004). Studies of habitat requirements of SAV have focused on light availability and on water column and benthic parameters that modify water clarity and light availability over SAV beds. Epiphytes, total suspended solids, chlorophyll concentration, and nutrients are the most important factors commonly considered (Gallegos 2001; Kemp et al. 2004). Suitable SAV habitats for Chesapeake Bay and its tidal tributaries have been defined by relating SAV presence or absence to five water quality variables (Dennison et al. 1993; Batiuk and Bergstrom 2000) and six physical, geological, and chemical variables (Koch 2001).

In contrast to studies focused on water quality conditions near SAV beds, landscape analysis has been increasingly applied to identify watershed effects on estuarine responses (Comeleo et al. 1996; Paul et al. 2002; King et al. 2005; Bilkovic et al. 2006; Rodriguez et al. 2007). Watershed land cover characteristics can be strong indicators of degraded estuarine health (Hale et al. 2004; Brooks et al. 2006). Watershed development has been associated with lower estuarine species diversity,

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altered food webs, and altered benthic community composition (Dauer et al. 2000; Lerberg et al. 2000; Breitburg 2002; Deegan et al. 1997; Desmond et al. 2002). Previous studies at the Smithsonian Environmental Research Center reported that local watershed land cover provided significant indicators of marsh bird diversity (DeLuca et al. 2004), blue crab and bivalve abundances (King et al. 2005), and toxicants in fish (King et al. 2004). The most commonly used landscape indicators of estuarine condition include simple and distance-weighted land cover proportions (e.g., Paul et al. 2002; Hale et al. 2004; King et al. 2005).

Historically, SAV inhabited the shorelines of creeks and embayments of major and minor tributaries of Chesapeake Bay. Such shallow estuarine embayments are biologically active interfaces between the land and the sea. Embayments temporarily retain water within the shallow nearshore zone, concentrating the effects of local watershed inputs and prolonging their residence in shallow areas. We focused on small subestuaries with well-mixed (nonstratified) estuarine tidal waters where the entire water column interacts with benthic processes. These well-mixed estuarine waters are a mixture of fresh water from their local watersheds and more saline water from adjacent estuarine or coastal waters. Within a subestuary, salinity can range from fresh to polyhaline. Subestuaries can differ in their internal salinity ranges, in the proportions of waters of various salinities, and in tidal marsh area. Small subestuaries are semi-enclosed and are relatively shallow, so the dilution of nutrients and suspended solids due to the interactions with the main channel of the Bay should be lower than in larger subestuaries and more open waters. These factors could make the linkage of small subestuaries to their local watersheds relatively strong.

We sought to identify the controls of variability in SAV abundance among Chesapeake Bay subestuaries. In our underlying conceptual model, watershed stressors affect estuarine water quality, which in turn affects SAV abundance. The linkages from watershed stressors to water quality and then to SAV are modulated by estuarine characteristics. In our ideal analysis, data on watershed characteristics, estuarine characteristics, water quality, and SAV abundance would be available for every subestuary of Chesapeake Bay. Such a data set could support a multivariate analysis in which causal pathways could be statistically traced from watershed stressors through intermediate water quality variables to SAV effects (e.g., structural equation modeling; Pugesek et al. 2003; Ahronditsis et al. 2007). Available water quality data were insufficient to support a causal analysis (see Discussion). Extensive spatial data were available on watershed characteristics, estuarine characteristics, and SAV abundance. We could apply landscape analysis and statistical modeling to identify watershed and estuarine characteristics that correlate strongly with differences in SAV abundance among subestuaries and to develop multivariate statistical models for predicting SAV abundance from the geographic characteristics. To quantify SAV abundance, we used digital maps of aerial survey data collected from 1984 to 2003 (Moore et al. 2000). This valuable data set is unique in providing complete spatial coverage of a large estuary over two decades. All the data were collected after the major SAV decline of the 1960s and 1970s (Orth and Moore 1983); our analysis addresses factors that control post-decline variation in abundance among subestuaries, not the factors that caused the decline.

We applied a number of statistical analyses to relate the variation in SAV abundance among subestuaries to landscape characteristics and to annual precipitation. We grouped subestuaries by the dominant land uses in their watersheds, and then tested for differences in SAV abundance among those dominant land use categories in average, wet, and dry years. We explored the univariate correlations of SAV abundance with several watershed and estuary metrics. Some of those relationships were strongly nonlinear, so we also applied a change-point analysis to test for threshold responses of SAV abundance to landscape stressors. We used regression tree analysis to combine the landscape metrics in multivariate models that account for much of the variability in SAV abundance among subestuaries. These analyses tested our hypotheses that anthropogenic stressors (such as farming, housing, or point source discharges) in a watershed have negative effects on SAV abundance in receiving estuaries and that estuarine characteristics modulate the effects of those stressors. In the discussion, we consider the limitations of our approach and possible directions for future research.

Materials and Methods

Study Area and Subestuary Selection

One hundred and one small subestuaries within Chesapeake Bay and their associated local watersheds were included in this study. We initially selected 128 watershed-subestuary systems (Fig. 1), but we eliminated 25 that had already been identified as no-grow zones for SAV (USEPA 2003). Two additional subestuaries (Mattawoman and Piscataway Creeks of the upper Potomac) were excluded because unusually high SAV abundances in certain years were driven by the boom and bust

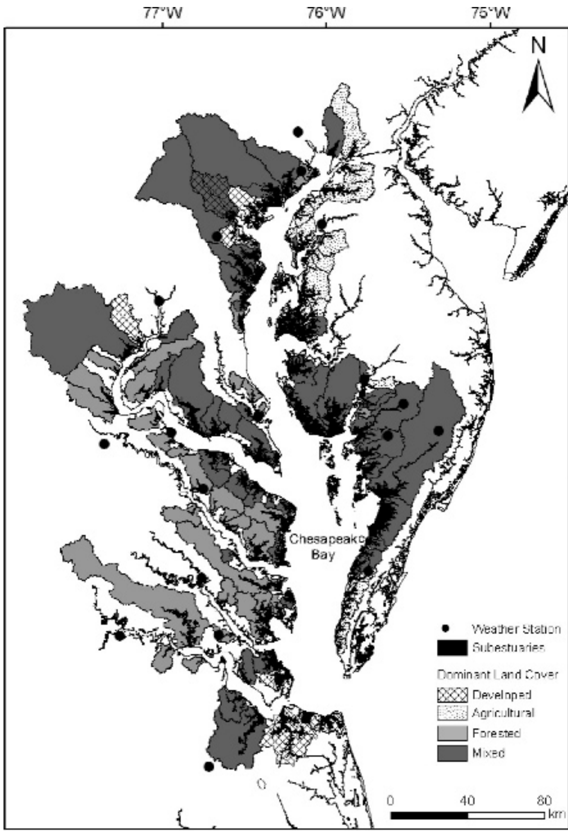

Fig. 1. Subestuaries of Chesapeake Bay and their local watersheds, dominant land cover categories, and weather stations.

cycle of the invasive freshwater plant Hydrilla, which was not tied with water quality issues (Orth personal communication). All the selected subestuaries had one or more mapped perennial streams flowing into the subestuary.

