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Long-term nutrient reductions lead to the unprecedented recovery of a temperate coastal region

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Humans strongly impact the dynamics of coastal systems, yet surprisingly few studies mechanistically link management of anthropogenic stressors and successful restoration of nearshore habitats over large spatial and temporal scales. Such examples are sorely needed to ensure the success of ecosystem restoration efforts worldwide. Here, we unite 30 consecutive years of watershed modeling, biogeochemical data, and comprehensive aerial surveys of Chesapeake Bay, United States to quantify the cascading effects of anthropogenic impacts on submersed aquatic vegetation (SAV), an ecologically and economically valuable habitat. We employ structural equation models to link land use change to higher nutrient loads, which in turn reduce SAV cover through multiple, independent pathways. We also show through our models that high biodiversity of SAV consistently promotes cover, an unexpected finding that corroborates emerging evidence from other terrestrial and marine systems. Due to sustained management actions that have reduced nitrogen concentrations in Chesapeake Bay by 23% since 1984, SAV has regained 17,000 ha to achieve its highest cover in almost half a century. Our study empirically demonstrates that nutrient reductions and biodiversity conservation are effective strategies to aid the successful recovery of degraded systems at regional scales, a finding which is highly relevant to the utility of environmental management programs worldwide.

submersed aquatic vegetation | seagrass | eutrophication | global change | ecosystem management

Nutrient pollution is a leading threat to nearshore ecosystems (1), including marshes (2), mangroves (3), kelps (4), and especially seagrasses (5, 6). The global cover of seagrasses has declined by over 29% in the last century, largely because of nutrient and sediment runoff (5, 6). As a result, humanity has lost associated ecosystem services worth trillions of dollars, including habitat and nurseries for commercially important species, shoreline protection, nutrient cycling, and carbon storage (5, 7, 8). With such high stakes for human well-being, coastal managers are working to mitigate nutrient inputs and restore the functionality of coastal ecosystems. Recent syntheses, however, indicate that many coastal ecosystems, including seagrasses and other underwater vascular plants—collectively known as submersed aquatic vegetation (SAV)—are failing to meet their recovery potentials (9–13). With few instances of effective and large-scale restorations to validate past management actions, current recommendations are often guided more by theory than empirical evidence, leading to less-than-desirable outcomes and creating an urgent demand for successful examples to shape current and future efforts (10, 11).

Most reported examples of successful recovery occur at small scales (1–10 km^2) and over short periods (<10 y) (10), whereas many coastal systems are much larger and respond to influences distributed over greater areas and longer time frames (14). Chesapeake Bay has 18,803 km of coastline, a diversity of habitats, and is among the most consistently studied and managed regions in the world (15). It therefore presents a unique opportunity to resolve the effects of human activities on essential SAV habitat. Since 1950, the population of the Chesapeake Bay watershed has doubled to 18 million people, leading to changes in land use and adding to the substantial nutrient and sediment runoff from previously established urban and agricultural lands (15). From the 1950s through the 1970s, tens of thousands of hectares of SAV were lost in the largest decline documented in over 400 y (16). Concern over the loss of SAV and declines in the overall health and economy of the bay led to unparalleled cooperation among federal, state, local, and scientific agencies, whose joint efforts identified nutrient pollution and subsequent loss of SAV as the two most critical issues facing Chesapeake Bay (15). These agencies instituted measures to reduce nutrient inputs, as well as long-term monitoring programs to gauge their effectiveness, thereby establishing Chesapeake Bay as one of the few places on Earth where comprehensive long-term data exist to mechanistically link human impacts and ecological restoration at broad scales (15).

In this study, we evaluate the relationship between nutrient pollution and SAV using aerial surveys conducted from 1984 to 2015, in situ biogeochemical monitoring data, historical information

Significance

Human actions, including nutrient pollution, are causing the widespread degradation of coastal habitats, and efforts to restore these valuable ecosystems have been largely unsuccessful or of limited scope. We provide an example of successful restoration linking effective management of nutrients to the successful recovery of submersed aquatic vegetation along thousands of kilometers of coastline in Chesapeake Bay, United States. We also show that biodiversity conservation can be an effective path toward recovery of coastal systems. Our study validates 30 years of environmental policy and provides a road map for future ecological restoration.

