Modeling the past to predict the future: forecasting the relative role of climate change and habitat management on Chesapeake Bay submersed aquatic vegetation (SAV)

Key Messages:

- Temperature rise and successful nutrient reductions over the last two decades have facilitated a shift in dominant SAV species throughout the Chesapeake Bay- from eelgrass to widgeongrass and in tidal fresh/oligohaline communities.
- Mechanistic predictions on how both climate change and regional management will affect each SAV community are required to update restoration plans and prepare for unprecedented climate futures.
- Using detailed analyses of the past applied to novel predictive modeling and sophisticated Chesapeake Bay Modeling Workgroup future climate scenarios, we found that none of our 8000 simulations reached the Bay-wide SAV restoration goal by 2060 but continued nutrient reductions are essential to ensure a vegetated Chesapeake Bay under climate change.
- Continued nutrient reductions will most benefit widgeongrass and tidal fresh/oligohaline communities that currently make up ~70% of all SAV, while reductions will also keep eelgrass from going locally extinct.
- Current nutrient reduction targets will foster the maintenance and expansion of SAV in Chesapeake Bay under climate change conditions but, to reach SAV restoration targets within this century, nutrient reduction targets must be significantly expanded and designed to benefit the new dominants.
- Species-specific monitoring and management combined with experimental investigations on the effect of species shifts on food webs, fisheries, and blue carbon is an essential next step in predicting the future.

Executive Summary:

Global change is re-organizing coastal habitats in the Chesapeake Bay; climate extremes and human activities are changing both the major stressors and dominant species that make up valuable submersed aquatic vegetation (SAV) habitat. To prepare SAV management plans that support coastal food webs and fisheries, protect shorelines, and sequester tons of carbon into the future across the whole Chesapeake Bay, we must address three explicit challenges: First, the *strength and seasonality of climate and anthropogenic controls will continue to change into the future to create increasingly novel environmental conditions unseen by past and present SAV communities*. Next, *17 species of SAV occupy the*

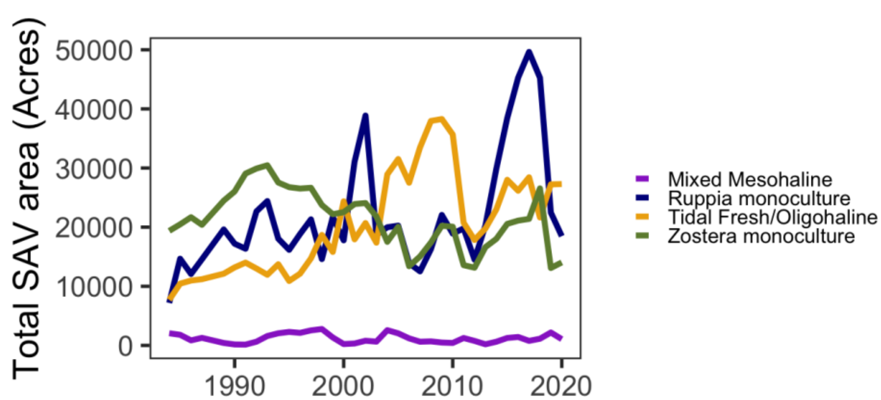

Figure 1. Total SAV area (HA) of each community over time in Chesapeake Bay shallow water habitat (green = eelgrass, blue = widgeongrass, yellow = freshwater, purple = mixed mesohaline)

Chesapeake Bay and species identity and life history determine different responses to these conditions, driving annual vegetation change. Finally, *future ecosystem change is uncharted by historical observations and habitat management that usually operates off of past knowledge may not apply to future environments*. Overall, predicting a future that is outside of the realm of the past requires interdisciplinary collaborations and big data synthesis to inform local and regional management decisions that maintain a sustainable relationship between humans and the Bay.

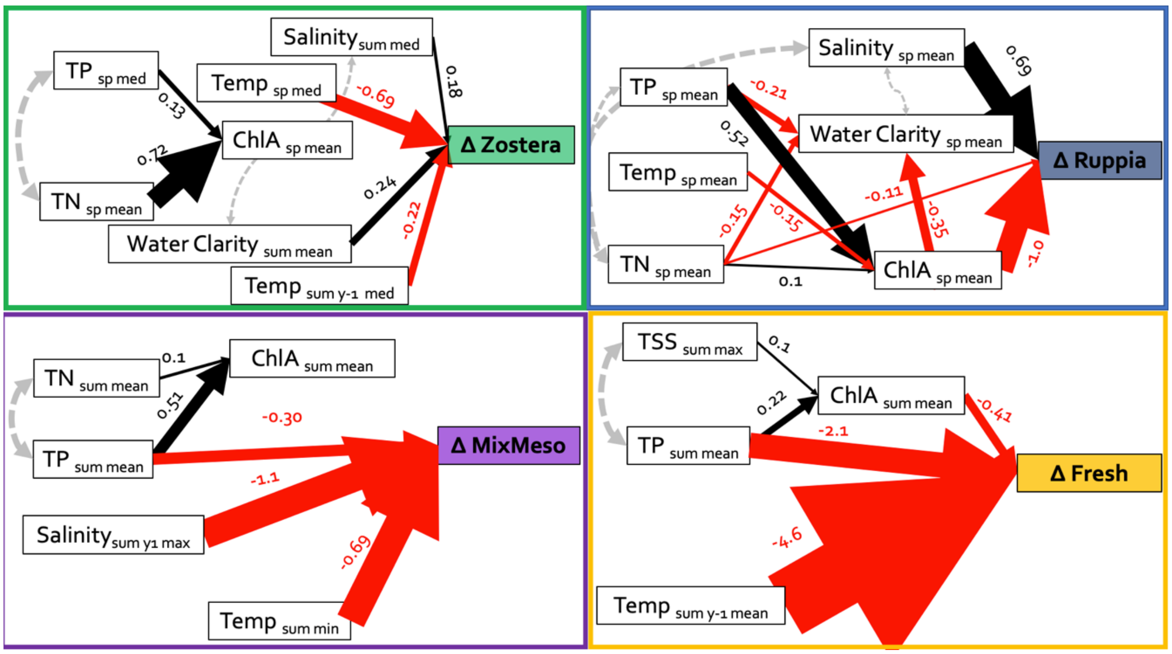

Figure 2. Structural equation modeling results showing environmental controls drive annual variation across each of the four major SAV communities in the Chesapeake Bay