Boundaries for the study subestuaries were taken from a 1:24,000 digital shoreline map of Chesapeake Bay (FGDC 2001; http://www.ngs.noaa.gov/newsys_ims/shoreline). For each subestuary, we added a line across the mouth to the digital shoreline to form a closed polygon representing the water surface. The local watershed boundaries were delineated from digital elevation maps and stream maps. We used the Spatial Analyst Tools of the ArcInfo. 9.1 (ESRI, Inc.) geographic information system (GIS) to analyze 1:24,000 DEM data (Caruso 1987; http://edc.usgs.gov/geodata/) and vector stream maps derived from the same 7.5 minute quadrangles (USGS 1999; http://nhd.usgs.gov). In Coastal Plain landscapes with low relief and low variation in elevation, we manually corrected the automated watershed delineation results (Baker et al. 2006) and checked local watershed boundaries with the boundaries of U.S. Geological Survey 12 or 14-digit hydrologic unit code (Allord 1992; http://water.usgs.gov/GIS/huc.html).

Data Sources

SAV

The data on SAV presence and density came from digital maps of aerial SAV surveys prepared by the Virginia Institute of Marine Sciences for the Chesapeake Bay Program (CBP; Moore et al. 2000; http://www.vims.edu/bio/sav). Bay-wide aerial surveys of SAV have been done annually from 1984 to 1987 and 1989 to 2003. Photography was acquired from an altitude of approximately 12,000 feet, yielding 1:24,000 scale photographs following 130–200 flight lines each year around the entire Chesapeake Bay (Orth 2004). The photographs were examined to identify all visible SAV beds, and the photographs covering SAV beds were scanned and orthorectified into digital mosaics. Outlines of SAV beds were interpreted on-screen and edge-matched to yield a digital database containing the locations and areas of visible SAV beds. Beds were also classified into one of five coverage density classes (no SAV 0% coverage, very sparse 0–10%, sparse 10–40%, moderate 40–70%, and dense 70–100%). The aerial photograph interpretations were verified and corrected with extensive ground survey data (Orth 2004). From 1985 to 1996, over 10,000 SAV ground survey observations were incorporated (Moore et al. 2000). A 1990 accuracy assessment demonstrated a strong linear relationship ($r^2 = 0.99$, $p < 0.001$) between mid points of SAV density classes from photo interpretation and ground survey measurements (Moore et al. 2000). Aerial survey methods have also been widely applied to map SAV presence and abundance in many published scientific studies (e.g., Ferguson et al. 1993; Lehmann et al. 1997; Robbins 1997; Kendrick et al. 1999; Zharikov et al. 2005).

We intersected each annual SAV map with the boundaries of our selected subestuaries and with a map of the maximum extent of potential SAV habitat. The potential habitat map included all areas less than 2 m deep, except for areas that have been judged unlikely to support SAV (no-grow zones) because of historical observations of continuous SAV absence since 1930s or unfavorable exposure regimes (Orth et al. 1992; USEPA 2003). Restoring SAV to all of this potential habitat area has been designated as the Tier III restoration goal by the CBP (USEPA 2003). For each subestuary polygon, the map of individual SAV beds was summarized into the overall percentage of SAV abundance (SAV_a) using the equation:

$$\%SAV_a = \frac{\sum(\%SAV_d \times A_b)}{\sum A_{T3}}, \qquad (1)$$

where SAV_d is the SAV density observed in an SAV bed, A_b is the area of the SAV bed, A_{T3} is the Tier III estimate of potential SAV habitat in the bed, and $\sum$ represents summation over all the SAV beds in the subestuary. We simplified the five reported density classes for SAV beds by replacing each density range with its median value (no SAV 0%, very sparse 5%, sparse 25%, moderate 55%, and dense 85%). If A_{T3} were replaced with the area of a different restoration goal (USEPA 2003), then Eq. 1 would yield SAV abundance relative to that restoration goal rather than to the Tier III area.

Land Cover

Watershed land cover information was calculated from the second generation of the National Land Cover Dataset (NLCD 2001; 30 m resolution; Homer et al. 2004), which was derived from Landsat 7 satellite remote sensing imagery. This national standard data set incorporates improved methods for classifying land-cover data from satellite imagery (Homer et al. 2004), and cross-validation analysis demonstrates an overall classification accuracy of 77% across the mapping zone that contains the Chesapeake Bay (NLCD zone 60; metadata file at http://www.mrlc.gov/show_data_nlcd.asp?ID=60). In each watershed, we calculated the percentages of cropland, forest, and developed land because these land cover proportions are useful predictors of nutrient and sediment delivery (Jordan et al. 1997a; Weller et al. 2003). As in earlier work (King et al. 2005; Brooks et al. 2006), we classified each watershed into one of six land cover categories based on the dominant land cover type: (1) forested ($\geq$ 60% forest + forested wetland), (2) developed ($\geq$ 50% developed land), (3) agricultural ($\geq$ 40% cropland), (4) mixed-developed (15–50% developed), (5) mixed-agricultural (20–40% cropland), and (6) mixed-undisturbed. The last category includes all watersheds that can not be classified into any of the other five categories and are dominated by mixtures of forest, grassland, and wetland.

Point Source Nutrient Discharges and Septic System Density

To quantify wastewater nutrient loading to subestuaries, we used publicly available point source discharge data (Wiedeman and Cosgrove 1998) to calculate monthly and annual total nitrogen (TN) and total phosphorus (TP) loads from 1984 to 2003 for each study watershed. Since 1984, the Environmental Protection Agency CBP office has compiled point source discharge data from active industrial, municipal, and federal facilities discharging directly to surface waters within the Chesapeake Bay watershed (Wiedeman and Cosgrove 1998). Septic system density was estimated for each watershed from 1990 U.S. Census data on households with and without public sewer service (www.census.gov).

Precipitation

To explore the effect of precipitation regimes on SAV abundance, we summarized monthly precipitation data for 1984–2003 that were recorded at 22 weather stations (Fig. 1) around the Chesapeake Bay (National Oceanic and Atmospheric Administration, National Climatic Data Center, http://cdo.ncdc.noaa.gov/ancsum/ACS). For each study subestuary, we used data from the nearest weather station and calculated annual precipitation and seasonal precipitation for spring (March-May) and summer (June-August). We categorized the weather regime of each watershed in each year as average (annual precipitation within 1/2 standard deviation [SD] from the mean), dry (annual precipitation more than 1/2 SD below the mean), or wet (annual precipitation more than 1/2 SD above the mean).

Salinity

Each study subestuary was assigned one of four salinity categories (tidal fresh [TF] 0–0.5, oligohaline [OH] 0.5–5, mesohaline [MH] 5–18, and polyhaline [PH] $>$ 18) by intersecting our subestuary boundaries with a CBP map of salinity zones (USEPA 2004). The map was derived from 12 yr (1985–1996) of salinity data from monitoring stations. Each station was assigned to one of the four salinity regimes based on the 12-yr grand mean of the monthly mean surface salinities, but bottom grand mean salinity was also considered in borderline decisions. To create a Bay-wide map, 0.5 salinity isopleths were interpolated from the monitoring station data, and segment lines were constructed at the isopleth breaks using the salinity classifications described above (USEPA 2004).