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on land use and fertilizer application, and watershed model estimates for the loads of nutrients and sediments from diffuse land runoff (nonpoint sources) and from discrete locations such as wastewater treatment plants (point sources). We unite these data using structural equation modeling (17) to quantify both the direct and indirect controls on SAV. To bridge terrestrial and aquatic realms, we conducted two separate analyses: one exploring 120 independent subestuaries that could be directly coupled to local watershed nutrient loads across multiple salinity zones, and the other linking local environmental conditions to SAV throughout the bay.

Results and Discussion

Both analyses reveal that nutrients play a dominant role in reducing SAV cover (Figs. 1 and 2). At the watershed scale, increasing nonpoint source nitrogen (Fig. 1) and phosphorus (*SI Appendix*, Fig. S1) loads reduce SAV. For the freshwater and oligohaline regions of the bay, this effect is independent of other variables (Fig. 1*A*). In the meso- and polyhaline regions, the nutrient effect becomes more negative as freshwater discharge from the watershed increases (a nutrient-by-flow interaction, Fig. 1 *B* and *C*). This interaction presumably reflects increased nutrient runoff with increased precipitation (18). We further find that high nutrient loads result from fertilizer application in all salinity zones (Fig. 1 and *SI Appendix*, Fig. S1 *A* and *C*), with an additional clear linkage to manure application in the mesohaline zone only (Fig. 1*B* and *SI Appendix*, Fig. S1*A*). Fertilizer and manure loads are positively associated with agriculture (Fig. 1 *B* and *C* and *SI Appendix*, Fig. S1) except in tidal freshwater/oligohaline areas (Fig. 1*A*), reflecting the agricultural sector's dominance as a source of nutrient loads to Chesapeake Bay. Many subestuaries in the tidal freshwater/oligohaline zone are highly urbanized, and nonfarm fertilizer applications (such as to residential lawns) in these areas may weaken the fertilizer-to-agriculture link. Urban development is also positively associated with increased nutrient loading in most areas of the bay, through increased runoff and/or through nonfarm application of fertilizer (Fig. 1 *A* and *B* and *SI Appendix*, Fig. S1 *A* and *B*). In summary, at the watershed scale, we find a cascade triggered by agricultural practices that apply manure and fertilizer which, together with urbanization, increase nutrient runoff that ultimately decreases SAV.

Higher loads from the watershed increase the concentration of nutrients in the bay and, accordingly, the larger bay-wide analysis shows that observed water column nitrogen and phosphorus concentrations reduce SAV through two pathways. First, phosphorus promotes phytoplankton blooms (increased chlorophyll-*a*), which shade the water column (decreased Secchi depth, a measure of clarity) and indirectly reduce SAV by restricting light penetration (Fig. 2). Second, nitrogen acts directly to reduce SAV, presumably by stimulating epiphytic algae that overgrow the blades (Fig. 2) (19, 20), or possibly through other means such as accumulation of sulfides (21). Moreover, the direct effect of nutrients on SAV is three times more negative than the indirect