Here, we utilize the Chesapeake Bay's unique long-term, large-scale data sources to build a mechanistic understanding of the past to predict how climate change and human activities will affect dominant SAV habitat into the next 40 years. We first use aerial survey and ground observation data to identify and map the dominant communities of SAV throughout the Bay (Objective 1). Then, we combine nearly 40 years of Bay-wide aerial survey and water quality data to quantify the major climate (e.g., temperature) and human (e.g., total nitrogen) controls on each community (Objective 1), using structural equation modeling to describe how different seasonal variables have controlled annual cover in each community across the Bay to date. Next, we combine the projected effects of climate change (i.e., temperature rise, precipitation fluctuations) and human activities (i.e., nutrient input management) to create two future scenarios that depict the future landscape of environmental conditions across the Bay (Objective 2) using climate modeling projections applied in the structural equation model of SAV for the years 2021-2060. Both scenarios incorporate predicted 2055 increase in temperature and precipitation volume and intensity. The "No Further Action" scenario assumes the case of no further Chesapeake Bay Program (CBP) nutrient reductions with nutrient control levels remaining as they were since 1985. The "Nutrient Reduction" scenario applies nutrient reductions in nitrogen and phosphorus throughout the Bay brought about the CBP Phase 3 Watershed Implementation Plan (Shenk et al. 2021). Finally, we implement a novel predictive modeling technique across every hectare of vegetated Chesapeake shallow water habitat to predict future responses of each community to anticipated conditions (Objective 2). Our interactive web-based tool then allows managers, scientists, and citizens to visualize how climate change and management scenarios will influence local rivers, basins, and communities (Objective 3).

By quantifying change in areal cover and total proportion of the Bay occupied by each of the 4 major SAV communities from 1984 to 2020, we find that **the last two decades of large-scale fluctuations in total Bay-wide SAV are mainly a result of major gains and die-backs in widgeongrass monocultures** (*Ruppia maritima*) **and in the oligohaline/tidal fresh community** (several species including *Vallisneria americana, Hydrilla verticillata)* (Figure 1). **While summer temperature extremes and poor water clarity have caused the gradual decline of the historically dominant eelgrass (*Zostera marina*), we find that the now-dominant communities are not only controlled by different seasonal variables but also have benefitted the most from successful nutrient reductions**; year-to-year widgeongrass cover responds most strongly to springtime freshwater flow and phytoplankton levels (chl-*a*) while the tidal fresh community responds to summer phosphorus concentrations and high temperatures. Overall, we find that each major community is controlled by a different combination of climate and human stressors, while variation in widgeongrass and freshwater communities are explained by different variables than the formerly dominant eelgrass (Figure 2).

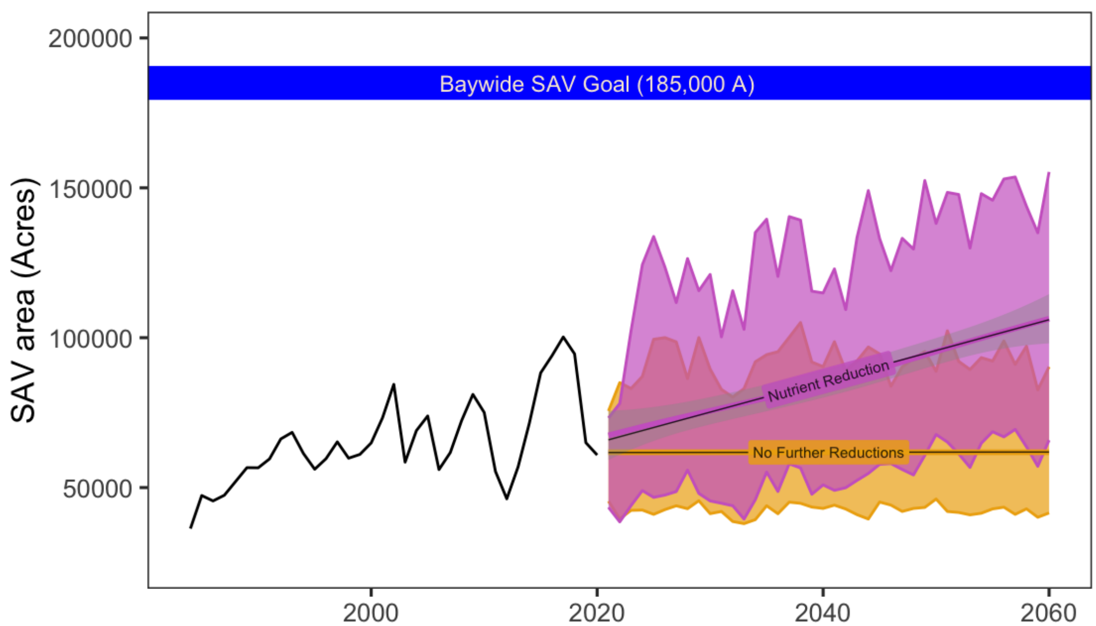

Figure 3. Future predicted total annual SAV area (acres) for both No Further Reductions (yellow) and Nutrient Reduction (purple) scenarios. Trendlines show mean and ribbons show the 95% credible interval for 1000 simulations. Blue bar represents the Chesapeake Bay SAV restoration goal of 184,889 acre. Overlapping ribbons can be interpreted as no significant difference between simulated scenarios

By examining 8,000 simulated futures in our predictive modeling framework, we find that, **while temperature extremes will exacerbate shifts in dominant species identity, expanded nutrient reductions have a critical role in mitigating the risks of climate change for sustained cover of Chesapeake Bay submersed aquatic vegetation**. We simulated 1,000 different futures annually from 2021-2060 for two potential scenarios: (1) a Nutrient Reduction scenario, under estimated 2055 climate change conditions combined with the Phase 3 WIP nitrogen and phosphorus reductions, and (2) a No Further Action scenario, under 2055 climate change conditions and 1985 (at the start of the CBP) nutrient management conditions (i.e., no actions to reduce nutrients). Using our structural equation models and these scenarios, applied starting in 2021, right after the last observed data year of 2020 and run for 40 years to 2060. Our modeling suggests that continued reductions in both nitrogen and phosphorus generates the only future with temporal stability for all seagrass communities (Figure 3). Most importantly, **nutrient reductions specifically support further large-scale expansion of the dominant, climate-tolerant plants in the mid- and upper-Bay (i.e., widgeongrass monocultures and freshwater communities) to fuel total Chesapeake vegetated area (Figure 4).** While our predictions indicate that uncontrollable summer temperature rise will continue to slowly decrease total eelgrass cover, nutrient reduction scenarios do help maintain eelgrass cover into the future even if historical cover is unrealistic to obtain.

Ecological predictions allow us to identify options for better managing our relationship with ecosystems, and Chesapeake Bay SAV management can be at the forefront of predictive ecology and foresight-driven conservation of changing coastal seascapes. Adaptations, acclimation, and recovery potential elevates Chesapeake Bay SAV as a potential winner in the Anthropocene, while predicting the future for these ecosystems will help create a sustainable relationship between humanity and nature. Now, our understanding of both the past and the future allows us to build tailored management and restoration plans for SAV communities throughout every segment, basin, and river. Additionally, we call for increased species-specific monitoring, including research on how shifting species dominance in SAV communities affects fisheries, carbon sequestration, and other ecosystem services.