Coastal Vulnerability

We intersected our subestuary boundaries with a 1:2,000,000-scale digital map of coastal vulnerability (Thieler and Hammar-Klose 1999) to derive four additional independent variables describing each subestuary: coastal slope, relative sea-level rise, mean tidal range, and mean wave height. The attributes in this data set were based on a coastal hazards database for the U.S. East Coast (Gornitz and White 1992) updated with data from more recent sources (Thieler and Hammar-Klose 1999). Coastal slope was calculated from a grid of topographic and bathymetric elevations extending

TABLE 1. Landscape metrics of Chesapeake Bay subestuaries and their local watersheds.

Metric	Description	Median value	Value range or categories
SubestArea	Subestuary area in km^2	8.0	0.1–100.8 km^2
SubestPerim	Subestuary perimeter in km	54.9	6.7–500.0 km
SubestVol	Subestuary volume in $km^3 \times 1000$	9.6	0.1–205.8 km^3
DepthMean	Subestuary mean depth in m	1.6	0.3–8.3 m
Mouth width	Subestuary mouth width in km	1.3	0.1–10.8 km
Mouth area	Subestuary mouth area in vertical cross-section, in $km^2 \times 1000$	2.7	0.01–57.4 km^2
Shallow water	Percentage of area shallower than 2 m in each subestuary	63.2	4.9–100.0%
Elongation ratio	Subestuary elongation ratio, defined as the diameter of a circle with the same area as subestuary divided by the length of the subestuary	0.4	0.07–0.86
Fractal dimension[a]	Subestuary fractal dimension, defined as 2 times the logarithm (ln) of subestuary perimeter (m) divided by logarithm (ln) of subestuary area (m^2)	1.39	1.27–1.58
SubestPerim:Area	Subestuary perimeter to area ratio	7.6	2.5–62.6
SubestPerim:Volume	Subestuary perimeter to volume ratio	5.8	0.9–366.1
SubestLength:MouthA	Subestuary length to mouth area ratio	3.0	0.4–1524.2
ShorlineLength:Area	Subestuary shoreline length to area ratio	18.6	6.4–60.5
WshdArea	Local watershed area of the subestuary in km^2	87.1	6.3–1664.0 km^2
WshdPerim	Local watershed perimeter of the subestuary in km	72.3	15.4–356.0 km
Land cover	Local watershed category of dominant land cover	NA	forested, developed, agricultural, mixed-agricultural, mixed-developed, mixed-undisturbed
WshdArea:SubestArea	Local watershed area to subestuary area ratio	9.5	1.0–3934.0
WshdArea:SubestVolume	Local watershed area to subestuary volume ratio	6.7	0.5–5374.0
Tidal range[b]	Mean tidal range in m	0.5	0.3–0.8 m
Wave height[b]	Mean wave height in m	0.9	0.4–1.0 m
Sea rise[b]	Relative sea-level rise in mm yr^{-1}	3.1	2.5–4.0 mm yr^{-1}
Salinity	Salinity regime	NA	TF, OH, MH, PH

[a] Fractal dimension is a measure of shoreline complexity (see calculation in Ferrarini et al. 2005).
[b] Mean tide range, mean wave height, and relative sea-level rise data are from Thieler and Hammar-Klose (1999).
NA means not applicable.

approximately 50 km landward and seaward of the shoreline. Relative sea level was interpolated from annual mean water elevations measured over time at 28 National Ocean Service data stations along the coastline. Tidal range data were interpolated among 657 tide stations, and mean wave height was interpolated from 151 U.S. Army Corps of Engineers Wave Information Study stations along the U.S. coast (Hubertz et al. 1996).

Subestuary Metrics

We derived descriptive metrics for the size and shape of each subestuary and its watershed through GIS analysis of watershed boundaries, subestuary shorelines, and bathymetric data (Cohen 1994; http://www.ngdc.noaa.gov/mgg/bathymetry/maps). The metrics included: subestuary area, subestuary volume, subestuary mouth width, local watershed area, and other measures of shape or structure (Table 1).

Statistical Analyses

Variation in SAV Abundance with Dominant Land Cover

To investigate the effects of dominant land cover on SAV abundance, we used one-way repeated-measures analysis of variance (ANOVA; SAS Institute, Inc. 1999) with the category of dominant watershed land cover as the main effect and year of measurement as the repeated time factor. The analysis was done for all subestuaries using all years of data; for four subsets of subestuaries representing the four salinity regimes (TF, OH, MH, and PH); and for three subsets of years corresponding to average rainfall years, dry years, and wet years. When the overall effect of dominant land cover was statistically significant ($p < 0.05$), we used the Student-Newman-Keuls (SNK) method of multiple comparisons (O'Rourke et al. 2005) to identify significant difference between specific dominant land covers.

Univariate Correlations of SAV Abundance with Watershed and Estuarine Characteristics

We used principal components analysis to select a few representative independent variables in each metric group, and then examined univariate correlations of the separate independent variables with the abundance of SAV. The variables having stronger relationships with SAV were included in further analyses (below).

TABLE 2. Repeated-measures ANOVA for variation of SAV abundance among Chesapeake Bay subestuaries during 1984–2003. *Significant at $p < 0.05$.

Factor	Land cover		Year		Land cover × Year	
	F	p	F	p	F	p
All subestuaries	45.04	<0.0001*	3.50	0.0038*	3.53	0.0035*
TF	6.95	0.0013*	0.58	0.4483	6.92	0.0014*
OH	3.42	0.0049*	28.27	<0.0001*	3.46	0.0045*
MH	4.10	0.0011*	23.81	<0.0001*	4.13	0.001*
PH	6.40	<0.0001*	14.92	0.0001*	6.48	<0.0001*
Dry years	5.93	0.0152*	1.93	0.0872	1.91	0.0910
Wet years	6.51	0.011*	1.67	0.1412	1.68	0.1386
Average years	5.12	0.0239*	1.66	0.1407	1.66	0.1423

Threshold Responses of SAV Abundance to Watershed and Estuarine Characteristics

We tested for potential threshold responses of SAV abundance to selected factors using nonparametric change-point analysis, a technique explicitly designed for detecting threshold responses using ecological data (Qian et al. 2003). This analysis is based on the idea that a structural change in an ecosystem may result in a change in both the mean and the variance of an ecological response variable used to indicate a threshold. When observations are ordered along a stressor gradient, a change point is a value that separates the data into the two groups with the greatest difference in means and variances. Change-point analysis works well even when stressor-response relationships are nonlinear or heteroscedastic. We conducted threshold analyses using the custom function chngp.nonpar (Qian et al. 2003) in S-Plus 6.2 for Windows (Insightful Corp., Seattle, Washington).

Combined Effects of Watershed and Estuarine Characteristics on SAV Abundance

We used regression tree analysis to quantify the overall relationships between SAV abundance and environmental factors. Ecological data are often complex, nonlinear, unbalanced, and heteroscedastic (Urban 1987), and may also include both numerical and categorical variables. Traditional regression analyses often fail with such data, but classification and regression tree analysis (CART) is especially appropriate for such situations (Urban 1987). CART has been successfully applied to quantify estuarine responses to environmental variables (De'Ath and Fabricius 2000; King et al. 2005). Using the RPART library in S-Plus (Therneau and Atkinson 1997; Venables and Ripley 2002), we built four separate regression tree models relating average SAV abundance in all subestuaries to selected independent variables. The four CART models considered SAV abundance averaged across all years, and across subsets of years classified as dry, wet, and average rainfall years. We defined a minimum number of splits as five and a minimum observation number of terminal node as three. We pruned the tree in each CART model using cross validation (Therneau and Atkinson 1997).

