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Unexpected resurgence of a large submersed plant bed in Chesapeake Bay: Analysis of time series data

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Abstract

An historically large (> 50 km^2) submersed plant bed in upper Chesapeake Bay virtually disappeared in 1972, following Tropical Storm Agnes. The bed experienced little regrowth until the early 2000s, when plant abundance rapidly increased. Here, we analyze a suite of recent (1984–2010) and historical (1958–1983) time series datasets to assess alternative explanations for the submersed plant resurgence. Change-point analysis showed that spring nitrogen (N) loading increased from 1945 to 1988 and decreased from 1988 to 2010. Analysis of variance on recent time series showed a significant difference in submersed aquatic vegetation (SAV) abundance percent change during wet years ($-7 \pm 11\%$) and dry years ($53 \pm 20\%$), indicating that floods and droughts likely contributed to SAV loss and growth, respectively. In the historic dataset, however, increasingly poor water quality led to SAV loss despite an extended drought period, indicating that underlying water quality trends were also important in driving change in SAV abundance. Several water quality variables, including N concentration and turbidity, were lower inside the SAV bed than outside the SAV bed, implying the presence of feedback processes whereby the bed improves its own growing conditions by enhancing biophysical processes such as sediment deposition and nutrient cycling. Together, these analyses suggest that stochastic extremes in river discharge and long-term water quality trends synergistically facilitated sudden shifts in SAV abundance and that feedback processes likely reinforced the state of the bed before and after the shifts. Management efforts should consider these dynamic interactions and minimize chronic underlying stressors, which are often anthropogenic in origin.

Change is ubiquitous in natural systems because the environmental conditions that affect biota are also inherently variable. Seagrass and associated submersed aquatic vegetation (SAV) communities, in particular, undergo episodes of decline and recovery that span seasons to multiple decades. Reports of decline dominate the literature, with many examples of SAV loss attributed to chronically degraded water quality associated with eutrophication (Kemp et al. 1983) or extreme weather events such as hurricanes, flooding, and temperature stress (Preen et al. 1995). Recent studies, however, have also reported instances of SAV recovery. Most relate expanded plant cover to improved water clarity resulting from management actions, such as sewage treatment plant upgrades (Burkholder et al. 2007; Rybicki and Landwehr 2007). Climate-related factors, such as decreased storminess (Reise and Kohlus 2007), have also been cited. The rate of both negative and positive trends can be substantially modified by the combined effects of short-term climatic drivers and long-term trends in anthropogenic stressors (Cardoso et al. 2004).

Change in SAV abundance can be abrupt, either as a linear response to an acute event or as a nonlinear threshold effect in which a sudden shift occurs after gradually changing environmental conditions cross some critical threshold (Scheffer et al. 2001; van der Heide et al. 2007). Theory suggests that feedback processes, through which a plant bed modifies its environment in ways that enhance its own growth, may facilitate threshold responses. For example, SAV beds attenuate wave energy and current velocity, which causes suspended particles to sink, improves ambient water clarity, and, thus, enhances plant growth (Ward et al. 1984; Gruber and Kemp 2010). SAV beds also decrease water column nutrient concentrations, thereby precluding the growth of phytoplankton and epiphytes and allowing more light to reach the leaf surface (Moore 2004). Positive feedbacks help maintain a suitable growing environment despite changes in external conditions. However, beyond a critical threshold (e.g., a minimum light level needed for plant growth), feedback processes no longer buffer against disturbance, and the system suddenly shifts to a degraded state (Scheffer et al. 1993). As conditions approach this threshold, resilience decreases and a small change in environmental conditions can drive the system beyond its "tipping point."

In some instances, plant reestablishment in bare sediment requires more stringent conditions than those needed to maintain an already established bed (Scheffer et al. 2001). As a result, restoration of a degraded submersed plant bed can be extremely difficult. The initiation of positive and negative shifts at different critical conditions (a pattern known as hysteresis) also means that different system "states" (e.g., bare sediment and sediment colonized by SAV) can exist under the same set of environmental conditions (e.g., turbid and clear water).

An abrupt increase in submersed plant abundance recently occurred in a broad shallow region in the upper Chesapeake Bay known as Susquehanna Flats. SAV at "the flats," historically extolled by fishermen and waterfowl enthusiasts as prime wildlife habitat, began to decline when nutrient loading and eutrophication intensified in the 1960s (Bayley et al. 1978; Kemp et al. 2005). Following Tropical Storm Agnes in 1972, submersed plants virtually disappeared for nearly three decades until the early 2000s,

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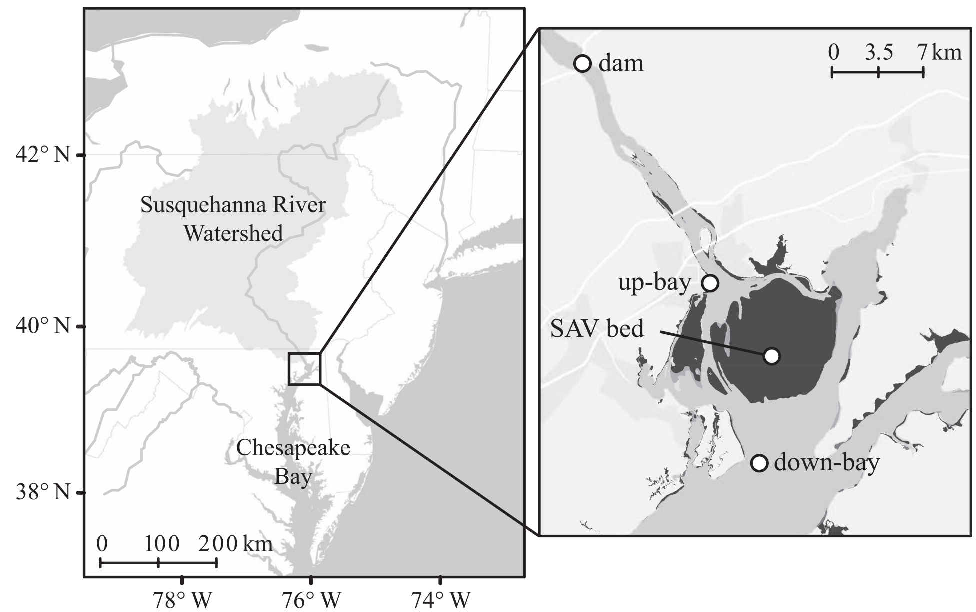

Fig. 1. Location of the Susquehanna River and water quality sampling sites. Dark shaded area in the figure on the right indicates the SAV bed aerial extent in 2010.

when they rapidly recolonized nearly the entire region (> 50 km^2). Whereas an extreme flood event apparently triggered the historic demise of SAV at Susquehanna Flats, the extended lack of recovery is puzzling because it appears that environmental conditions have generally satisfied the habitat requirements for SAV in oligohaline regions of Chesapeake Bay since water quality monitoring began in 1984 (i.e., April–October median light attenuation coefficient < 2.0 m^{-1}, total suspended solid and dissolved inorganic phosphorous concentrations < 15 mg L^{-1} and 0.67 μmol L^{-1}, respectively; Dennison et al. 1993; Kemp et al. 2004).