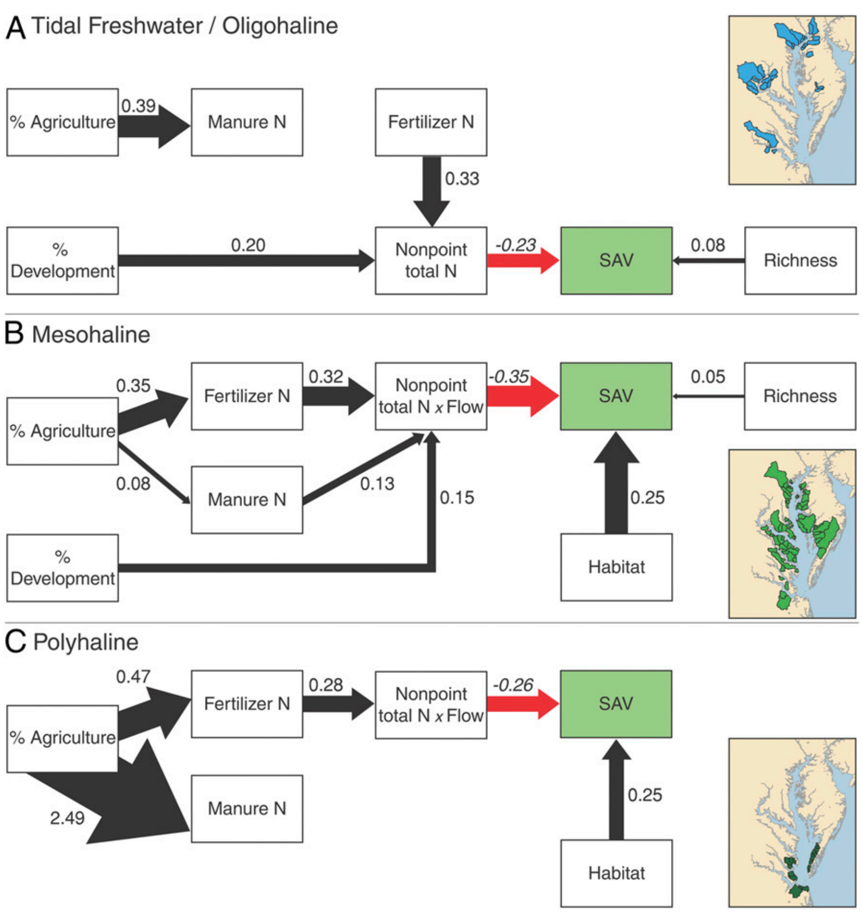

Fig. 1. Structural equation models for total nitrogen (N) fit to subestuaries and their watersheds by salinity zone. (*A*) Tidal freshwater/oligohaline (0–5 psu), (*B*) mesohaline (5–15 psu), and (*C*) polyhaline (15–25 psu). Arrow width is proportional to the standardized effect size, given next to the arrows. Black arrows denote positive effects; red arrows, negative effects. Nonsignificant relationships ($P > 0.05$) have been omitted for clarity, including the nonsignificant effects of point source nutrients and total suspended solids (TSS) (*SI Appendix*, Fig. S5). Map *Insets* denote the location of watersheds. Units and unstandardized path coefficients are given in *SI Appendix*, *Supplementary Materials*.

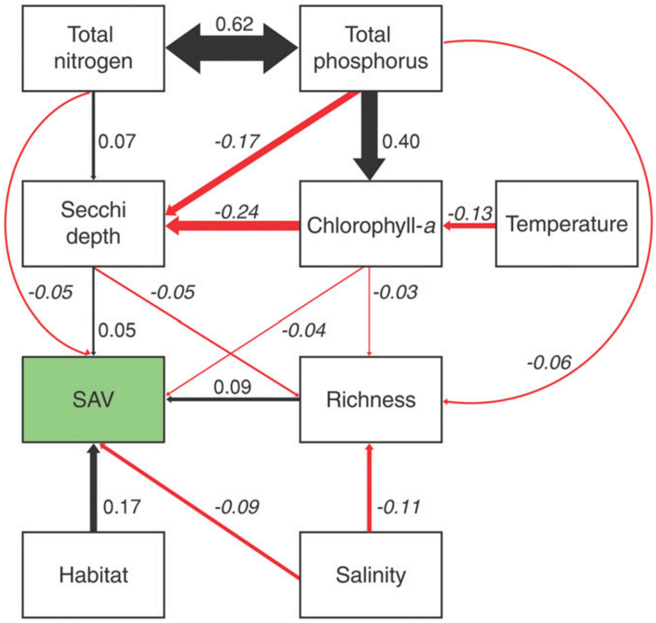

Fig. 2. Bay-wide structural equation model representing the effects of water quality on SAV cover. Arrow width is proportional to the standardized effect size, given next to the arrows. Black arrows denote positive effects; red arrows, negative effects. Nonsignificant relationships ($P > 0.05$) have been omitted for clarity, including the nonsignificant effects of total suspended solids (TSS) (*SI Appendix*, Fig. S6). Units and unstandardized path coefficients are given in *SI Appendix*, *Supplementary Materials*.

effect mediated by water column chlorophyll-*a* and Secchi depth (based on computed indirect effects, Fig. 2), suggesting that direct fouling is more detrimental to SAV than low clarity (22). The weaker effect of clarity may be explained by the patchiness of phytoplankton blooms, and by variability in the effect of particulates on light penetration due to differences in the types and properties of the suspended particles (23). Both mechanisms are widely recognized in Chesapeake Bay (24, 25) and elsewhere (22, 26, 27), but we demonstrate that they operate simultaneously and at large scales, a key finding that validates small-scale experimental work (19) and has direct implications for nutrient management.