Results

Characteristics of Watershed-Subestuary Systems

The areas of selected subestuaries and their local watersheds varied widely. Subestuary areas range from 0.1 to 101 km^2, and their associated local watershed areas range from 6 to 1664 km^2 (Table 1). Watershed land cover percentages range from 6% to 81% forest, 1% to 64% cropland, 2% to 38% grassland, and 0.3% to 89% developed land.

Among watersheds and years, wastewater discharge volumes ranged from 0 to 30.2 $m^3\ yr^{-1}$ with an average of 0.8 $m^3\ yr^{-1}$. Only seven of the 101 study watersheds received average annual wastewater discharges greater than 1 $m^3\ yr^{-1}$, and 49 watersheds received no major point source discharges during 1984–2003.

Variation in SAV Abundance with Dominant Land Cover and Annual Precipitation

We analyzed SAV abundance responses to the dominant land cover of the local watershed, to the year of measurement, and to the interaction of dominant land cover and year using repeated-measures ANOVA of data from 1984 to 2003 (Table 2). The overall effect of dominant land cover on SAV abundance was statistically significant ($p < 0.05$) for all subestuaries together, for all four subsets of subestuaries representing four different salinity regimes, and for all three subsets of subestuaries representing three different precipitation regimes. The effect of the year factor on SAV abundance was statistically significant ($p < 0.05$) for all subestuaries together and for the subsets corresponding to three salinity regimes (OH, MH, and PH), but the year factor was not significant for the TF salinity regime or for subsets representing dry, wet, and average annual precipitation (Table 2). The interaction of dominant land cover and

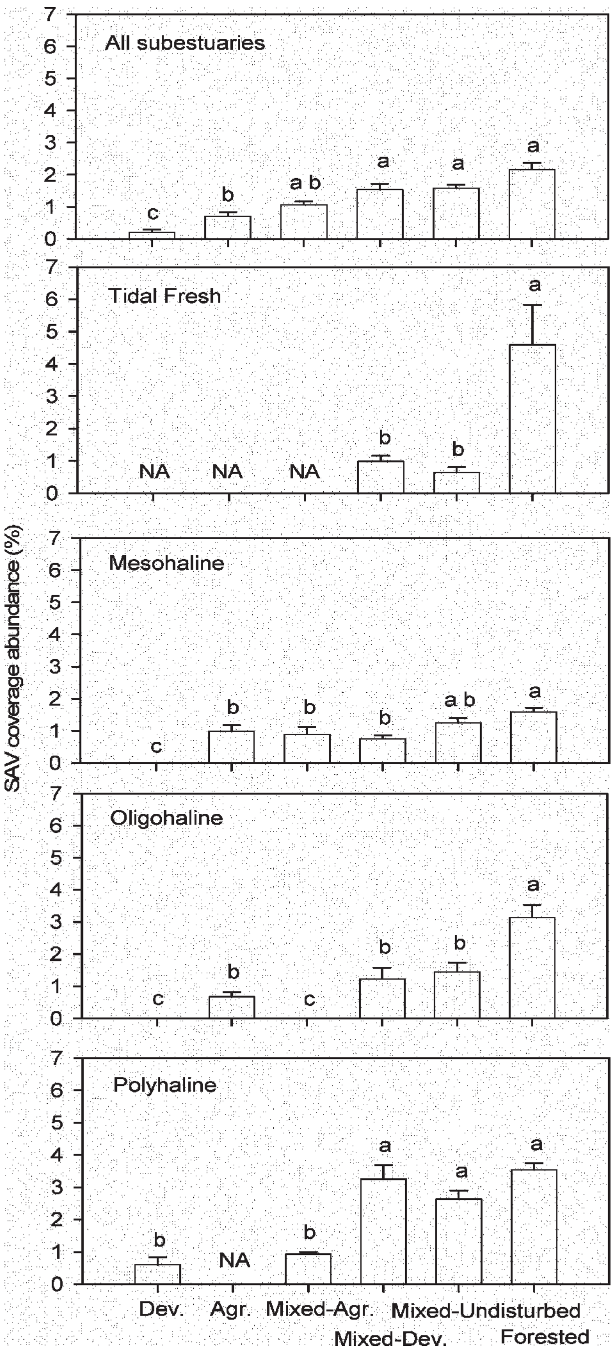

Fig. 2. SAV abundance for different dominant land covers across all subestuaries and for each salinity regime. Bars are standard errors of the means. Different letters indicate significant differences ($p < 0.05$) based on the Student-Newman-Keuls test. For some salinity regimes, there were no watersheds dominated by developed, agricultural, or mixed-agricultural land uses (NA).

year significantly affected SAV abundance ($p < 0.05$) for all subestuaries together and subsets of all four salinity regimes, but not for subsets representing dry, wet, and average annual precipitation.

Multiple mean comparisons (SNK tests) indicated that the general ordering of mean SAV abundance among dominant land cover types was developed land < agricultural land < mixed land < forested land, but the pattern of statistically significant differences among land cover types varied with salinity regime (Fig. 2). The same general ordering of SAV abundance was also consistent across analyses considering all years or subsets for dry, wet, or average years; but the patterns of significant differences again changed among the subsets (Fig. 3). The effect of precipitation regimes on SAV abundance was not statistically significant for all subestuaries together ($p > 0.05$). Across all subestuaries, the average SAV abundance was 1.21% (all years), 1.10% (wet years), 1.43% (dry years), and 1.14% (average years). Subestuaries with agriculturally dominated watersheds had lower SAV abundances in wet years (0.44%) than dry years (0.99%) and this difference was statistically significant ($p < 0.05$). There was no significant difference between wet and dry years for watersheds dominated by developed land. SAV abundance was generally lower in wet years for mixed lands, but higher in wet years for forested land.

Univariate Correlations of SAV Abundance with Watershed and Estuarine Characteristics

Linear correlations of individual independent variables with SAV abundance were generally weak (Table 3). The proportions of developed land and crop land were negatively correlated with SAV abundance, and forest proportion was positively correlated with SAV abundance, but these correlations were weak and not statistically significant ($p > 0.05$). The proportion of developed land is more strongly correlated with SAV ($r = -0.77$, $p = 0.002$) among subestuaries with higher proportions (> 20%) of developed land (Fig. 4). SAV abundance was not correlated with the ratio of local watershed area to subestuary area ($r = -0.18$, NS), but the correlation was much stronger ($r = -0.62$, $p = 0.04$) among subestuaries where the proportion of developed land was greater than 20%.