Given the valuable ecological services that submersed plant beds provide, such as nutrient uptake and habitat for economically important fisheries, it is imperative that we refine our understanding of why they disappear and what conditions are required for their return. In the Chesapeake Bay region, monitoring programs have generated a wealth of detailed time series datasets measuring submersed plant abundance since 1958, water quality since 1984, and climate-related variables, such as temperature and river discharge, since the late 1800s. Here, we rigorously examine and analyze these diverse time series datasets to develop an explanatory model for the recent rapid recovery of the large SAV bed at Susquehanna Flats. Specifically, we investigate (1) how patterns and trends in anthropogenic and climatic variables relate to SAV abundance, (2) whether the sudden resurgence could reflect a threshold response to change in environmental conditions, and (3) whether feedback processes could have played a role in this resurgence. Whereas retrospective data analysis is inherently limited because, for example, the data are restricted to what is available and often contain gaps, the inferences developed through such exercises can facilitate interpretation of current ecological dynamics as well as prediction about the future. Our broader motivation lies in the idea that the methods used and explanatory model derived here can be applied elsewhere to explore similar plant bed dynamics worldwide.

Methods

Study site—Susquehanna Flats is a broad, tidal freshwater region located near the mouth of the Susquehanna River at the head of Chesapeake Bay (Fig. 1a). The shallow flats, formed from sand and silt deposited where the Susquehanna River broadens as it flows into the Bay, cover roughly 50 km^2, with a relatively narrow but continuous channel (3–7 m deep) bordering the western side and also relatively deep but discontinuous channels to the east and south of the flats. As of 2010, SAV covered most of Susquehanna Flats with dense stands of as many as 13 plant species, co-dominated by *Vallisneria americana*, *Myriophyllum spicatum*, *Hydrilla verticillata*, and *Heteranthera dubia*.

Data sources—The data described herein were collected by various agencies and organizations at a range of sampling intervals and durations (Table 1). Water quality data were collected at 2–4 week intervals beginning in 1984. We used data from the sampling station CB1.1, which we call "up-bay," located at the mouth of the Susquehanna River, for most analyses (Fig. 1). Because upper Chesapeake Bay hydrology is dominated by Susquehanna River outflow (Schubel and Pritchard 1986), data from this station are likely representative of water flowing into and around the plant bed. This study focuses on chlorophyll *a* (Chl *a*), total suspended solids (TSS), Secchi depth, total nitrogen (TN), dissolved inorganic nitrogen (DIN), particulate nitrogen (PN), total phosphorous (TP), dissolved

Table 1. Summary of data sources, sampling intervals, and date ranges.

Data type	Source	Sampling interval	Date range
SAV cover	Virginia Institute of Marine Science http://web.vims.edu/bio/sav/index.html	Annual	1984–2011
SAV relative abundance	Bayley et al.1978 study and Maryland Department of Natural Resources (MDDNR)	Annual	1958–1988
Water quality	Chesapeake Bay Monitoring Program, http://www.chesapeakebay.net/data/downloads/cbp_water_quality_database_1984_present	2–4 weeks	1984–2011
Water quality	MDDNR Continuous Monitoring Program Calibration Data, http://www.chesapeakebay.net/data/downloads/cbp_water_quality_database_1984_present	2–4 weeks	2007–2010
Water quality	MDDNR Continuous Monitoring Program, http://mddnr.chesapeakebay.net/eyesonthebay/index.cfm	15 min	2007–2010 (spring–fall)
Susquehanna River discharge	U.S. Geological Survey (USGS), http://waterdata.usgs.gov/md/nwis/uv?01578310	Daily	1890–2011
Susquehanna River TN, TP, and TSS loading rate	USGS	Monthly	1978–2010
Susquehanna River TN loading rate	Zhang et al. 2013	Monthly	1945–1978

inorganic phosphorous (DIP), particulate phosphorous (PP), particulate carbon (PC), the diffuse downwelling attenuation coefficient (K_D), and water temperature (temp). We also examined high sampling frequency (four per hour) water quality data for dissolved oxygen (DO), pH, Chl *a*, turbidity, and temperature measured continuously from April through October since 2007. From 2007 to 2009, biweekly to monthly water quality data were available for several additional locations around Susquehanna Flats, including inside the SAV bed and down-bay from the SAV bed. Salinity was not included in this analysis because values in and around the plant bed were generally < 1.0, well within the tolerance range of the dominant submersed plant species populating the study site (Haller et al. 1974). Susquehanna River flow rates were measured at gauging stations located at Conowingo Dam (1968 to present) and at Harrisburg, Pennsylvania (1890 to present). Daily mean TN, TP, and TSS (1978–2010) loading rates at Conowingo Dam (Fig. 1) were calculated for each month based on streamflow and water quality concentrations using the weighted regressions on time, discharge, and season (WRTDS) method (Hirsch et al. 2010). Mean TN loading rates from 1945 to 1978 were estimated based on loading rates calculated for Harrisburg (Hagy et al. 2004; Zhang et al. 2013).

Annual estimates of total SAV cover and crown density from 1984 to 2010 were based on geo-referenced aerial photographs (Table 1). Previous studies using aerial survey data focused on total area occupied by plants, which we call "bed area" (Orth et al. 2010). However, we felt that, for this region, using a measure of plant abundance that reflected plant density was particularly important. From 1984 to 2000, plants were sparsely distributed throughout Susquehanna Flats. Whereas the bed area was large, the actual abundance of plants was low. Therefore, we calculated SAV bed area weighted for density using a multiplier based on crown density categories (1–4) to estimate an index of total plant biomass, which we call "bed abundance" (Moore et al. 2000; Rybicki and Landwehr 2007). We characterized temporal SAV trends in terms of both bed area and bed abundance, although our statistical analyses focused on the latter. We also determined the mean depth of the bed perimeter, which we call "perimeter depth," with geographic information systems (GIS) software (Esri ArcGIS) by overlaying SAV shape-files on bathymetric data and extracting the depth of the SAV shape-file perimeter. Historical SAV data for the period 1958–1975 (Bayley et al. 1978) and 1971–1988 (Maryland Department of Natural Resources unpubl.) were reported as a unitless annual plant abundance rating based on material recovered with a standard rake collected along four transects crisscrossing Susquehanna Flats (Bayley et al. 1978).

Data analyses—Whereas relative SAV abundance, river discharge, and N loading data were available since 1958 and earlier, regular water quality monitoring did not begin until the 1980s. Thus, our overall approach was to first rigorously analyze and synthesize the recent time series datasets (1984–2010), which include SAV abundance, water quality, river discharge, and loading, to generate a detailed explanatory model for the recent sudden SAV resurgence. We then conducted limited statistical analysis on the historical datasets (1958–1983) and used the relationships established through analysis of the recent data to make logical assumptions about the underlying mechanisms driving change across the entire time series. We performed all calculations and plotted all figures with the statistical computing and graphics software R with its "base" and "stats" packages, unless otherwise noted.

We used change-point analysis to characterize the sudden change in features of the SAV bed. A change-point is defined as the point at which the statistical properties of a time series abruptly change. In this case, we performed segmented regression analysis to test for sudden and sustained changes in trend trajectories for bed area, bed abundance, and perimeter depth. We used the R package "segmented" for this analysis (Muggeo 2008). The sample size (n) was 26 years (aerial SAV surveys were not conducted at Susquehanna Flats in 1988). This method constrains the segments to be continuous; however, trends in the historic SAV time series were clearly discontinuous. Therefore, we used a slightly different approach for this dataset, in which change-point selection was based on minimizing the mean squared error from iteratively generated two-segment piecewise regression models (Crawley 2007). Although this approach allows for a more accurate characterization of discontinuous breaks in trends, it does not calculate confidence intervals or p-values.