We also find a consistent role for biodiversity (i.e., species richness of SAV) in promoting cover (Figs. 1 and 2). At the bay-wide average richness of three species, one additional species would result in a 1.8-fold increase in total SAV cover. Because salinity strongly affects species' distributions in Chesapeake Bay (18), the consequences of increasing diversity applies primarily to oligohaline and freshwater regions (Fig. 1 *A* and *B*), where more than a dozen SAV species coexist (*SI Appendix*, Table S1) and where recovery has been greatest (Fig. 3*A*) (28). The importance of richness in our models was unexpected, as its inclusion was meant only to distinguish monospecific stands of species like *Zostera marina* and *Hydrilla verticillata*, which are known to respond differently than other SAV species in this system (8, 15). We believe this result is robust because we accounted for sampling effort through rarefaction (Figs. 1 and 2), and we modeled extrinsic controls on cover such as sampling area, nutrient concentration, and light availability that might generate otherwise spurious correlations (e.g., ref. 24; see also *SI Appendix*). The richness effect is consistent with global studies of terrestrial plants and fishes (29, 30) and provides large-scale confirmation of diversity effects reported for local seagrass plots in the Indo-West Pacific (31). Our finding confirms, then, that conservation or restoration of species diversity could further enhance recovery of underwater grasses.

Examination of long-term nutrient trends from in situ observations show that water column nitrogen concentrations have declined, on average, by 23%, and phosphorus concentrations by 8% since 1984, with the biggest reductions occurring in the mid-1990s (Fig. 3 *B* and *C*). Declining nutrient levels coincided with a 316% increase in SAV cover during the same period, from 7,878 ha in 1984 to 24,874 ha in 2015, based on data from the aerial surveys (Fig. 3*A*). Given our finding that nutrients reduce SAV from our model results, we propose that much of the SAV recovery has been a direct result of intensive efforts to reduce inputs and lower nutrient concentrations in Chesapeake Bay over the last 30 y. We also show that nutrients from land use activities (i.e., nonpoint sources) have a more significant impact than those from specific sources (e.g., sewage treatment plants) (Fig. 1 and *SI Appendix*, Fig. S1). There are, however, instances where mitigation of point sources may be key to restoring SAV, particularly at the scale of individual subestuaries (25). We suggest that a combination of the two efforts is therefore required to continue the trajectory of SAV recovery.

While we did find a role for water clarity in enhancing SAV (Fig. 2), total suspended solids (TSS) did not emerge as a strong predictor of cover, either as loads or observed concentrations (Fig. 1 and *SI Appendix*, Figs. S1 and S2), despite TSS being linked to light penetration (32). Two possible explanations are that TSS provide little explanatory power at large scales beyond Secchi depth, which is a more integrated measure of clarity, and that phytoplankton play a larger role in light attenuation in much of the bay (*SI Appendix*, Fig. S2). Furthermore, local TSS concentrations were available for only 17 of the 30 study years, limiting our power to detect an effect of TSS in the bay-wide analysis (*SI Appendix*, Fig. S2). Our finding does not imply that TSS are unimportant. Rather, reducing TSS may represent an alternative route for further maximizing SAV recovery, although more data are required to validate this conclusion.

Our study contributes to the limited but growing number of examples of successful reversal of human impacts and subsequent recovery of coastal habitats (10, 13). The Chesapeake Bay, however, is distinguished in the degree of recovery, the spatial and temporal scale, and our ability to discern specific mechanisms using structural equation modeling. Other regions have seen large resurgences in seagrass cover with improved water clarity, such as in Tampa Bay, Florida (33), or improved sediment stability, as in the Wadden Sea (34); but the Chesapeake Bay has seen greater total and proportional recovery than any other SAV restoration project of which we are aware. There have also been well-documented increases in kelp forests after the cessation of trawling or implementation of no-take reserves in the Gulf of Maine (35), Norway (36), and Tasmania (37), and on coral reefs in the Bahamas (38), although these studies generally extrapolate from local observations or model predictions to the regional scale. While recovery in these systems is undeniably sizable, the lack of actual cover data contrasts these examples against shallow subtidal SAV systems where regional cover can be accurately quantified. Our precise measures of SAV cover makes a strong case for the Chesapeake Bay as one of the preeminent ecological restorations reported to date.