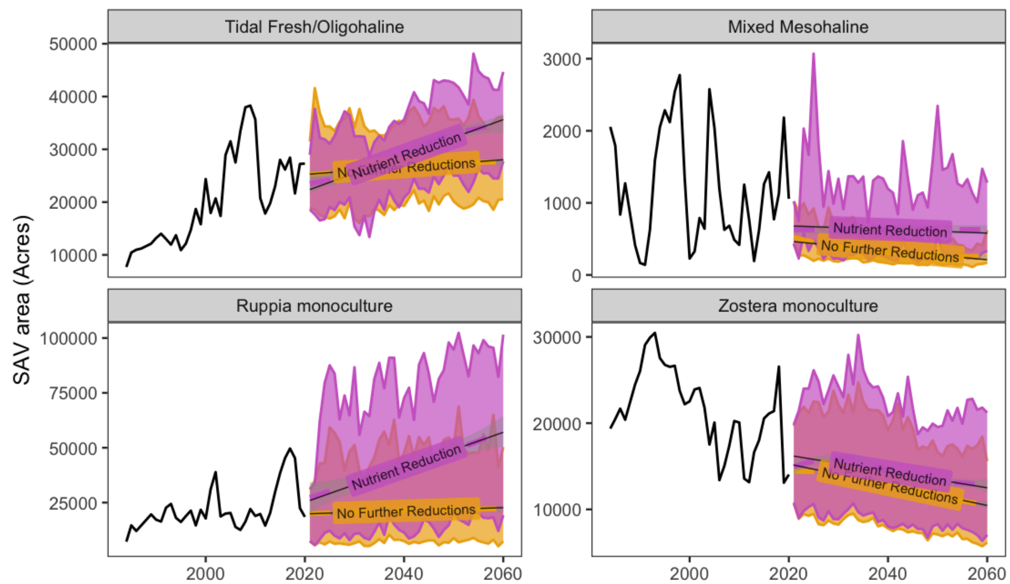

Figure 4. Future projections in SAV area (acres) for each of the four major communities. Yellow trendline represent the mean of 1000 No Further Reductions simulations, with the yellow ribbon representing 95% of said simulations. Purple line and ribbon represent the Nutrient Reduction scenario. Overlapping ribbons can be interpreted as no significant difference between simulated scenarios where non-overlapping ribbons show periods of time where one scenario is significantly different than the other.

Background: Empowering SAV management by leveraging the past to predict unprecedented futures

Climate change and human activities have shifted both the major stressors and dominant species in nearshore habitats. These shifts create challenges for continued ecosystem management not only because species respond differently to climate and human stressors, but also because future environmental conditions will be outside the realm of the recent past. In the Chesapeake Bay, seagrasses and aquatic plants (hereafter refered to as SAV, submersed aquatic vegetation) enhance coastal structure, function, and health by providing habitat for productive fisheries, buffering thousands of kilometers of shoreline, improving water quality, and sequestering tons of carbon across each year. The large spatial scale of the Bay generates substantial variation in abiotic factors like salinity to create different SAV communities that may need to be managed individually. In fact, Chesapeake Bay SAV is comprised of fresh- and saltwater plants that make up four distinct communities and have already shown significant difference to both climate change and human management.

Importantly, SAV communities and environmental factors across the Bay have changed over time. For example, in the middle and lower Bay, recent evidence suggests that eelgrass is unable to handle the combined rising summer temperatures and poor water quality of the last two decades (Lefcheck et al. 2017). Yet, large-scale eelgrass decline has been offset by massive gains in temperature-tolerant, opportunistic widgeongrass in response to successful nutrient reductions (Hensel et al *submitted*). Thus, trade-offs in life history traits and stressor-recovery capability create different responses for major species to the combined effects of temperature rise, increase precipitation volume and intensity, and nutrient inputs. These novel environmental conditions threaten the long-term resilience of SAV habitat, but proactive management informed by a mechanistic understanding of the causes of annual change can prepare Chesapeake Bay SAV for the unprecedented future. *To meet conservation goals including reaching the Baywide SAV area restoration targets, we must now determine how current and future climate change interacts with variation in multiple, simultaneous stressors to drive cover of each of the significant SAV communities across the Chesapeake.*

Project Objectives

Objective 1: ***Quantify the effect of past changes in water quality, habitat availability, land cover, and climate (rainfall, runoff, temperature) on interannual variation of the four major SAV communities and total Bay-wide trends across the Chesapeake Bay***.

i) Use aerial surveys and ground observations to identify the major SAV communities across the Chesapeake Bay,
ii) use aerial surveys to describe how SAV community relative abundance and contribution to total Baywide SAV cover has changed over time,
iii) use CBP water quality data to describe past changes in environmental conditions across the Bay,
iv) use structural equation modeling to quantify the major climate and management variables that have controlled the annual cover of each of the four dominant SAV communities since 1984

Objective 2: ***Predict how climate change and nutrient management scenarios will affect individual SAV communities and total Bay-wide SAV across the Bay into the future.***

i) Use predicted environmental data from the CBP Modeling Workgroup and past environmental changes to build future climate scenarios for every hectare of habitable shallow water across the Bay
ii) use simulation models parameterized with information from Objective 1 to predict how each SAV community and total Bay-wide SAV will respond to changes in temperature, precipitation, sea level rise, and watershed land use (i.e., nutrient management) every year until 2060.

Objective 3: ***Build an interactive web-based tool to explore how climate change and management scenarios will influence SAV in the future***.

i) build a web-based map/graph tool to depict both future scenarios and predicted effects on each SAV community. Users will be able to select segments and basins, communities, and total Bay-wide projections for each scenario.

Methods Summary:

Objective 1: ***Quantify the effect of past changes in water quality, habitat availability, land cover, and climate (rainfall, runoff, temperature) on interannual variation of the four major SAV communities and total Bay-wide trends across the Chesapeake Bay***.

i) *To identify the major SAV communities and map community distribution across the Chesapeake Bay*, we combined annual SAV aerial coverage data from the VIMS aerial survey with SAV community and species identity information from the VIMS ground survey dataset. To determine the dominant community types across the Bay, we analyzed the recent history of reported SAV species in meadows within each of the 108 vegetated Chesapeake Bay Program (CBP) water quality stations (i.e., site) in the long-term database of SAV species observations (http:// web.vims.edu/bio/sav/field_observations.html) collected annually by researchers, natural resource managers, and trained volunteers. These sites are used throughout all analyses in all objectives, and act as independent replicates by assigning each 30-meter vegetation-cover cell to the nearest monitoring station and collating the total vegetation proximate to each station. Water quality station zones have been treated as independent replicates (as in: (Lefcheck et al. 2017, 2018)) and correspond with sampling stations for the Chesapeake Bay Program Water Quality Monitoring Database (http://www.chesapeakebay.net/data). Vegetation cover in the CBP water quality stations is eventually converted to vegetation cover in the CBP Segments, for visualization in the web-based tool of Objective 3.