We also characterized patterns and trends in environmental drivers. We calculated seasonal means for river discharge and water quality. Seasons are defined as follows: growing season, June through October; winter, December through February; spring, March through May; summer, June through August; fall, September through November. For variables that were sampled at multiple depths, we calculated the water column mean before calculating seasonal means. We then conducted segmented regression analysis on these growing season means to detect change-points. We also tested for long-term trends using the nonparametric Mann–Kendall trend test, which is often the preferred method of trend analysis for characteristically nonnormal and/or skewed time series datasets (Hirsch et al. 1982). Sample sizes ranged from 23 to 26. In addition, because light availability is often a key driver of SAV growth (Dennison 1987), we used the nonparametric Spearman rank-order test to calculate correlations between K_D and the growing season means for parameters with significant long-term trends. To broadly demonstrate how all of the environmental variables included in this study were interrelated, we performed standardized principal component analysis (PCA) on growing season mean values for all surface water quality variables and then tested for correlation between the first principal component and growing season mean river discharge using the Spearman rank-order test.

To show how environmental variables were related to bed abundance, we constructed simple linear regression models using seasonal means and medians for each climatic and water quality parameter as the predictor variable and bed abundance as the response variable. We tested the residuals of each model for normality, independence, and heteroskedasticity using the Shapiro, Durbin–Watson, and nonconstant error variance tests, respectively. We performed data transformations (e.g., log) as necessary. Because the bed abundance data were autocorrelated, we used differencing to obtain a time series reflecting interannual change in bed abundance (i.e., the first difference of y at time t is equal to $y(t) - y(t-1)$), which we call "bed change." Even after transformation, the relationship between bed change and environmental time series was clearly nonlinear (i.e., the relationship between predictor and response variables changed over time). Whereas environmental variables and bed change appeared to be unrelated when bed change was minimal, linear relationships were apparent when bed change $\neq 0$. Thus, we partitioned the bed change dataset into two time periods: "stable" (1984–1998 and 2009–2010, characterized by little interannual change) and "transition" (1999–2008, when bed abundance rapidly increased). We then conducted piecewise regressions on these segments.

The nonlinear nature of these relationships may suggest that the change in SAV abundance was related to a threshold response to changes in environmental conditions. Segmented regression, in addition to detecting points in time at which a temporal trend trajectory shifts, can also be used to identify the threshold value at which at the slope of the relationship between predictor and response variables changes. Because, again, light is a critical resource for SAV growth, we used segmented regression to detect a potential threshold response of bed abundance to change in the light environment, as indicated by growing season mean K_D.

In addition, because extreme weather events can modify SAV trends, we also tested for relationships between bed change and extremes in river discharge. We classified years with river discharge values exceeding the 75th percentile of growing season mean river discharge as "wet years" and those that fell below the 25th percentile as "dry years" (U.S. Geological Survey http://md.water.usgs.gov/waterdata/chesinflow/wy/). We classified "normal" river discharge values as those between the 25th and 75th percentiles. We then used Kruskal–Wallis one-way analysis of variance (ANOVA) by ranks to further investigate how weather-related mechanisms affected bed change by testing for differences in percent change in bed abundance during wet years, dry years, and average years. This test was a better choice than parametric ANOVA because the groups were unequal in size and variance was not homogeneous over time. We then calculated post hoc individual comparisons using the Mann–Whitney test.

To quantify spatial differences in water quality, which may indicate how the SAV bed affected ambient growing conditions, we calculated the mean difference and a 95% confidence interval between monitoring data collected inside and outside the SAV bed for each month during which data were collected (April–October). Turbidity, Chl a, DO, and pH were measured at 15 min intervals with continuous monitoring data sondes, whereas grab samples analyzed for DIN were collected every 2–4 weeks. Because sample sizes were large ($n > 2000$ for most parameters, with the exception of DIN), we felt that a significance test (e.g., t-test) would be inappropriate; with so many samples, such tests usually yield significant results even if the actual differences are minimal (McBride 1993). Rather, we quantified the magnitude of differences (effect size) between sample stations, which, in this context, is more ecologically meaningful.

Results

There was a change-point indicating sudden plant loss in 1972, which coincided with Tropical Storm Agnes (Fig. 2a). Several change-points were also evident in the recent SAV time series for bed abundance, bed area, and perimeter depth. Bed abundance was near zero with little

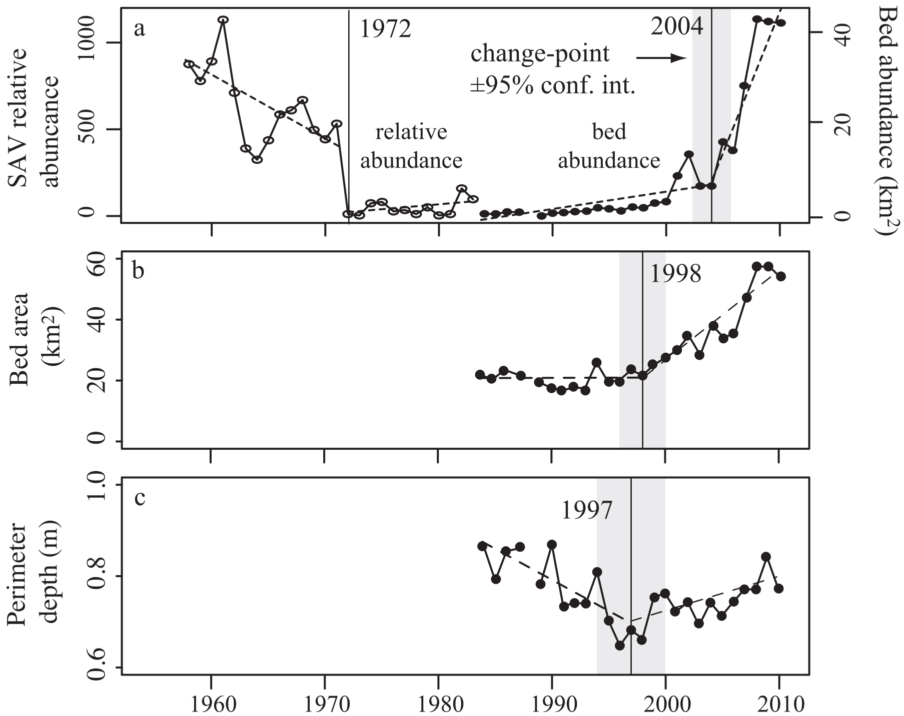

Fig. 2. Time series for (a) SAV relative abundance (1958–1983) and bed abundance (1984–2010), (b) bed area, and (c) perimeter depth. Solid vertical lines and gray shaded areas in the time series plots indicate estimated change-points ± 95% confidence intervals (conf. int.). Dashed lines indicate linear trends before and after each change-point.

change from 1984 to 2000, but it increased gradually between 2001 and 2004 and then rapidly increased to > 40 km^2 after the 2004 change-point (Fig. 2a). Bed area was generally constant from 1984 to ~ 1998 and then increased to nearly 50 km^2 by 2010 (Fig. 2b). Perimeter depth decreased between 1984 and 1997 and then increased, following a change-point around 1997 (Fig. 2c). These trends are illustrated in more detail by the series of SAV maps generated through analysis of aerial photographs (Fig. 3), which show that submersed plant cover was persistently sparse (< 10% cover) through much of the 1980s and 1990s and then rapidly increased in size and density between 2000 and 2006. The bed remained persistently large and dense after 2007.

There were several significant long-term trends in the surface water quality time series data (Table 2). Notably, water clarity, indicated by K_D, improved by ~ 40% between 1984 and 2010. TP, PP, PN, and PC concentrations also significantly decreased and temperature increased. There was also a change-point in spring N loading, which gradually increased prior to 1988 and then began to decrease after 1988 ($p < 0.01$; Fig. 4a). Most significant trends for individual seasonal means (winter, spring, summer, fall) were also significant for the entire growing season (June–August). Therefore, we simply report trend test and change-point results for growing season means. However, one exception was the significant change-point in only spring N loading, as reported above. Of the trending variables, K_D was correlated with N load ($\rho = 0.62$, $p < 0.05$, where ρ is the Spearman rank correlation coefficient), TP ($\rho = 0.65$, $p < 0.001$), PP ($\rho = 0.66$, $p < 0.001$), PC ($\rho = 0.49$, $p < 0.05$), and temperature ($\rho = -0.86$, $p < 0.001$).