The Chesapeake Bay Program, which is responsible for overseeing the SAV restoration reported here, is also a unique example of cooperation among federal, state, and local agencies. While most other recoveries have occurred in one or few jurisdictions, the Chesapeake Bay watershed spans six US states and the District of Columbia. The coordination, monitoring, and enforcement of regulations pertaining to water quality and habitat protection have therefore posed a significant challenge. Despite these difficulties, sustained efforts have yielded a substantial positive outcome for the overall health of the bay (Fig. 3). Studies that provide positive examples of successful human intervention have been shown to strengthen public support for

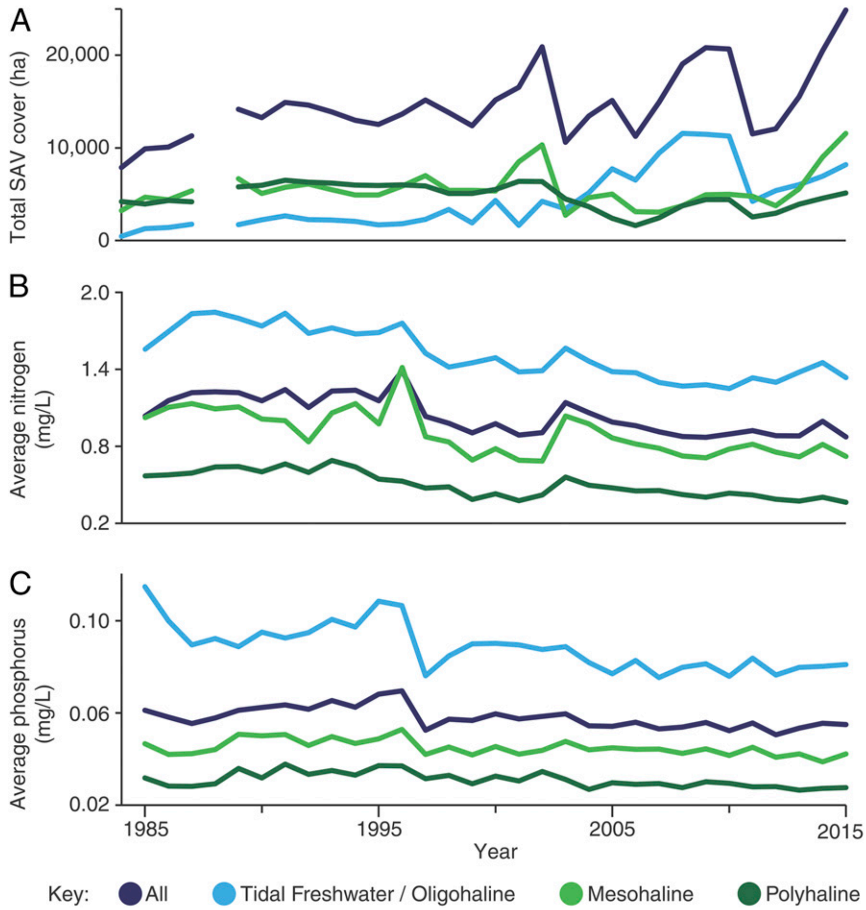

Fig. 3. Annual bay-wide trends, and trends by salinity zone, in (*A*) total observed SAV cover (hectares, from aerial monitoring survey), (*B*) mean water column nitrogen, and (*C*) mean water column phosphorus concentrations (milligrams per liter, from in situ water quality monitoring). SAV cover was not obtained for 1 y (1988).

environmental conservation (39, 40), and long-term studies like ours have also demonstrated a disproportionate ability to inform environmental policy (41). Our findings validate the importance of both continued nutrient reductions and continued monitoring in the Chesapeake (and elsewhere), as well as the implementation of other measures to revitalize impacted ecosystems. For example, the Chesapeake Bay Program does not currently consider biodiversity in its recommendations. Our finding that species richness was the only predictor (other than habitable area) to have a positive effect on SAV cover (Figs. 1 and 2) suggests that enhancing diversity of foundation species like SAV could both restore and stabilize future habitat. Evidence from other systems has also shown that high biodiversity may buffer against further change caused by other stressors, such as climate change (30, 42).

Reducing nutrient inputs is a central component of coastal restoration efforts worldwide, including the US Environmental Protection Agency's Chesapeake Bay Program, Great Lakes Restoration Initiative, San Francisco Bay Program, and Gulf of Mexico Program, as well as similar partnerships in Long Island Sound, Puget Sound, and Lake Champlain (https://www.epa.gov/nutrientpollution), and in many areas of Europe (e.g., HELCOM in the Baltic Sea, www.helcom.fi/action-areas/agriculture). These programs seek to restore some of the most productive, valuable, and iconic bodies of water in the world, all of which are facing similar challenges. Our study speaks directly to the value of such coordinated, multipartner restoration efforts to enhance coastal habitats at the regional scale.