To characterize the average species composition within each site, we combined all ground survey observations from 2000-2020 to create a summed station × species occurrence observation matrix for the entire period of record. The number of observations of each species was then converted to percentages of total observations for each station to normalize for differences in the frequency with which the different stations were surveyed. The SAV communities were characterized using non- metric multidimensional scaling (NMDS) in R using the meta-MDS function in the Vegan package, which performs an iterative analysis at random starts to prevent selecting a local optimum fit rather than the global optimum (Oksanen et al. 2014). The sites were then classified into community categories using an unweighted pair-group method using arithmetic averages for an average linkage clustering method in the Vegan Library. The observers report species identifications coded by location and date, and has been previously used to characterize the communities in SAV beds across Chesapeake Bay (Moore et al. 2000, Patrick et al. 2017).

ii) *To describe how SAV community relative abundance and contribution to total Baywide SAV cover has changed over time*, we assembled all the above SAV species identity data with annual cover data from the VIMS aerial surveys (https://www.vims.edu/sav). In each of the 108 sites, we calculated annual SAV area (hectares) and density weighted mean area (ha) of each community from 1984-2020. To explicitly understand year-to-year vegetation dynamics, account for variation in the size of sites, and to ensure that large beds are not overrepresented in data analyses, we calculated the annual proportional change in density-weighted bottom coverage at each site. At each site every year, we computed total density-weighted bottom cover by multiplying the site area by the midpoint of its percent cover class (very sparse - 5%, sparse – 25%, dense – 55%, very dense – 85%). Then, to compute the proportional change in density-weighted bottom cover, we quantified the total potential habitable area for seagrass at each site by calculating the maximum density-weighted mean composite area over all years of data. Using this maximum value, we scaled widgeongrass coverage at each site each year between 0 and 1, where 1 was the maximum density weighted mean composite area and 0 was no cover. Finally, we calculated proportional change in scaled density weighted mean area between two consecutive years at each site. We also quantified total Bay-wide SAV by summing the annual area of every site.

iii) *To describe past changes in environmental conditions across the Bay,* we assembled monthly data through present (1984-2021) *via* CBP Water Quality Monitoring Program (https://www.chesapeakebay.net/what/programs/monitoring), examining *in situ* water quality data from nearby sampling stations in the Chesapeake Bay Program Water Quality Monitoring Database (http://www.chesapeakebay.net/data). We summarized seven variables collected bi-weekly at each water quality monitoring stations from 1984-2020: temperature, salinity, water clarity, and water column concentrations of total nitrogen and total phosphorus, and chlorophyll-*a*. While measurements are taken at multiple depths, we used values at 0.5 or 1 m depth to best reflect conditions in nearshore shallow waters. At each station, temperature and salinity were measured along a hydrographic profile with a multiparameter sonde, water clarity was estimated with Secchi disk depth using a black and white Secchi disk and a measuring line dropped over the side of the sampling vessel, while water samples were collected from the surface and several depths and sent to a laboratory for analysis of nutrient concentrations, chlorophyll-a, and total suspected solids. For our analyses we calculated mean, median, maximum, minimum, range, and step-wise change values for each variable and summarized each variable into seasons (i.e., annual, spring, summer, fall, winter).

iv) To determine how both climate and management have controlled the annual cover of each of the four dominant SAV communities since 1984, we used structural equation modeling (SEM) to develop a mechanistic understanding of how changing environmental conditions have affected annual density change of the four dominant SAV communities in the Chesapeake Bay. SEM is a powerful tool for understanding cascading effects, such as from the watershed to shallow water seagrass habitat, because variables can be both predictors and responses. Piecewise SEM, or local estimation, allows variables to be modeled to a wide variety of distributions and hierarchical structures, and incorporates statistical interactions better than in previous iterations of SEM (Lefcheck 2016). A key feature of SEM is that it assumes causal (i.e., directional) relationships. One can support causal inferences by including previous experimental and observational evidence, biological knowledge, and logical intuition about the system. Given how well the Chesapeake Bay has been monitored and studied, we have a higher degree of confidence in the causal nature of the associations identified in our data. Such expert knowledge is an inherent feature in the structuring and evaluation of multivariate causal hypotheses. In addition, we have carefully structured our models to improve causal inference. The 'back-door criterion' proposes that adding covariates that explicitly block the confounding effect of other factors on the response of interest can be used to open the possibility of causal linkages. For example, nutrients can affect freshwater vegetation change directly or indirectly by increasing chl-*a* or decreasing Secchi depth. In other words, these linkages to nutrients provide a statistical control that reduces the probability of spurious correlation. For each community, we used generalized linear mixed effects models with ARMA correlation structures for the individual models. The relationships specified in the mainstem analysis were derived from *a priori* knowledge of Chesapeake Bay SAV ecosystems. All SEMs generated a set of meaningful independence claims, so we could assess global goodness-of-fit using Fisher's *C*.

For all sets of SEMs, we computed standardized path coefficients. These are scaled by the standard deviations of the variables involved, so the standardized coefficients are unitless measures of association that can be compared across the same relationship in different models and across different relationships within and among models. Standardized coefficients are also useful for computing indirect effects. Because they are unitless, the strength of indirect pathways can be obtained by multiplying the standardized coefficients along the path. For example, we can compute the indirect pathway from phosphorus to chlorophyll-*a* to Secchi to widgeongrass by multiplying the path coefficients.

Objective 2: *Predict how climate change and nutrient management scenarios will affect individual SAV communities and total Bay-wide SAV across the Bay into the future.*

i) To build future climate scenarios for every hectare of habitable shallow water across the Bay, we obtained predicted changes from 2021-2060 in all water quality variables from the Chesapeake Bay Program Modeling Workgroup. Each decadal climate change scenario (2025, 2035, 2045, and 2055) uses *in situ* environmental variables collected at each site from 1991-2000 as a baseline and applies temperature and precipitation scalars based on the estimated future decadal climate scenarios scenario while using the hydrology of 1991-2000 as baseline using the delta approach to climate change modeling (Shenk et al. 2021). The projected data applied decadal scalars to trends in water temperature, salinity, nitrogen, phosphorus, water clarity, total suspended solids, and chlorophyll-*a* at every monitoring site from 2021-2060. The atmospheric deposition estimates are for 2030 conditions for all scenarios. Estimates of changes in temperature, meteorology, and precipitation are based on an ensemble of global climate models (Shenk et al. 2021).