PCA results show that TN, TP, DIN, DIP, PP, TSS, Secchi depth, and K_D were interrelated (Fig. 5a). These variables all projected strongly onto the first principal component (PC1), which accounted for 53% of the variance in water quality. PC1 was significantly correlated with river discharge ($\rho = 0.57$, $p < 0.01$; Fig. 5b). Chl *a*, PN, and PC projected strongly onto the second principal component (PC2), which represented 20% of the variance in water quality.

Bed change was related to river flow and several water quality variables during the transition period but not during the stable time period (Fig. 6; Table 3). Generally, winter and spring environmental conditions were not related to bed change, with the exception of spring TN concentration ($R^2 = 0.45$, $p < 0.05$) and possibly TN loading ($R^2 = 0.47$, $p < 0.07$). Relationships between bed change and most environmental variables were stronger during the summer and were weaker, but often significant, in the fall. Summer mean river flow explained the greatest proportion of variance in bed change ($R^2 = 0.88$ $p < 0.001$). Bed change was, however, not related to Chl *a*, DIN, PN, or PC during any season. Regression results also indicated several weaker but significant positive relationships during the stable period between bed change and winter and fall TN, as well as weak but significant negative relationships with spring water temperature. Regression analyses using historical TN loading and river discharge as predictors and SAV relative abundance as the response

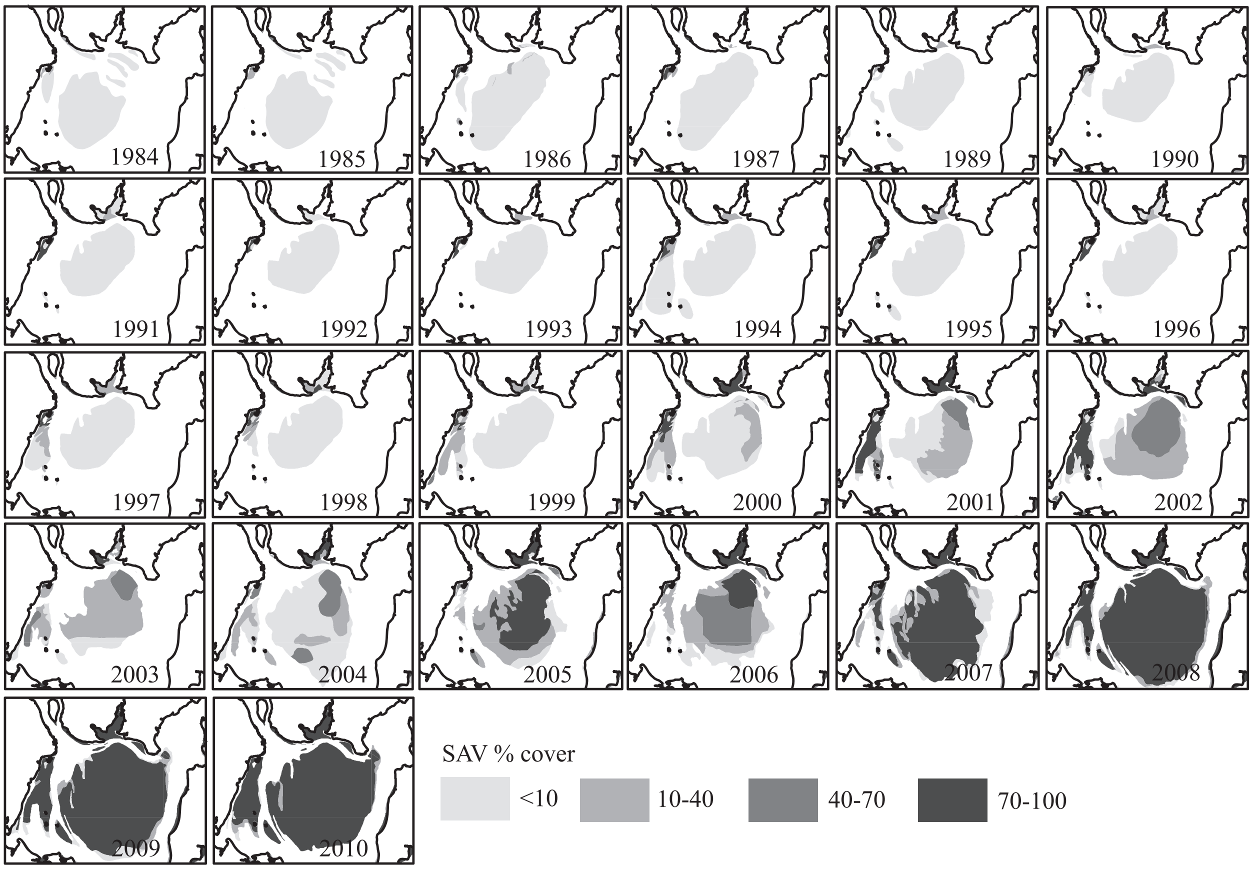

Fig. 3. 1984–2010 SAV cover at Susquehanna Flats. Shades of gray indicate SAV density classes. Images were generated through digital analysis of aerial photography. Surveys were not flown in 1988.

variable yielded no significant results. We used both seasonal mean and median values to construct regression models, and we report results for whichever explained more variance in bed change. Segmented regression on bed abundance and growing season mean K_D indicated that the rapid increase in bed abundance occurred around a threshold K_D value of 1.3 m^{-1} ($p < 0.001$) with a 95% confidence interval of 1.1 to 1.5 m^{-1}.

Table 2. Mann–Kendall trend test results for annual loading rates at Conowingo Dam and growing season (June–October) mean water quality variables from 1984 to 2010. Kendall's τ, associated p-values, and trend slopes are listed. Rows in bold are significant at the 0.05 level.

Parameter	τ	p	Slope
TN loading	−0.19	0.18	−0.50
TP loading	−0.03	0.82	−0.01
TSS loading	0.19	0.18	1.42
TN	−0.13	0.36	−0.48
DIN	0.07	0.65	0.07
PN	**−0.30**	**0.03**	**−0.10**
TP	**−0.28**	**0.04**	**−0.01**
DIP	−0.01	0.97	0.00
PP	**−0.40**	**0.00**	**−0.01**
PC	**−0.31**	**0.03**	**−0.01**
Chl *a*	−0.19	0.17	−0.09
TSS	−0.04	0.80	−0.02
Secchi	0.14	0.31	0.00
K_D	**−0.44**	**0.00**	**−0.03**
Temp	**0.50**	**0.00**	**0.10**

Extremes in river discharge were related to shifts in bed abundance. In 2003, growing season mean river flow was particularly high (1449 m^3 s^{-1}; Fig. 4b), and bed abundance declined by 45%. Conversely, from 1995 to 2002, there were no wet years, and no daily flow rates exceeded 10,000 m^3 s^{-1}. The change-point in SAV total area occurred during this time, and bed abundance rapidly increased shortly thereafter (Fig. 2). On average, bed abundance increased by 53 ± 20% and 21 ± 10% during dry years and normal flow years, respectively, and decreased by 7 ± 11% during wet years (Fig. 7). Kruskal–Wallis ANOVA results indicate that percent change in bed abundance was significantly different depending on growing season flow conditions (wet years, average flow, dry years; $\chi^2 = 7.63$, $p < 0.05$). Post hoc comparisons indicate a significant difference between bed change during wet years and that during dry years ($p < 0.05$). Although the 1972 demise of SAV was clearly linked to a record river discharge maximum (Figs. 2, 4), this relationship could not be generalized across the entire historical dataset, as ANOVA resulted in no significant differences in bed change under different flow conditions.