Materials and Methods

Subestuary Data. Subestuary watersheds were identified as in refs. 18 and 43, and grouped into three salinity zones: 0–5 (low), 5–15 (oligohaline), and 15–25 practical salinity units (psu) (polyhaline). Land use information came from the US Geological Survey (USGS) National Water Quality Assessment Wall-to-Wall Anthropogenic Land Use Trends dataset (44). Within each watershed, we aggregated the areas of crop, pasture, hay, and grazing lands into one agricultural land category, and we aggregated commercial, industrial, recreational, and residential lands into one developed category. To normalize for differences in watershed size, we expressed agricultural and developed land uses as their percentages of watershed area. We used spline interpolation among the years of reported land use to assign values to missing years.

Fertilizer and manure data were collated by the USGS from various sources. Annual county-level fertilizer loads and manure nutrient mass were decomposed into separate nitrogen and phosphorus components (in $kg\ N \cdot y^{-1}$ and $kg\ P \cdot y^{-1}$), and summed for each watershed. Point and nonpoint source nitrogen, phosphorus, and total suspended solid loads were estimated using the Chesapeake Bay Program's phase 6 beta 4 watershed model (CBWM) (www.chesapeakebay.net/groups/group/modeling_team). These loads (in $kg \cdot y^{-1}$) and water discharge (in cubic meters, our independent variable "flow") are simulated daily from 1984 to 2012 at a subcounty scale and summed for each watershed in each growing season. Because fertilizer and manure records were only available through 2012, the entire subestuary dataset was restricted to 1985–2012. Further details on the delineation of watersheds and calculations of summary statistics can be found in *SI Appendix*.

SAV Data. SAV bed area and density class were mapped from aerial imagery acquired annually from 1984 through 2015 (except for 1988) as part of the Virginia Institute of Marine Science Submersed Aquatic Vegetation Monitoring Program (web.vims.edu/bio/sav/) (see ref. 8). Annual maps of SAV were converted to raster maps with 30 m cells, each of which was assigned to a density bin. Total density-weighted bottom cover was computed by multiplying the cell area by its percent cover. The area of habitable bottom was calculated using 1- and 2-m contour data that were produced to support the development of Chesapeake Bay SAV restoration goals. Species richness of SAV and community composition data were based on presence/absence surveys conducted during the growing season by researchers, government agencies, and trained individuals, including citizen scientists (18, 45). To account for variable effort over time, we rarefied richness for each subestuary across all years (46). Further details on mapping and biodiversity data are given in *SI Appendix*.

Water Quality Data. Water quality data were obtained from the Chesapeake Bay Program Water Quality Monitoring Database (www.chesapeakebay.net/data), including: temperature, salinity, turbidity (Secchi depth), and water column concentrations of nitrogen and phosphorus, chlorophyll-*a*, and total suspended solids. We utilized 112 stations with consistent data coverage from 1985 to 2014. To create replicate units, we assigned each SAV cell to the nearest monitoring station and then summed the total SAV cover proximate to each station. Further details concerning water quality data can be found in *SI Appendix*.

Statistical Analysis. To mechanistically link watershed characteristics and water column variables to SAV cover, we constructed structural equation models (SEMs). This technique allows for fitting of complex networks where variables can be both predictors and responses, facilitating the identification of cascading effects. Because SAV cover is temporally and spatially autocorrelated, we modeled cover using general linear mixed effects models in a piecewise SEM (17). Models were fit with subestuary or monitoring station as a random effect, and an additional autoregressive moving average (ARMA) correlation structure with a 2-y lag (47). We fit separate SEMs for nitrogen and phosphorus in the subestuary analysis, and with and without total suspended solids for the bay-wide analysis. Model assumptions were assessed visually, and fit was determined using Fisher's *C* statistic and calculation of individual model R^2 values (17). Further details on the structural equation modeling analysis, including derivation of conceptual models and evaluation of goodness of fit, can be found in *SI Appendix*.

Supplementary Materials. Supplementary methods and results, and all data and code used for the analyses, are given in *SI Appendix*.

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