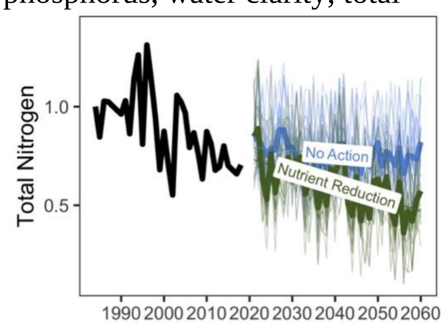

Figure 5. Projected mean springtime total nitrogen from both scenarios where nitrogen remains the same into the future (No Further Action, blue) and where nitrogen (and phosphorus) are reduced through habitat management (Nutrient Reduction, green). Small lines are individual simulations and thick lines are the mean of 100 future simulations

<u>Scenario 1: Nutrient Reduction Scenario</u> The Nutrient Reduction Scenario represents meeting the conditions of the Phase 3 Watershed Implementation Plan. The Phase 3 WIP meets nutrient reductions required for offsetting population growth by 2025 (Table 1) but does not respond to estimated nutrient reduction required for 2025 climate change which is a further 5 million pound nitrogen and 0.4 million pound phosphorus reduction. To generate estimated environmental variables to be used in our predictive models, the Nutrient Reduction scenario is run with 2025 land use throughout and 2025, 2035, 2045, and 2055 estimated decade by decade climate change conditions of increased temperature and precipitation volumes and intensities. The constant 2025 land use and 2030 atmospheric deposition is designed to isolate the future climate change effect. The scenario is based on the CBP Phase 6 integrated suite of airshed, watershed, and estuary models (Shenk et al. 2021, Tian et al. 2022, Linker et al. *in press*). Simulated temperature and salinity are

combined with simulated concentrations of total nitrogen, total phosphorus, total suspended solids and chlorophyll-*a* for the 108 vegetated water quality stations.

The point and nonpoint source controls under the Nutrient Reduction scenario also result in water clarity improvements. Simulated salinity at the monitoring station locations varies based on modeled 2025, 2035, 2045, and 2055 watershed hydrology and Bay hydrodynamics but does not increase nor decrease over time. Overall, this scenario over the 2021-2060 period utilized for our predictive models has a temperature rise of 2°C and an increase in flow, total nitrogen, total phosphorus, and total suspended solids (Table 1).

Scenario	Climate	Flow	TN	TP	TSS
Nutrient Reduction	2025	84274	204	14.0	19,287
Nutrient Reduction	2035	85363	208	14.6	20,142
Nutrient Reduction	2045	86005	212	15.4	20,890
Nutrient Reduction	2055	87421	220	16.7	22,016
No Action	2025	85639	417	42.5	21,636
No Action	2035	86732	424	44.5	22,862
No Action	2045	87375	432	47.5	23,822
No Action	2055	88792	446	51.6	25,395

Table 1. Nutrient Reduction and No Further Action scenario flows and loads for estimated climate change conditions of 2025, 2035, 2045, and 2055. Flows and loads are estimated for the entire Chesapeake watershed delivered to tidal waters. Flows are in units of cubic feet per second (CFS). Total nitrogen, total phosphorus, and total suspended sediment loads are in millions of pounds.

<u>Scenario 2: No Further Action Scenario</u> The No Further Action Scenario represents the condition where no further CBP nutrient reductions were made, simulating the level of nutrient management in Chesapeake Bay when point and nonpoint sources were unmanaged in 1985. Climate change occurs in this scenario just as it does with the Nutrient Reduction Scenario with decadal climate change represented for 2025, 2035, 2045, and 2055. The nutrient and sediment loads are higher than the Nutrient Reduction Scenario (Table 1). The atmospheric deposition nitrogen inputs, temperature rise, and salinity fluctuations are identical to Scenario 1. We included this scenario both to evaluate if the positive effect of the Chesapeake Bay Program and state budgets to reduce nutrients in the past will continue in the future as climate change becomes more extreme, and to quantify the value of continued reductions in the face of reevaluating Chesapeake Bay goals.

<u>Sea Level Rise:</u> To simulate the effect of sea level rise on the amount of habitable area, and then future SAV abundance per site, we obtained sea level rise data from NOAA prediction stations around the Bay using both intermediate SLR estimates and relative sea level trends to estimate mm/yr rise. We used this data to estimate, based on sea level rise changing habitat depth, changes in habitable area for SAV across our sites. We also estimated accretion rates for each

	Sea Level Rise (mean mm/yr)	Accretion rate (mean mm/yr)
Zostera monoculture	3.6	6
Ruppia monoculture	4.78	5.2
Mixed Mesohaline	3.44	9.2
Tidal Fresh/Oligohaline	3.78	5.5

Table 2. Mean estimates for sea level rise and accretion rates across community zones.

community from the literature. Based on the available data, we found that accretion rates will keep up with sea level rise during the course of our projected time period, as we calculated minimal change in habitable area across our sites by 2060. Thus, until we extend this prediction period further into the future, we do not report the effect of sea level rise.

ii) To predict how each SAV community and total Bay-wide SAV will respond to changes in temperature, precipitation, and watershed land use (i.e., nutrient management) every year until 2060, we use generalized linear mixed effects models, parameterized from the SEMs of past SAV change by community in Objective 1, to project annual change in SAV density across the Bay. We model the effect of future environmental conditions on annual SAV cover at each station for each community by setting station (i.e., site) as a random effect and seasonal water quality variables as fixed effects. We ran 1,000 simulations for each of the four communities for all scenarios in land use change and climate change over the next century, summing to 8,000 potential futures overall and 2,000 potential futures per community. Because the density of previous year's vegetation is an important predictor for current vegetation coverage, we fed 2020 SAV cover data per station, i.e., the most recent year of SAV data, into our model as initial coverage. Each subsequent year's "density of previous year's vegetation" then came from the model output.

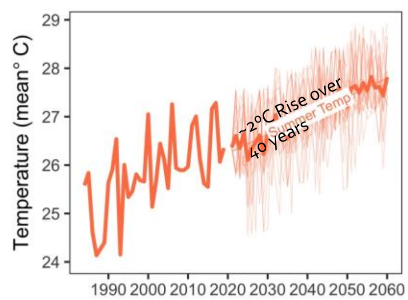

Figure 6. Projected mean summer temperature in both scenarios shows an increase of 2 degrees C from 2021-2060.