SAV abundance had significantly positive correlations with two subestuary metrics: mouth width ($r = 0.35$, $p = 0.0009$) and fractal dimension ($r = 0.22$, $p = 0.04$). SAV abundance was positively correlated with mean tidal range ($r = 0.22$, $p = 0.04$; Fig. 4). The septic system density in the local watershed was negatively correlated with SAV ($r = -0.19$, $p = 0.07$). TN and TP in point source nutrient

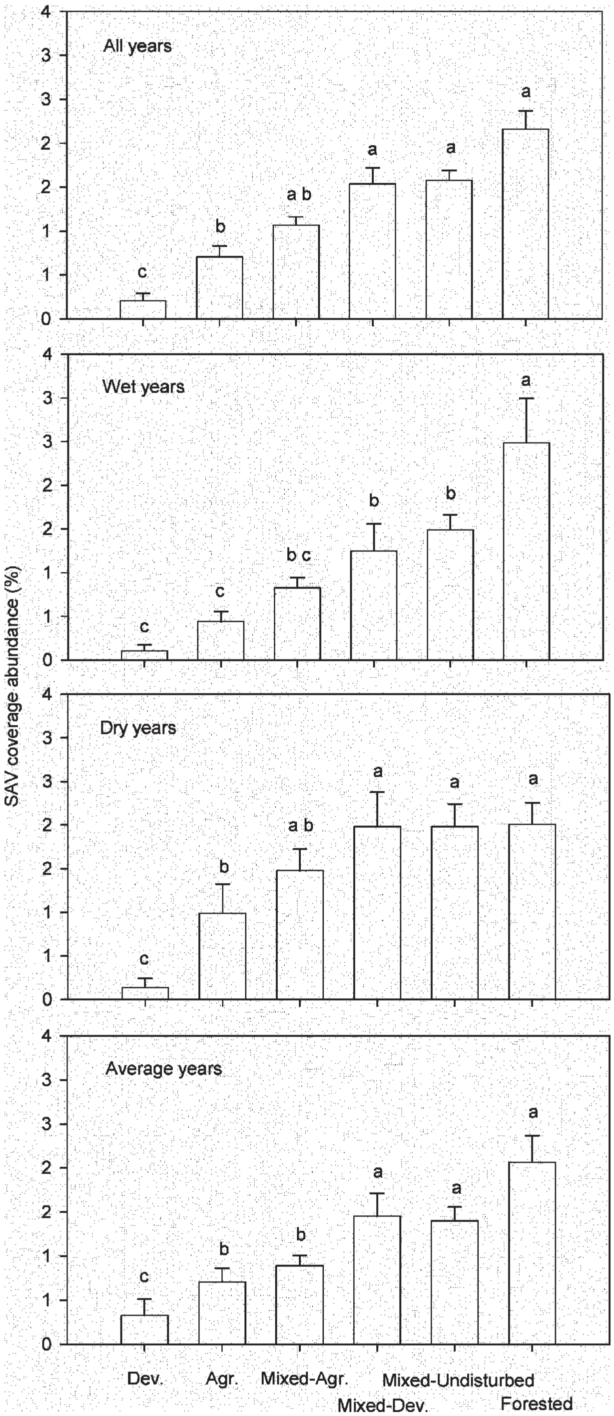

Fig. 3. SAV abundance for different dominant land covers across all subestuaries and for years of dry, wet, and average precipitation. Bars are standard errors of the means. Different letters indicate significant differences ($p < 0.05$) based on the Student-Newman-Keuls test.

TABLE 3. Pearson correlations of SAV abundances with landscape metrics, precipitation, septic system density, and point source discharges. Annual SAV abundances from 1984 to 2003 were compared with annual total nitrogen, total phosphorus, annual precipitation, and summer precipitation. All other metrics were compared with SAV abundances averaged across all years. *Significant at $p < 0.05$.

Metric	R	p
Developed land (%)	−0.12	0.2579
Crop land (%)	0.06	0.5463
Forest (%)	0.16	0.1415
Subestuary mouth width	0.35	0.0009*
Shoreline fractal dimension	0.22	0.0416*
WshdArea:SubestArea	−0.18	0.0993
Mean tidal range	0.22	0.0414*
Mean wave height	0.02	0.8427
Septic system density	−0.19	0.0738
Total nitrogen	−0.02	0.2616
Total phosphorus	0.01	0.5826
Annual precipitation	−0.01	0.6000
Summer precipitation	−0.04	0.1262

discharges had very low linear correlations with SAV, as did annual or summer precipitation.

Threshold Responses of SAV Abundance to Watershed and Estuarine Characteristics

Nonparametric change-point analysis detected change points in the relationships of average SAV abundance with several watershed or estuarine metrics (Fig. 5). The χ^2 test (Qian et al. 2003) indicated a statistically significant change point in the relationships of SAV abundance with the ratio of watershed area to subestuary area ($p < 0.001$), the septic system density in the watershed ($p < 0.044$), and the point source discharges of TN ($p < 0.002$) and TP ($p < 0.001$). For two variables (the ratio of watershed area to subestuary area and the septic system density in the watershed) there was a relatively sharply increasing probability of a change point in a narrow range of the independent variable. The value where there was a 95% probability of a change point occurred at 3.7 for the ratio of watershed area to subestuary area and at 39 km^{-2} for watershed septic system density (Fig. 5). The patterns of SAV responses to point source discharges of TN and TP were similar. The value where there was a 95% probability of a change point occurred at 17.6 kg N km^{-2} d^{-1} for TN and at 1.3 kg P km^{-2} d^{-1} for TP. For TN, the watershed land cover at the right side of the change point at 95% probability was dominated by developed land; for TP, the land cover was dominated by developed land and mixed land.

Combined Effects of Watershed and Estuarine Characteristics on SAV Abundance

Sixty percent of the variation among subestuaries in average annual SAV abundance could be