Water quality variables measured in and around the SAV bed varied over space and time. Turbidity and Chl *a*

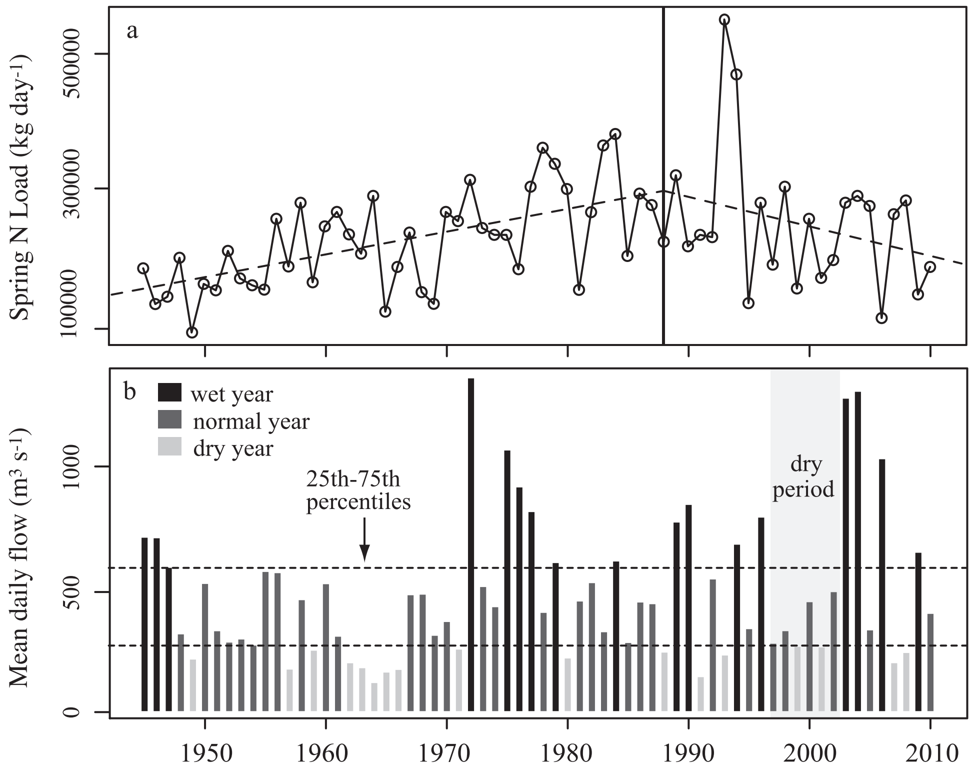

Fig. 4. 1945–2010 time series for (a) spring daily mean TN loading and (b) growing season (June–October) mean Susquehanna River flow with "wet years" (> 75th percentile) and "dry years" (< 25th percentile) highlighted.

were lower inside the bed than up-bay from the bed, whereas pH and DO were higher inside the bed (Table 4; Fig. 8). DIN was lower inside the SAV bed compared to both up-bay and down-bay stations and was slightly lower down-bay compared to the up-bay station. Generally, the magnitude of these differences was smaller early in the growing season and increased as the SAV growing season progressed. The difference in DIN, which was > 30 times lower inside the bed compared to up-bay in July and August during peak biomass, was particularly striking. Monthly mean DIN concentrations inside the bed ranged from 1.6 μmol L^{-1} to 2.3 μmol L^{-1} during the summer (July–September), whereas up-bay concentrations ranged from 39 μmol L^{-1} to 54 μmol L^{-1}.

Discussion

Here, we first examine the results of our analyses separately to explore potential causes and/or effects of each set of observations. We then take a step back and consider these disparate observations together to construct an explanatory model of the SAV resurgence. Our overall

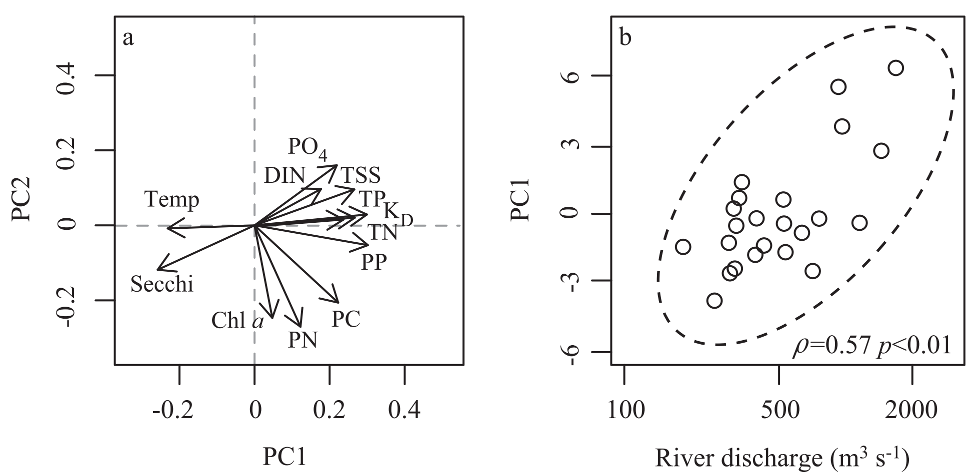

Fig. 5. (a) Biplot illustrating relative loadings of water quality variables onto the first and second principal components (PC1 and PC2) and (b) correlation between river discharge and PC1.

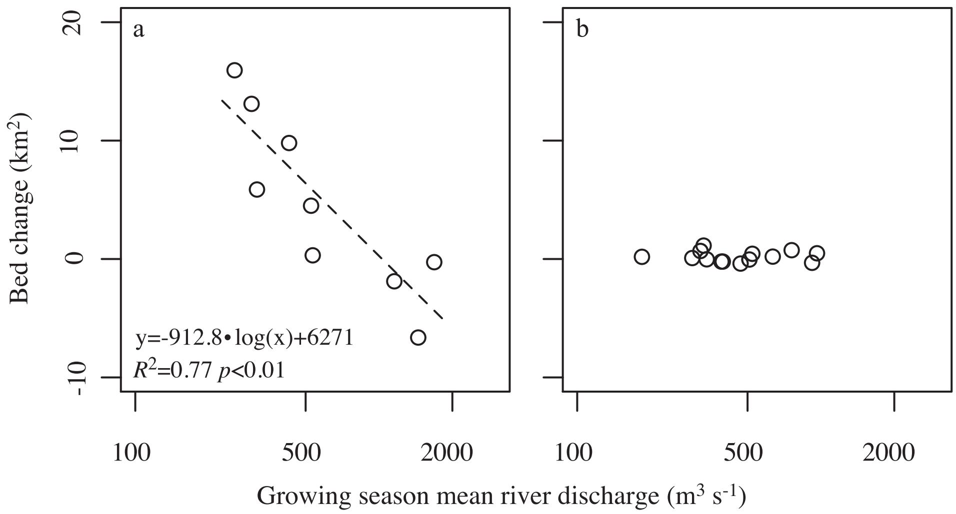

Fig. 6. Relationship between growing season mean Susquehanna River discharge and SAV bed abundance during (a) the transition time period (1999–2008) and (b) the stable time period (1984–1998; 2009–2010).

line of reasoning begins with the hypothesis that reductions in nutrient loading led to long-term water clarity improvement and, thus, a long-term increase in light availability for plant photosynthesis. Then, during a dry period from 1997 to 2002, a critical light threshold was crossed, which, together with an absence of storm events, provided ideal conditions for new plant growth. As a result, the bed began to expand and colonize deeper water. Finally, as plant density increased, positive feedback effects between the bed and ambient water quality facilitated the subsequent rapid SAV resurgence. The following paragraphs provide a detailed explanation of this sequence of logic.