All code and data used for the climate projections can be found at the public repository: https://github.com/mhensel/Predicting-SAV

Objective 3: ***Build an interactive web-based tool to explore how climate change and management scenarios will influence SAV in the future***.

i) To build a web-based map/graph tool to depict both future scenarios and predicted effects on each SAV community. Taking the predicted density output from simulations in Objective 2, we first converted all vegetation data from CBP Stations to CBP Segments using data on the overlap between the two methods of dividing up the Bay. For all vegetation of every community in each segment in each simulation every year, we summed the vegetation from the component stations. In cases where a full station zone was found within a segment, no correction was needed. We calculated the mean, maximum, and minimum vegetation across all simulations in every segment for every year. For all environmental variables in each segment in each simulation, we took a mean and median of the component stations

We then created a Shiny application in the open-source statistical software R, where users can view the future of Chesapeake Bay SAV on a whole Bay, individual community, or segment scale using both the No Further Action and the Nutrient Reduction Scenario.

Major findings and results

Objective 1: ***Quantify the effect of past changes in water quality, habitat availability, land cover, and climate (rainfall, runoff, temperature) on interannual variation of the four major SAV communities and total Bay-wide trends across the Chesapeake Bay.***

Over the last four decades, climate extremes (i.e., heatwaves and precipitation extremes) and positive human activities (i.e., nutrient reductions) have shifted the relative abundance of Chesapeake Bay SAV communities, where climate-tolerant species are now dominant and respond the strongest to years of low nutrients

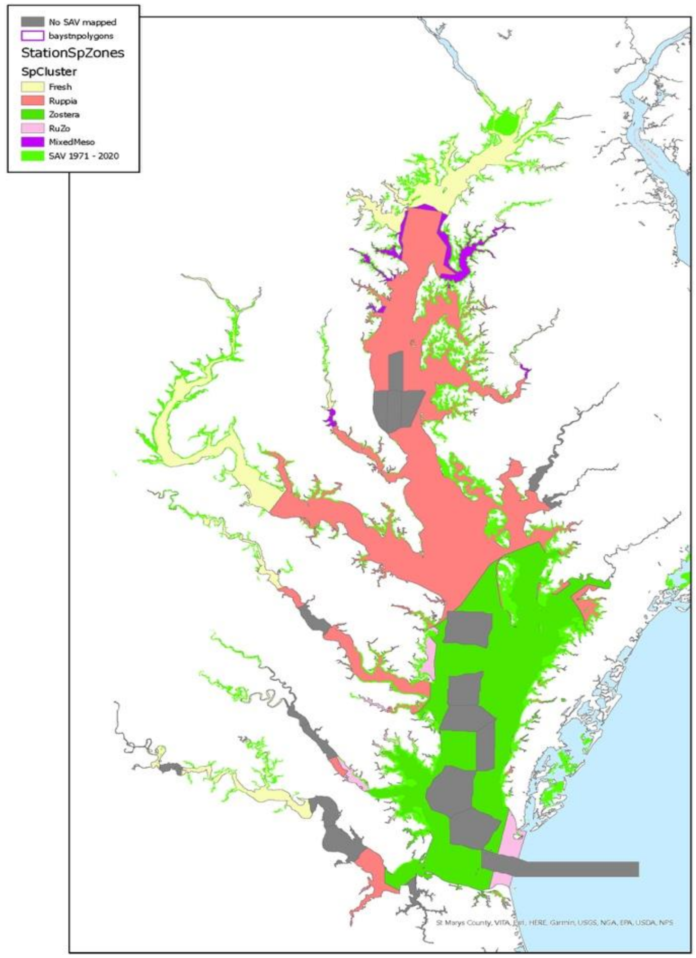

Figure 7: Major SAV communities, widgeongrass (red), eelgrass (green), mixed mesohaline (purple), and freshwater (yellow)

i) The four major SAV communities in Chesapeake Bay are eelgrass monoculture, widgeongrass monoculture, tidal fresh/oligohaline community, and mixed mesohaline community. The combination of cluster analyses and expert opinions mapped out the current and recent locations (Figure 6) of the eelgrass (*Zostera marina*) monoculture in the higher salinity lower Bay, the widgeongrass (*Ruppia maritima*) monoculture in the lower and middle Bay, a mixed mesohaline community made up of *Potamogeton perfoliatus*, *R. maritima*, *Zannichellia palustris*, and *Stuckenia pectinata*) in the upper Bay, and an oligohaline/tidal fresh community (i.e., "freshwater SAV") made up of *Vallisneria americana, Heteranthera dubia, Hydrilla verticillata, Ceratophyllum demersum*, *Elodea canadensis*, *Myriophyllum spicatum*, and several species of both *Najas* and *Potamogetons*. .

ii) Both SAV community relative abundance and contribution to total Baywide SAV cover has changed over time, with the widgeongrass and freshwater SAV communities occupying over 15,000 hectares at various points during the last 20 years (Figure 1). While the eelgrass monoculture accounted for nearly half of the whole Bay's vegetation at the beginning of the Bay-wide aerial survey, consistent declines in proportional occupation has left eelgrass to only occupy less than 30% of the Bay's vegetated bottom in recent decades (Figure 7). Massive gains in both hectarage (Figure 1) and spatial dominance (Figure 7) now puts widgeongrass and freshwater SAV as the dominant space-holding SAV in Chesapeake Bay. Major vegetative crashes of the last two decades have also been due to fluctuation in these two communities: the most recent (2018-20) baywide crash was driven by widgeongrass die-back, as widgeongrass lost over 12,000 ha from its high point in 2017. Eelgrass also lost nearly half of its total area during this crash, dropping eelgrass coverage to its lowest recorded point in the survey in 2019.

iii) Temperature rise and nutrient decreases are the defining changes in environmental conditions across the Bay. Increases in mean summer temperature (Figure 5), and the Bay wide decreases in total nitrogen and phosphorus (Figure 4), from climate change and successful nutrient management, respectively, have created environmental conditions that may be unique to modern Chesapeake SAV communities.

iv) Each community of SAV responds to a different set of seasonal variables, as both expansions and die-backs are controlled by different climate (e.g., mean summer temperature) and anthropogenic factors (e.g., median spring total phosphorus) (Figure 2). Briefly, previously dominant foundation species eelgrass (*Zostera marina*) dramatically responds to rises in summer temperatures with rapid die-offs that are exacerbated by a general decline in water clarity (i.e., low Secchi depth). The currently spatially dominant foundation species widgeongrass (*Ruppia maritima*) is highly vulnerable to increased nutrients from springtime run-off events but expands rapidly in response to high salinity (i.e., low spring freshwater flow) conditions. While salinity fluctuations can be a result of oceanic water intrusion, we interpret responses to salinity as mostly a response to freshwater flow from the watershed. The two variables are closely related in this community (Hensel et al *submitted*) and we expect similar relationships in other communities. The mixed mesohaline community, which includes *P.perfoliatus, S. pectinata* and *Z. palustris* as well as widgeongrass, makes up the smallest area of the bay and responds strongly to freshwater and nutrient influxes in the summer. Oligohaline and tidal fresh communities are diverse and makes up the second largest area of the Bay, with rapid expansions associated with lower summer temperatures and lower summer nutrients (namely total phosphorus). Overall, seasonal climate effects (e.g., summer temperatures and spring salinity) and seasonal human effects (e.g., summer TP, spring TN, spring chl- *a*) all appear to have different relative importance across the large spatial scale of Chesapeake Bay.