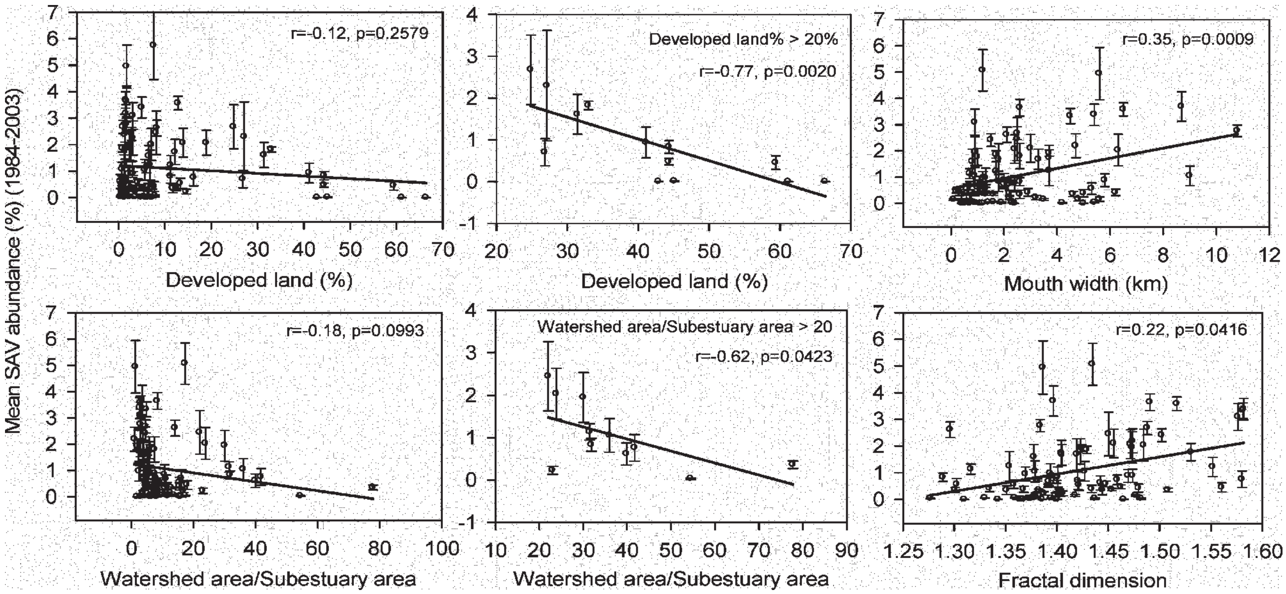

Fig. 4. Correlations of SAV abundance with watershed and subestuary characteristics: proportion of developed land, proportion of developed land (percent developed land > 20%), mouth width of subestuary, ratio of watershed area to subestuary area, ratio of watershed area to subestuary area (ratio > 20), fractal dimension of shoreline. Bars are standard errors of the mean of SAV abundances within each subestuary during 1984–2003.

explained by a regression tree model based on five independent variables: subestuary fractal dimension, mean tidal range, local watershed land cover, the ratio of watershed to subestuary area, and mean wave height (Fig. 6). Fractal dimension, a measure of subestuary shape complexity, appeared at the highest level of the tree. SAV was least abundant (0.4%) when fractal dimension was less than 1.38. The average tidal range was at the second level of the tree. Average SAV abundance was 0.9% when the tidal range was less than 0.4 m. At the third level of the tree, 50 watersheds were split into two groups: 37 subestuaries with developed, agricultural, mixed-developed, mixed-agricultural, or mixed-undisturbed land had lower average SAV abundance of 1.4%, while 13 subestuaries with forested land cover had higher SAV abundance of 3.0%. Thirteen subestuaries with forested land cover were then split into two groups by average wave height, which had a negative effect: average SAV abundance was 2.5% where average wave height was higher than 1.05 m and 3.8% where wave height averaged lower than 1.05 m. For subestuaries with all other land covers, the ratio of watershed to subestuary area had a negative effect on SAV abundance (Fig. 6).

Similar explanatory power was found in regression tree models fit for average, wet, or dry years only (Fig. 6). For years with average precipitation, the tree split pattern and independent variables were the same as for all years, but the regression tree models differed for observations split by wet and dry years. In wet years, fractal dimension was still at the highest level of the regression tree. The importance of the ratio of watershed to subestuary area rose to the second level. SAV abundance in subestuaries with a higher ratio of watershed to subestuary area was then dependent on the salinity regime: nine mesohaline subestuaries had lower SAV abundance (0.3%) while other salinity regimes had higher SAV abundance (1.5%). The land cover effect appeared at the lower level than in the regression tree for all years, and subestuaries with forested watersheds had higher SAV abundance. In dry years, the independent variables selected for the regression tree were similar to those chosen for wet years, but the pattern of splitting was very different. The ratio of watershed to subestuary area was the most important variable in dry years, followed in order of importance by fractal dimension, salinity regime, and the ratio of watershed to subestuary area or watershed land cover.

Discussion

Influence of Landscape Factors on SAV Abundance among Subestuaries

We succeeded in identifying watershed and estuarine characteristics that are useful predictors of variation in SAV abundance among subestuaries. Previous research on SAV habitat requirements has demonstrated that SAV presence and growth are strongly dependent on light attenuation and its

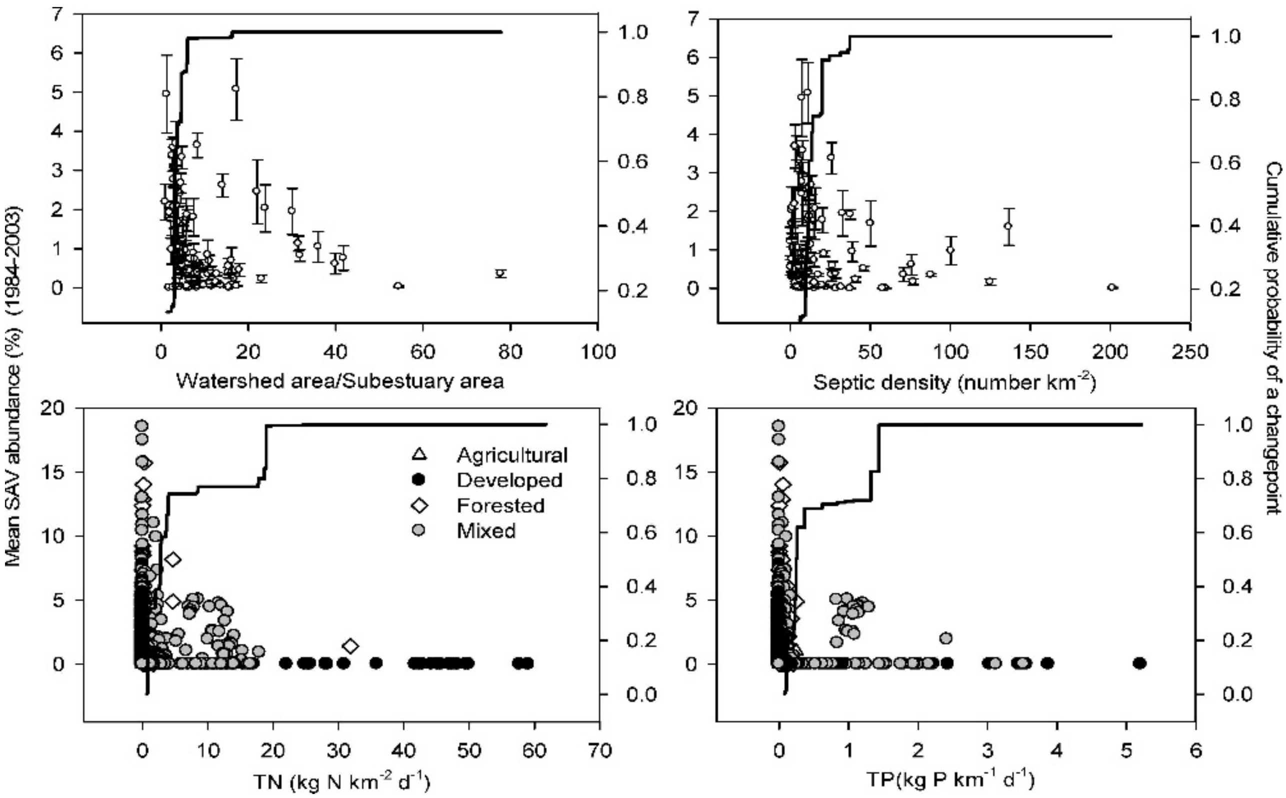

Fig. 5. Threshold responses to SAV abundance: ratio of watershed area to subestuary area, watershed septic system density, total nitrogen discharge from point source facilities, and total phosphorus discharge from point source facilities. The lines indicate the cumulative probability of a change point. Bars are standard errors of the means of SAV abundances within each subestuary during 1984–2003.

controlling factors, particularly water quality (Dennison et al. 1993; Stevenson et al. 1993; Batiuk and Bergstrom 2000; Gallegos 2001; Kemp et al. 2004). In this study, we focused instead on other watershed and estuarine characteristics that may be drivers or correlates of nearshore water quality and can indirectly influence SAV abundance. Our regression tree models showed that variation in SAV abundance among subestuaries was statistically related to watershed land use, estuarine morphological features, estuarine hydrological energy, and salinity regime. Multivariate combinations of these characteristics explained much of the variance in SAV abundance among subestuaries (Fig. 6, $r^2 = 0.49$–0.60), but no single variable could serve as a univariate indicator of SAV abundance (Figs. 4, 6 and Table 3).