Environmental drivers—It has been well established that light availability is the most important constraint on the growth of submersed plants when other habitat requirements, such as substrate composition, wave exposure, and flow regime, are satisfied (Dennison 1987). Our analyses show that water clarity increased over time and that N loading has been decreasing over the last several decades. We suggest that these trends may have been a key component in the SAV resurgence. Other instances of SAV restoration have been attributed to decreased nutrient loading and associated declines in phytoplankton abundance (Burkholder et al. 2007). Therefore, we were surprised to find no significant decline in Chl *a* concentration and no significant correlations between Chl *a* and K_D or Secchi depth. There were, however, declines in PN, PC, TP, and PP. Of these trending parameters, PC, TP, and PP were correlated with K_D. In addition, PCA showed that Chl *a*, PN, and PC tended to covary (Fig. 5). Thus, decreases in particulates, possibly the result of reduced nutrient loading, may have been responsible for improved water clarity. Furthermore, in tidal freshwater regions of Chesapeake Bay, epiphytes can contribute 20–60% additional shading beyond light attenuation by dissolved and suspended material in the water column (Kemp et al. 2004). Thus, reductions in nutrient loading may have also limited the growth of epiphytes, allowing more light to reach the SAV leaf surface.

Our analyses also suggest that interannual change in bed abundance around the trend of recovery was driven by stochastic weather variability, at least during transition years. Physical and biological processes in estuaries are often directly linked to watershed rainfall and, subsequently, downstream river discharge into the estuary. In the present study, correlation between PC1 and river discharge demonstrates that Susquehanna River outflow and, thus, rainfall, was a major driver of change for many key water quality parameters, which covaried as a result of their collective response to river flow. Consequently, bed change was also strongly related to river flow during the transition period. Because water quality variables often covary (van der Heide et al. 2009), it is difficult to identify which variables were specifically responsible for bed change. However, significant correlation among TSS, Secchi depth, K_D, and river discharge suggests that flow controlled the concentration of suspended particles, which affected water clarity and, in turn, bed change. TN and TP were also related to river discharge and could have affected epiphyte growth. Because river discharge was related to bed change, it comes as little surprise that extremes in river discharge were related to substantial SAV loss and growth (Fig. 7). Interestingly, however, Chl *a*, PN, and PC were not related to bed change or river discharge (Fig. 5; Table 3). Thus, although these parameters appeared to be related to long-term water clarity improvement, they were unrelated to weather-driven interannual variation in and river discharge and bed change.

The strong relationships between bed change, river discharge, and water quality during June through August, in particular, demonstrate that the annual change in size and density of the SAV bed is largely a function of summer river discharge. Because the dominant macrophyte species at Susquehanna Flats do not generally emerge until late spring to early summer (Carter et al. 1985), winter and

Table 3. Linear regression results for transition (1999–2008) and stable (1984–1998; 2009–2010) time periods. For each regression, bed change was the response variable; seasonal means (or medians, if indicated) for each environmental parameter were the predictor variables. Bold values are significant at the 0.05 level.

Predictor variable	June–October			Winter			Spring			Summer			Fall		
	Slope	R^2	p	Slope	R^2	p	Slope	R^2	p	Slope	R^2	p	Slope	R^2	p
Transition															
River flow	**−**	**0.76***	**0.002**	−	0.04*	0.739	−	0.04*	0.629	**−**	**0.88***	**0.000**	−	**0.57†**	**0.018**
N load	−	0.00	0.941	−	0.37	0.108	−	0.47	0.061	−	0.01	0.781	−	0.00	0.917
P load	−	0.01	0.805	−	0.21	0.256	−	0.32	0.138	−	0.05	0.588	−	0.04	0.626
TSS load	−	0.03	0.708	−	0.08	0.498	−	0.22	0.240	−	0.09	0.464	−	0.08	0.504
TN	−	0.20	0.223	−	0.41	0.062	**−**	**0.45†**	**0.049**	−	0.18	0.252	−	0.15	0.307
TP	**−**	**0.67†***	**0.007**	−	0.01	0.767	−	0.04	0.627	**−**	**0.70***	**0.005**	−	0.32	0.112
DIN	−	0.14	0.313	−	0.30	0.129	−	0.08	0.448	−	0.11	0.386	−	0.17	0.273
DIP	**−**	**0.71***	**0.004**	−	0.04	0.587	−	0.21	0.214	**−**	**0.54***	**0.022**	−	0.18	0.249
PN	**+**	0.00	0.975	+	0.29	0.138	−	0.02	0.690	+	0.05	0.553	−	0.05	0.566
PP	**−**	0.40	0.067	+	0.13	0.333	+	0.00	0.955	**−**	**0.52**	**0.029**	**−**	**0.02**	**0.049**
PC	**−**	0.17	0.264	+	0.39	0.071	−	0.00	0.933	−	0.02	0.689	**−**	0.05	0.566
TSS	**−**	**0.75†**	**0.021**	−	0.14	0.320	−	0.05	0.582	**−**	**0.62†**	**0.011**	−	0.10	0.397
Chl *a*	+	0.14	0.330	+	0.04	0.589	+	0.09	0.443	+	0.11	0.384	+	0.05	0.562
K_D	**−**	**0.61†**	**0.013**	−	0.01	0.795	−	0.04	0.623	**−**	**0.61†**	**0.014**	**−**	**0.50†**	**0.049**
Secchi	**+**	**0.61**	**0.012**	+	0.32	0.13	+	0.00	0.994	**+**	**0.62**	**0.011**	**+**	**0.48**	**0.037**
Temp	**+**	**0.67**	**0.007**	+	0.21	0.213	+	0.06	0.525	+	0.43	0.056	+	0.19	0.247
Stable															
River flow	−	0.01	0.770	−	0.06	0.391	+	0.00	0.817	−	0.00	0.954	−	0.03	0.561
N load	+	0.00	0.884	−	0.00	0.887	−	0.04	0.514	−	0.00	0.847	+	0.01	0.719
P load	+	0.00	0.997	−	0.00	0.926	−	0.04	0.516	−	0.00	0.837	+	0.00	0.904
TSS load	−	0.00	0.845	−	0.00	0.918	−	0.05	0.424	−	0.01	0.711	−	0.00	0.911
TN	−	0.00	0.948	**+**	**0.27**	**0.047**	+	0.01	0.803	−	0.12	0.217	**+**	**0.28**	**0.041**
TP	+	0.10	0.258	+	0.22	0.077	−	0.03	0.531	+	0.01	0.805	+	0.09	0.292
DIN	−	0.06	0.378	+	0.22	0.075	+	0.00	0.941	−	0.26	0.051	+	0.16	0.137
DIP	+	0.06	0.388	+	0.19	0.105	+	0.04	0.456	−	0.02	0.608	+	0.12	0.198
PN	+	0.07	0.342	+	0.03	0.569	−	0.03	0.567	+	0.18	0.128	−	0.00	0.986
PP	+	0.05	0.408	+	0.19	0.102	−	0.02	0.579	+	0.06	0.371	+	0.02	0.593
PC	+	0.16	0.145	−	0.07	0.366	−	0.01	0.722	+	0.26	0.062	+	0.02	0.585
TSS	+	0.15	0.152	+	0.16	0.146	−	0.03	0.571	+	0.02	0.633	+	0.04	0.453
Chl *a*	+	0.01	0.741	−	0.01	0.700	−	0.06	0.397	+	0.06	0.365	−	0.03	0.559
K_D	+	0.08	0.366	−	0.02	0.721	−	0.09	0.313	+	0.03	0.603	+	0.20	0.140
Secchi	−	0.07	0.326	−	0.01	0.797	+	0.10	0.248	−	0.04	0.458	−	0.01	0.793
Temp	−	0.03	0.552	+	0.08	0.316	**−**	**0.28†**	**0.043**	+	0.00	0.847	−	0.00	0.937

* Log(predictor variable).
† Annual median for predictor variable was used instead of the mean.

spring flow has little effect on the SAV bed. On the other hand, summer river discharge explained nearly 90% of the variability in bed change because plants are especially sensitive to turbidity during this critical stage in the growth cycle, when they emerge from the sediment and begin to actively grow. These results support modeling studies, which simulate severe effects on SAV beds by storms that occur during the height of the growing season but muted effects for storms occurring after biomass has peaked (Wang and Linker 2005).