Our major assessment of direct anthropogenic forcing factors found that, across the Bay's community zones, higher levels of seasonal TN and TP provide consistent enhancement of phytoplankton abundance (i.e., chlorophyll-*a*). While the mixed mesohaline and freshwater communities do respond to the direct effect of TP in summer, all nutrient-sensitive communities (i.e., all communities besides *Zostera*) were negatively affected by seasonal chlorophyll-*a* levels.

The dominant climate variables controlled different aspects of different parts of the bay, with temperature rise having the strongest effects on the upper and lowermost communities in the Bay. *Zostera* responds negatively to both summer and springtime temperature increases. We found a strong negative effect of the previous summer's temperature on Freshwater SAV growth and on the mixed mesohaline community, suggesting that heatwaves can have a lasting effect on the germination of late season SAV. Salinity, an indication of freshwater influxes from precipitation or river flow, was an important predictor of gains in the widgeongrass community (i.e., if springtime salinity is high due to few precipitation events, widgeongrass expansions were most common) and a predictor of retraction in the mixed mesohaline community (i.e., summer saltwater influxes contribute to plant die-back).

Objective 2: ***Predict how climate change and nutrient management scenarios will affect individual SAV communities and total Bay-wide SAV across the Bay into the future.***

Continued nutrient reductions, specifically to benefit the widgeongrass and tidal fresh/oligohaline communities, are required for the Chesapeake Bay to offset the declines from heatwave induced eelgrass loss over the next 40 years.

i) As outlined in the Methods Summary, our three future scenarios apply relevant reductions in nitrogen and phosphorus into the future (Figure 5). Corresponding variability in chl-*a*, salinity, and Secchi depth are factored into these scenarios. Temperature increase of 2° C over the next four decades is applied in both scenarios (Figure 6).

ii) Our climate change projections suggest that continued nutrient reductions are a critical management step needed to maintain and increase SAV cover throughout Chesapeake Bay through 2060 (Figure 3). <u>While no simulations reached the baywide SAV goal of 180,000 acres by 2060, only Nutrient Reduction scenarios closed that gap and showed steady increases in SAV cover.</u> While 4% of No Action simulations reached total SAV area higher than historical (i.e., 2017 high) peaks, over 45% of Nutrient Reduction simulations reached this historical peak while many simulations continued to hit new peaks in Baywide cover, especially after another20 years of nutrient reductions. These future gains in SAV will be fueled by further increases in cover by widgeongrass and the freshwater community as eelgrass declines will continue despite nutrient reductions. Nutrient reductions do appear to be able to slow the decline of eelgrass.

Objective 3: ***Build an interactive web-based tool to explore how climate change and management scenarios will influence SAV in the future***.

We completed the development of our web-based tool, where users can explore how our scenarios are expected to affect SAV communities, the whole Bay, and segments. Access the tool here: [https://www.vims.edu/research/units/programs/sav/predicting-sav/index.php]

Conclusions, Future Recommendations, and Data Needs

Under the increasingly novel environmental conditions of the present and near-future, the dominance of climate-tolerant, invasive, or opportunistic species represents both challenges and opportunities for management to conserve ecosystems, ensure continued provision of key services, and to prepare them for continued climate change. *In Chesapeake Bay and elsewhere, managers seeking to understand, anticipate, and react to dynamic foundation species must adjust their assessment strategies and ultimate goals while not letting up on successful nutrient mitigation (i.e., Total Maximum Daily Loads).* Not only do we showcase that climate change has greatly increased the importance of watershed nutrient management, but we also demonstrate that current nutrient reduction targets contribute to persistent, stable meadows into the future, but not to the extent that baywide restoration goals are reached. Our community-specific simulations suggest that continued reductions in nitrogen, phosphorus, and total suspended solids to improve water quality throughout the Chesapeake Bay will (1) prevent local eelgrass extinction by stabilizing decline for decades in the face of rising temperatures, (2) create conditions that encourage widgeongrass regrowth throughout the large proportion of the bay that has driven record-setting recovery, and (3) alleviate the effects of summer temperature stress in mixed mesohaline and tidal fresh/oligohaline communities to encourage the massive gains in the upper bay. But only to an extent: to reach SAV restoration goals in Chesapeake Bay, the current nutrient reduction targets must be expanded.

We have a unique opportunity to mitigate for the variability and general unpredictability of global climate change through regional improvements in water quality by combining our mechanistic understanding of SAV community response to future change with the extensive Chesapeake Bay management infrastructure. <u>**Now, we can build new nutrient reduction goals for each SAV community based on the stressor-response relationships derived in our structural equation models**</u> and lay the path for continued and expanded nutrient management that focuses on the major drivers of the dominant tidal fresh/oligohaline community and widgeongrass (i.e., springtime nutrient influxes, TP and TN). Previously established water quality thresholds were based on conditions necessary for mature SAV beds to persist. Under current/future climates and species dominance, lower SAV bed stability will be a constant management hurdle as opportunistic SAV species may spend as much time re-establishing as persisting. Thus, water clarity will need to be adequate for germination and seedling survival, as well as mature plant and bed persistence. For example, springtime phytoplankton blooms (i.e., extremes in chl-*a*) are fatal specifically to the short (~3-10 cm) widgeongrass shoots that are present in the springtime. Summer water quality improvements are less likely to benefit widgeongrass both because springtime influxes may have already limited growth and because tall (~30cm+) reproductive shoots are less affected by lower clarity. Widgeongrass reproductive shoots not only reach the water surface, during low tide they lie horizontally on the water surface, increasing photosynthetic capacity for a significant portion of the day.