The local watershed of a subestuary can be a source of stressors, such as suspended sediment, nutrients, and colored dissolved organic matter; many studies have demonstrated that watershed characteristics affect the condition of estuarine organisms and communities (Comeleo et al. 1996; Paul et al. 2002; DeLuca et al. 2004; King et al. 2005; Bilkovic et al. 2006). Land cover characteristics of watersheds can be strong indicators of degraded benthic communities (Hale et al. 2004). Watershed land cover can affect SAV by elevating nutrient and sediment loading to estuaries (Staver et al. 1996), and SAV responses to watershed inputs have been considered in modeling estuarine water quality (Cerco and Cole 1993; Cerco 1995; Cerco and Moore 2001). Nonpoint source discharges of sediment and nutrients from watersheds go up with increasing proportions of either agricultural or developed lands (Frink 1991; Comeleo et al. 1996; Jordan et al. 1997a,b, 2000, 2003; Paul et al. 2002; Weller et al. 2003) and croplands discharge far more nitrogen than other rural land covers (Beaulac and Reckhow 1982; Jordan et al. 1997a,b). There are several possible sources of nutrients in developed land, including septic systems (Weiskel and Howes 1992; Nizeyimana et al. 1996; Short and Burdick 1996), sewage system leaks, lawn fertilizers, and industrial activity (Cerco et al. 2002). The discharges of suspended solids and associated

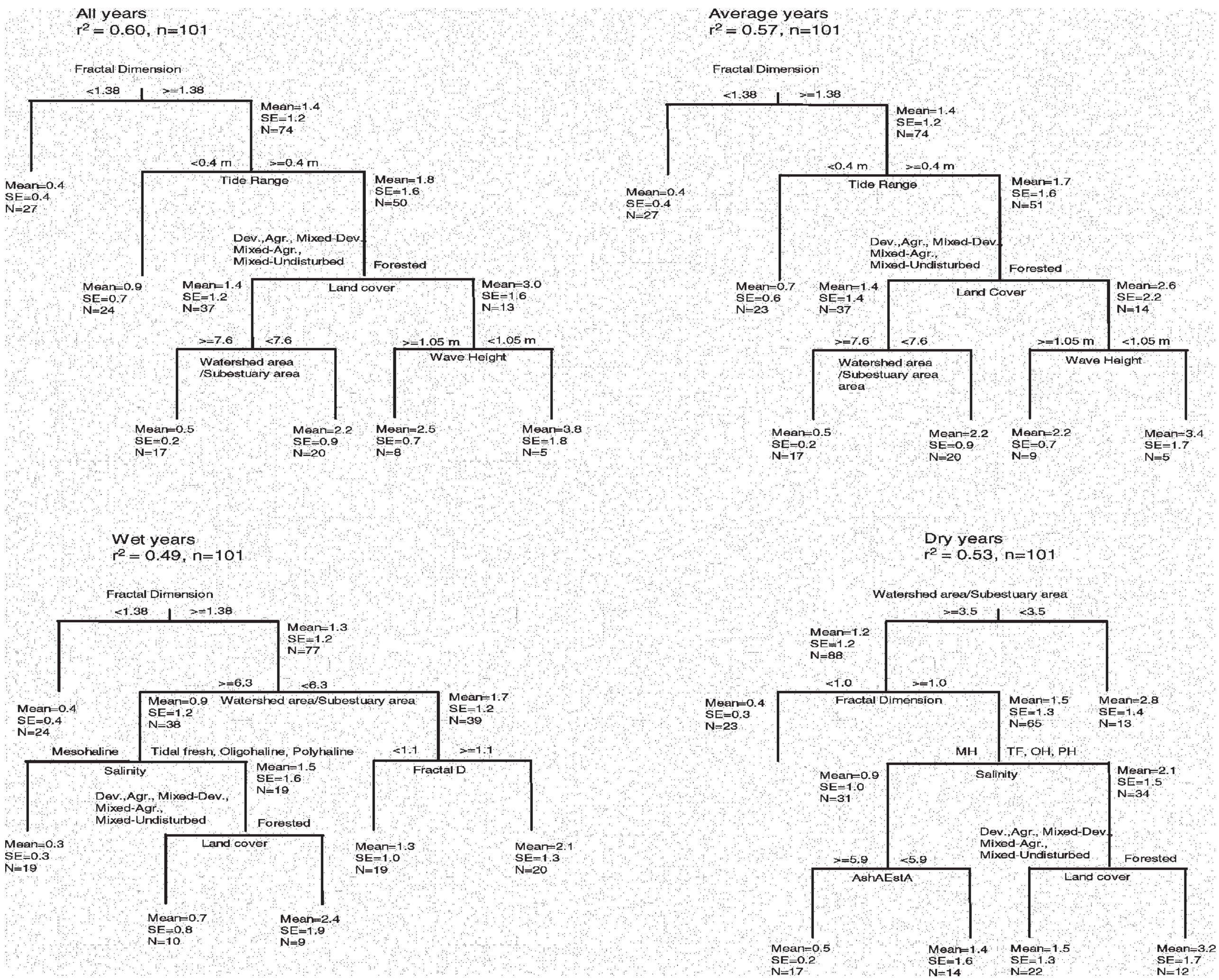

Fig. 6. Regression trees predicting SAV abundance from watershed and estuarine characteristics. Means, standard errors (SE), and number of subestuaries summarize the properties of the group to the left and right of each split. all years, average years, wet years, dry years.

nutrients from developed lands may also increase because of accelerated runoff from impervious surfaces (e.g., Schueler 1987).

Watershed Characteristics

We found that the subestuaries with watersheds dominated by either developed or agricultural land had significantly lower SAV abundances than subestuaries with predominantly forested watersheds (Figs. 2 and 3). This suggests that higher loads of nutrients and sediments from developed or agricultural lands degraded water quality and SAV habitat. The analysis of SAV abundance with the dominant land cover of the local watershed documented the significant influences of agriculture and development, even though the univariate correlations of individual land covers with SAV abundance were not significant (Table 3).