Although summer environmental conditions had the strongest effect on bed change, the relationships between bed change and spring TN concentration and TN loading (Table 3) are also worth noting. In estuarine ecosystems, ecological response often lags change in river flow (Hagy et al. 2004). Our analyses suggest that springtime N inputs may have had a similar lagged effect on the SAV bed, possibly because of a delayed response between N loading and phytoplankton and/or epiphyte production.

The absence of significant statistical relationships between bed change and external drivers during stable years, as well as the sudden nature of the SAV resurgence, implies a nonlinear threshold response to improving environmental conditions. It appears that a critical threshold in light availability was crossed during an extended period of low to normal river flow (1995–2002), when the light environment substantially improved. Before the dry period (1984–1994), the average percent of incident light reaching the bottom (PLB) was $\sim$ 17%, which we calculated by assuming a mean depth (z) of 1 m and inserting growing season mean K_D values into the Lambert–Beer relationship ($I_z/I_o = e^{-K_D z}$), where PLB ($100\ (I_z/I_o)$) is irradiance reaching the sediment surface (I_z) as a percentage of that at the water surface (I_o). We

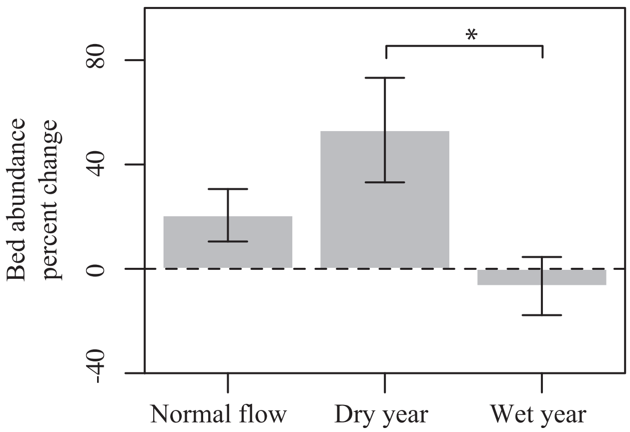

Fig. 7. Mean percent change in bed abundance ± standard error (SE) during normal river flow years, dry years, and wet years. An asterisk indicates significant difference at the 0.05 level.

estimated that PLB was ~ 27% during the dry period and ~ 25% after the dry period (2003–2010). The light threshold for tidal freshwater SAV in Chesapeake Bay is ~ 13–14% (Dennison et al. 1993; Kemp et al. 2004); however, this threshold generally applies to existing SAV beds rather than to initiation of a new bed. The fact that our estimated threshold is greater supports the idea that new SAV growth requires more light than an already established bed. Thus, although water quality gradually improved across the entire 1984–2010 time series, the SAV bed only began to expand after this critical threshold was exceeded.

Comparison of trends in river discharge, N loading, and SAV from 1958 to 1988 implies that the same processes described above occurred in reverse. In the decade prior to the 1972 SAV demise, bed abundance was declining despite an extended drought period (Figs. 2, 4). N loading was also increasing; and, consequently, chronic eutrophication led to poor water quality and widespread SAV loss (Bayley et al. 1978; Kemp et al. 1983, 2005). Tropical Storm Agnes then pushed the already deteriorating SAV system beyond its "tipping point" into a degraded state in 1972. Thus, it appears that the ultimate response of the SAV bed to precipitation patterns depended on underlying water quality trends. This may explain the lack of statistical differences in percent bed change during wet and dry years for these historical time series. Whereas the bed tended to expand during dry years in recent decades as water quality improved, deteriorating water quality from the 1950s through the 1980s likely precluded this response.

Internal feedback processes—Differences in water quality inside and outside the SAV bed suggest the presence of

Table 4. Mean water quality differences ± 95% confidence intervals between monitoring sites located inside and outside the SAV bed for Chl *a*, turbidity, dissolved oxygen, pH, and dissolved inorganic nitrogen.

	n	Mean difference	95% confidence interval			*n*	Mean difference	95% confidence interval	
Chl *a:* Up-bay, SAV bed					DIN: Up-bay, SAV bed				
Apr	597	2.92	2.65	3.19	Apr	10	13.99	0.70	27.28
May	2189	0.44	0.18	0.70	May	15	11.59	−3.05	26.24
Jun	1847	3.87	3.69	4.06	Jun	13	50.14	34.82	65.46
Jul	1248	3.13	2.99	3.28	Jul	15	70.61	65.57	75.66
Aug	2499	2.78	2.68	2.89	Aug	13	65.15	58.19	72.10
Sep	2290	3.06	2.95	3.17	Sep	13	63.04	56.67	69.40
Oct	2323	1.26	1.18	1.33	Oct	15	67.81	31.28	104.35
Turbidity: Up-bay, SAV bed					DIN: Down-bay, SAV bed				
Apr	623	−0.49	−0.91	−0.08	Apr	3	3.89	−10.71	18.50
May	1924	0.89	0.41	1.37	May	3	8.46	−7.41	24.32
Jun	1530	4.87	4.75	5.00	Jun	3	34.76	12.40	57.12
Jul	676	2.75	2.53	2.97	Jul	3	52.05	7.58	96.52
Aug	1237	1.23	1.14	1.31	Aug	3	47.82	−17.95	113.60
Sep	1945	1.69	1.55	1.83	Sep	3	37.12	8.31	65.93
Oct	1299	5.02	4.65	5.40	Oct	3	37.99	0.49	75.48
pH: Up-bay, SAV bed					DIN: Up-bay, down-bay				
Apr	626	−0.08	−0.11	−0.06	Apr	10	10.09	−5.75	25.94
May	2189	−0.83	−0.85	−0.81	May	15	3.14	−8.96	15.23
Jun	1696	−1.43	−1.45	−1.42	Jun	13	15.38	−8.76	39.52
Jul	1732	−1.51	−1.53	−1.49	Jul	15	18.56	−24.28	61.41
Aug	2540	−1.41	−1.43	−1.39	Aug	13	17.32	−44.91	79.56
Sep	2679	−1.41	−1.43	−1.40	Sep	13	25.92	1.11	50.73
Oct	2582	−1.21	−1.23	−1.19	Oct	15	29.83	8.71	50.95
DO: Up-bay, SAV bed									
Apr	625	−0.37	−0.44	−0.29					
May	2189	−1.53	−1.61	−1.45					
Jun	1901	−2.91	−3.00	−2.81					
Jul	1948	−2.16	−2.25	−2.07					
Aug	2745	−1.54	−1.63	−1.46					
Sep	2878	−1.49	−1.55	−1.43					
Oct	2586	−2.30	−2.37	−2.23					

strong positive feedback processes (Table 4). For example, low turbidity inside the plant bed (Fig. 8a) was likely the result of particle trapping or reduced sediment resuspension due to the effects of bed architecture on local hydrodynamics (Ward et al. 1984; Gruber and Kemp 2010). Reduced Chl *a* inside the bed (Fig. 8b) could also result from particle trapping or from nutrient limitation within the plant bed. Low DIN within the plant bed during summer months (Fig. 8c) is evidence of direct nutrient uptake by plants and/or enhanced denitrification within the plant bed (Caffrey and Kemp 1992). This effect on DIN may extend beyond the SAV bed, as down-bay DIN concentrations were substantially less than those measured up-bay. Elevated pH (Fig. 8d) and DO (Fig. 8e), which are indicative of plant photosynthesis, further illustrate the strong effects of dense vegetation on water quality. Seasonality in these spatial patterns demonstrates that as plant biomass increased throughout the growing season, so did the magnitude of the feedback effects.

These feedback processes may explain the threshold-type response of the SAV bed to change in environmental conditions. Feedbacks help maintain densely vegetated plant beds; however, in the absence of sediment-stabilizing vegetation, bottom sediments are easily resuspended, leading to elevated turbidity (Scheffer et al. 1993). As a result, the system tends to persist within one of these states (clear water with SAV or turbid water without SAV) until an externally driven change in water clarity induces a shift into the alternate state. We suggest that exceptional growing conditions during the drought period allowed the system to overcome the turbid water state, serving as a ‘‘kick-start’’ to facilitate the rapid resurgence.

Alternative explanations—An alternative explanation for sparse plant cover from the 1970s through the 1990s is lack of propagules, possibly the result of scouring or burial during Tropical Storm Agnes. The SAV increase in the early 2000s could, thus, be attributed to reintroduction of new propagules and bed expansion by rapid clonal growth. This occurred in Virginia's coastal bays, where historically abundant eelgrass (*Zostera marina*) disappeared in the 1930s due to a fungal disease and hurricane damage (Orth et al. 2006). When the area was reseeded through restoration efforts in 2001, eelgrass flourished because water quality was already suitable for plant growth. In contrast, SAV restoration efforts in and around Susquehanna Flats in the late 1980s were met with only marginal success, in part due to epiphytic growth on seedlings and transplants (Kollar 1989). If lack of propagules was the only limiting factor for plant growth in this system, then survival rates for

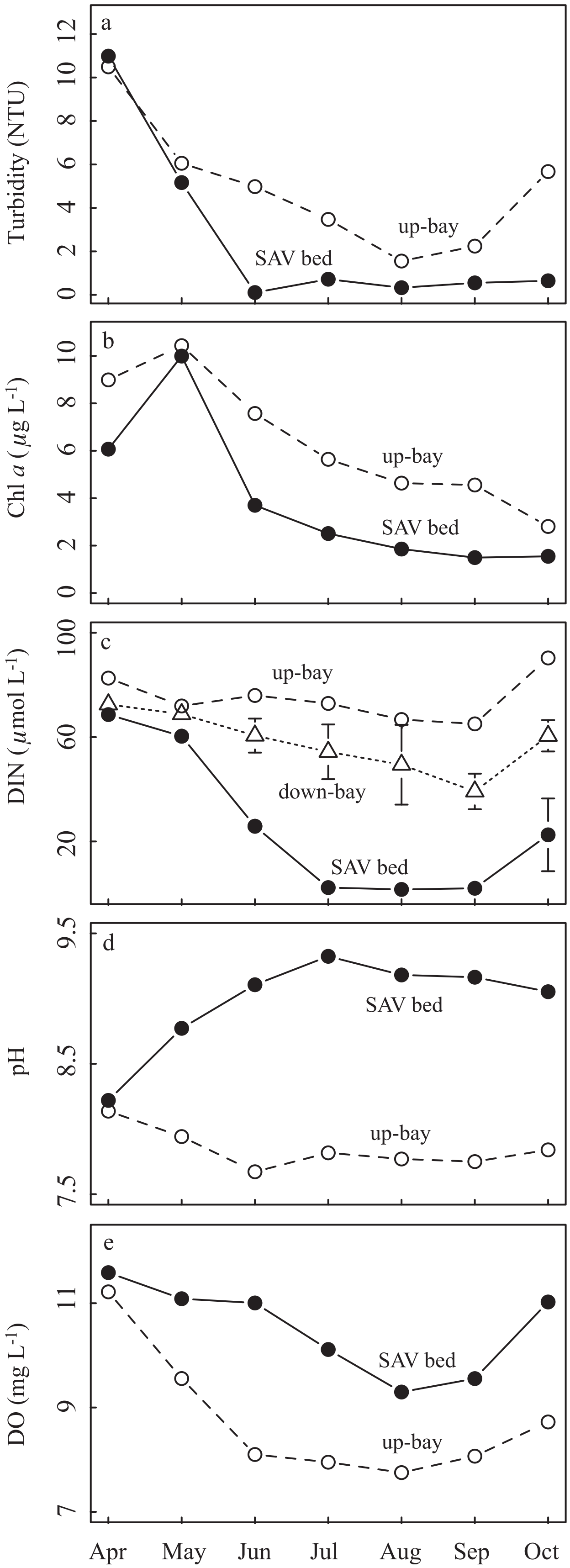

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Fig. 8. 2007–2010 monthly means ± standard error (SE) for several water quality parameters at sampling stations located inside the SAV bed, up-bay, and, in the case of dissolved inorganic nitrogen, down-bay from the SAV bed. Except for DIN, all other SE values did not exceed the radius of the data points. NTU, nephelometric turbidity units.

transplants and seedlings should have been greater in the absence of other limiting factors, such as light availability. Furthermore, patches of *M. spicatum* have persisted on Susquehanna Flats since at least the 1960s, and *V. americana* was always present and often abundant along the area's shoreline (Bayley et al. 1978; Kollar 1989). Presumably, these populations could have served as propagule sources for new plants. Therefore, we suggest that inadequate growing conditions are a more likely explanation for lack of SAV regeneration following their historic decline.

Another variable that warrants consideration is the trend of increasing growing season mean temperature, which continues to rise at 0.1°C per year (Table 2). Global warming is already causing temperature stress and diebacks for SAV species that prefer cold water, such as eelgrass, whose optimal temperature ranges from 10°C to 20°C (Nejrup and Pedersen 2008). For many freshwater SAV species, however, elevated water temperatures that are still within physiological tolerance ranges tend to promote increased plant production (Barko and Smart 1981). Because the optimal temperature for the dominant species at Susquehanna Flats exceeds 30°C (Van et al. 1976), warmer water could increase production. From 1984 to 1992, water temperature during the SAV growing season never exceeded 30°C; yet, between 1993 and 2010, 10–15% of water temperature measurements were greater than 30°C. Because, however, SAV were historically abundant in the upper Chesapeake Bay before this recent warming trend, we suggest that other factors were more important in driving the sudden SAV resurgence.

Future implications—These processes and patterns are not unique to Susquehanna Flats. Instances of nonlinear temporal trends in submersed plant systems have been suggested for the Dutch Wadden Sea (van der Heide et al. 2007) and U.S. mid-Atlantic Coastal Bays (Carr et al. 2010), as well as for shallow lakes in the United States (Carpenter et al. 2001) and Northern Europe (Scheffer et al. 1993). Whereas the variables affecting SAV systems may differ according to particular geographic features and plant species, the underlying mechanisms driving system dynamics are broadly relevant to our understanding of ecological change and can help guide SAV management. External perturbations that can shock a system are typically stochastic. However, the controlling variables that affect an ecosystem's resilience, or ability to withstand disturbance, are frequently related to anthropogenic activity (Walker 2004). Management efforts should consider dynamic interactions, which may include threshold effects, between SAV and relevant controlling variables. Particularly in light of predicted future increases in weather extremes, which are often the source of external perturbations, maximizing resilience by minimizing chronic anthropogenic stressors should be a core goal in the conservation of SAV ecosystems.

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