The strong threshold responses of SAV abundance to septic system density and point source discharges (Fig. 5) provided further evidence of the negative effects of development. Short and Burdick (1996) reported negative effects of housing development on seagrasses. They found that the coverage of seagrasses had a linear relationship with the house number in nearshore areas. When responses follow threshold patterns (Fig. 5), simple linear relationships (Table 3) can not effectively describe the responses. For example, the percentage of developed land had significantly negative effects on SAV abundance where developed land was more than 20%, but other factors may control SAV abundance where developed land is less than 20% (Fig. 4). Threshold responses may reflect sudden catastrophic changes in structure of ecosystem (Scheffer et al. 2001). Such catastrophic shifts may be due to the existence of alternative stable states in an ecosystem (Scheffer and Carpenter 2003; Rietkerk et al. 2004). The existence of threshold responses should be considered in managing SAV restoration activities in the Chesapeake Bay.

In this study, we considered the importance of developed land in the entire local watershed of a subestuary. It may also be important to apply spatial analyses to evaluate the differential effects of development close to the subestuary or to an individual SAV bed as well as the effects of shoreline modifications that often accompany nearshore development.

Human sewage is an important nutrient source to the Chesapeake Bay. In the James, York, and Rappahannock Rivers, point sources contributed 5–48% of nitrogen and 8–38% phosphorus discharges to Chesapeake Bay (Cerco et al. 2002). Our regression tree models did not select nitrogen or phosphorus discharges from sewage treatment plants as influential factors for predicting SAV abundance (Fig. 6); SAV abundance seemed to have a strong threshold response to point source discharges of TN or TP and to septic system density in the local watershed (Fig. 5). Where TN discharge reached 16.7 kg N km^{-2} d^{-1} or higher, or TP discharge reached 1.3 kg P km^{-2} d^{-1} or higher, SAV abundance declined to zero. In prioritizing SAV restoration sites or in managing watersheds to support SAV restoration, special attention should be given to reducing human waste inputs to subestuaries where any of these factors is higher than its threshold.

Estuarine Characteristics

Much of the habitat suitable for SAV in Chesapeake Bay occurs in the highly indented shorelines of creeks and embayments associated with major and minor tributaries to the Bay. Shallow subestuaries have local watersheds, but are also driven by exchanges of water at their seaward boundaries (Schubel and Pritchard 1986; Gallegos et al. 1992, 1997). SAV can be affected by subestuary characteristics, such as the shape or depth profile of the subestuary. Structural characteristics can be surrogates or indicators of how the influences of the local watershed and mainstem of Chesapeake Bay balance out in a subestuary. We found that SAV abundance declined sharply with the ratio of watershed area to estuary area when that ratio was higher than 20 (Fig. 4), suggesting that watershed influences are relatively more important when the local watershed is large relative to the size of the subestuary.

Our analyses also support the importance of subestuary physical structure to SAV abundance. Both mouth width and shoreline fractal dimension were significantly and positively correlated with SAV abundance (Fig. 4). Shoreline fractal dimension was also an important variable in all of the regression trees, and higher values of fractal dimension were always associated with higher SAV abundances (Fig. 6). Higher values of the fractal dimension reflect more shoreline length per unit of subestuary area and likely indicate more prevalence of sheltered embayments is conducive to SAV growth within a subestuary. Subestuary mouth structure is an important factor controlling water exchange between a shallow tributary and the main Bay, but its effect on SAV could be either positive or negative. A wider mouth could enhance water exchange and dilute nutrients and suspended solids input from the local watershed. In this case, the effect on SAV abundance could be positive. A wider subestuary mouth also could expose the subestuary to greater influence from the hydrodynamic energy of the main Bay. In our analysis, we excluded a priori those subestuaries where there is no historical observation of SAV presence, and this included some systems where high wave energy precluded SAV occurrence (Orth et al. 1992; USEPA 2003). Our analysis may then be more likely to detect the positive effects of mouth width from dilution rather than the negative effects from increased wave energy. Encouragingly, our simple subestuary metrics seemed to capture important aspects of physical circulation and exchange that could not be known more completely without doing a full physical model of estuarine hydrodynamics on each of the 101 subestuaries.

Coastal vulnerability factors can influence the abundance of SAV in some areas independently of the light attenuation conditions (Koch 2001). Very high wave energy may prevent SAV from becoming established, even when the light requirements are met (Clarke 1987). By reducing current velocity and attenuating waves, SAV beds create conditions that lead to the deposition of small and low-density particles within meadows or canopies (Kemp et al. 2004). This in turn can affect the availability of light at leaf surfaces (Kemp et al. 2004). Hydrodynamic effects on SAV can be either positive or negative. Waves with high energy can erode the edges of a SAV bed or suspend sediments to reduce light. Hydrodynamic energy can also attenuate flow and enhance water column mixing (Koch and Gust 1999) to improve water clarity in shallow subestuaries.

Precipitation

Neither annual nor summer precipitation was identified as a significant factor influencing SAV abundance in the univariate correlations or regression tree analyses (Figs. 4, 6 and Table 3). This seems to disagree with the conventional wisdom that lower precipitation favors better water quality and higher SAV abundance (Stevenson et al. 1993). We did observe some interesting contrasts in SAV responses to annual precipitation between subestuaries with disturbed watersheds and subestuaries with more pristine watersheds. In subestuaries with watersheds dominated by agriculture or developed land, SAV abundance was lower in wet years than in dry years, but the opposite was true for systems with forested watersheds (Fig. 3). These opposite patterns would cancel out when all subestuaries were considered together (Fig. 6 and Table 3), making it harder to observe responses to annual precipitation.

Limitations and Future Directions

Although we identified watershed characteristics that are strong predictors of variation in SAV abundance among subestuaries, we acknowledge some important limitations in our approach. Models based on the post-1984 SAV data can explain variations in SAV abundance under the low abundance conditions that have persisted since the catastrophic decline of SAV during the 1960s and 1970s (Orth and Moore 1983). The models do not explain the decline itself. If the Chesapeake Bay could be restored to pre-decline conditions, then the statistical relationships discovered here may no longer apply.

We were also unable to explore the complete chain of causal linkage from landscape characteristics to water quality and then from water quality to SAV. To achieve that objective with a Bay-wide statistical analysis (such as a structural equation model, Pugesek et al. 2003; Ahronditsis et al. 2007), we would need integrated data on the geographical characteristics, water quality, and SAV responses for each study subestuary. The required data are available for geographical characteristics and for SAV abundance, but not water quality. Other researchers have already noted that there are not enough current water quality data for analysis of SAV at the whole-Bay scale (Kemp et al. 2004). Most Chesapeake Bay water quality samples are collected from mid channel stations and there are fewer stations in shallow areas. The placement is not consistent among the few subestuaries sampled: in some subestuaries, the station is close to the mouth while in other subestuaries the station is nearer to the headwaters. The point data cannot be integrated to give a spatially and temporally integrated measure that represents an entire estuary and is equivalent among subestuaries. That is, the water quality can not be made commensurate with integrated, whole subestuary values of the SAV response and geographic characteristics. Despite the lack of water quality data, we did successfully identify useful, indirect predictors of SAV abundance. Future research should work to develop additional water quality data for subestuaries and include water quality intermediates in more complete models.

Our analysis also focused on metrics that represent the aggregated characteristics of entire subestuaries and entire watersheds. Future studies could apply spatial analyses at a finer scale to explore patterns of abundance within subestuaries, for example, by relating the locations of SAV beds to neighboring environments. The locations of land cover types or other stressors within the watershed could also be considered.

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