In tandem with developing community-by-community management and restoration plans that specifically target species life histories, we also recommend that managers use the findings from our project to re-evaluate local acreage goals. We can first focus on re-setting restoration goals for the mid and lower Chesapeake Bay because, with the climate change-driven shift to widgeongrass, acreage goals established for a species no longer suited to the system may be unrealistic. We find that, even with nutrient reductions, fluctuations and boom/bust years will occur in widgeongrass-dominated and, to a lesser extent, freshwater communities. Thus, to set realistic expectations and establish a true barometer for long-term success in the modern Chesapeake Bay, **we suggest that progress should be gauged using longer-term averages and trajectories to smooth year-on-year variability and prevent any one year from excessively derailing assessment of progress**. Adjustments in SAV recovery assessment are needed in both directions; widgeongrass expansion due to nutrient reductions has several segments in the mid bay now supporting SAV for the first time in our survey history. Additionally, we allow for adaptive management techniques; for example, during a high precipitation springtime, managers may be able to implement widgeongrass seed-based restoration and help recover lost vegetative coverage in the early growing season.

Our findings demonstrate the importance of recognizing species identity shifts through long-term monitoring programs and support the need for on-the-ground species surveys to quantify changes in species-specific cover over time. We quantified change in aerial cover within pre-defined zones using presence/absence data that is collected haphazardly but the continued and expanded implementation and funding of the a three-tiered hierarchical SAV monitoring program in Chesapeake Bay will be vital to fill data gaps as we move further into a climate-change impacted future. The aerial survey (Tier 1) that provides Bay-wide SAV distribution and density data is being supplemented by a volunteer-based point survey effort (Tier 2) that provides broad-scale condition assessments and identifies and quantifies driver/response relationships. The first two tiers are then further supported by a more in-depth Sentinel Site monitoring program (Tier 3) that will identify causal relationships by intensively monitoring drivers of change, ecosystem responses, and ecological processes (Neckles et al. 2012). Parallel assessments of how species shifts, and year-to-year fluctuations affect food webs and ecosystem processes through measurements of biodiversity, abundance of key fishery species, juvenile settlement substrate and blue carbon sequestration are required to simultaneously understand the causes of unanticipated variation and to assess the effects of this variability on long-term management success and ecosystem functioning. With this ecosystem function and food web data collection, we can begin to mechanistically predict how and where climate change and regional management will affect future SAV carbon sequestration, fishery habitat provisioning, and coastal protection.

Acknowledgements

We acknowledge that this research was funded by the US Environmental Protection Agency, the Chesapeake Bay Trust, and the Chesapeake Bay Program. The authors thank our steering committee, the Chesapeake Bay Program SAV Working Group and Modeling Working Group for feedback throughout the project.

References

Lefcheck, J. S. 2016. PIECEWISESEM: Piecewise structural equation modelling in R for ecology, evolution, and systematics. Methods in Ecology and Evolution 7:573–579.

Lefcheck, J. S., R. J. Orth, W. C. Dennison, D. J. Wilcox, R. R. Murphy, J. Keisman, C. Gurbisz, M. Hannam, J. B. Landry, K. A. Moore, C. J. Patrick, J. Testa, D. E. Weller, and R. A. Batiuk. 2018. Long-term nutrient reductions lead to the unprecedented recovery of a temperate coastal region. Proceedings of the National Academy of Sciences 115:3658–3662.

Lefcheck, J. S., D. J. Wilcox, R. R. Murphy, S. R. Marion, and R. J. Orth. 2017. Multiple stressors threaten the imperiled coastal foundation species eelgrass (Zostera marina) in Chesapeake Bay. Global Change Biology 23:3474–3483.

Moore, K. A., D. J. Wilcox, and R. J. Orth. 2000. Analysis of the Abundance of Submersed Aquatic Vegetation Communities in the Chesapeake Bay. Estuaries 23:115.

Murphy, R. R., W. M. Kemp, and W. P. Ball. 2011. Long-Term Trends in Chesapeake Bay Seasonal Hypoxia, Stratification, and Nutrient Loading. Estuaries and Coasts 34:1293–1309.

Neckles, H. A., B. S. Kopp, B. J. Peterson, and P. S. Pooler. 2012. Integrating Scales of Seagrass Monitoring to Meet Conservation Needs. Estuaries and Coasts 35:23–46.

Patrick, C. J., D. E. Weller, R. J. Orth, D. J. Wilcox, and M. P. Hannam. 2017. Land Use and Salinity Drive Changes in SAV Abundance and Community Composition. Estuaries and Coasts 41:85–100.

Shenk, G. W., G. Bhatt, R. Tian, C. F. Cerco, I. Bertani, and L. C. Linker. 2021. Modeling Climate Change Effects on Chesapeake Water Quality Standards and Development of 2025 Planning Targets to Address Climate Change. Page 145. Chesapeake Bay Program, Annapolis, MD.

Supplemental Tables:

Supplemental Table 1: Regression coefficient table for community structural equation models. Dens.percomp.change is the proportional change in SAV area per site and dens.percomp $_{y-1}$ is the scaled widgeongrass coverage in that site in the previous year. All values are springtime (March-May) means and have been $\log_{10}$-transformed. Asterisk (*) indicates interaction term, i.e., SAV_{y-1} * Salinity is the interaction between the previous year's grass coverage and springtime salinity. Abbreviations in this table include: Total Suspended Solids (TSS), chlorophyll-a (chl-A), total nitrogen and total phosphorus (TN, TP), while Turbidity is estimated via Secchi depth. Standardized coefficients (scaled by standard deviations) of significant values (P < 0.05) are marked with asterisks in the right most column. Correlations included in the model are at the bottom of the table.

Supplemental Table 1a: Ruppia monoculture change SEM coefficient table. Global goodness of fit: Fisher's C = 1.721 with P-value = 0.787 and on 4 degrees of freedom

Response	Predictor	Estimate	Std.Error	DF	Crit.Value	P.Value	Std.Estimate	
log10(Chla.spme)	log10(Temp.spme)	−0.4876	0.1156	1163	−4.2185	0.0000	−0.1117	***
log10(Chla.spme)	log10(TP.spme)	0.7272	0.0522	1163	13.9425	0.0000	0.5206	***
log10(Chla.spme)	log10(TN.spme)	0.1837	0.0531	1163	3.4633	0.0006	0.1433	***
log10(Secc.spme)	log10(Chla.spme)	−0.2513	0.0129	1162	−19.4713	0.0000	−0.3488	***
log10(Secc.spme)	log10(Temp.spme)	−0.3189	0.0535	1162	−5.9633	0.0000	−0.1014	***
log10(Secc.spme)	log10(TN.spme)	−0.1446	0.0275	1162	−5.2569	0.0000	−0.1566	***
log10(Secc.spme)	log10(TP.spme)	−0.0977	0.0277	1162	−3.5285	0.0004	−0.0971	***
dens.percomp.change	dens.percomp.y1	−1.6896	0.7699	1156	−2.1946	0.0284	−1.8064	*
dens.percomp.change	log10(Chla.spme)	0.0207	0.0274	1156	0.7564	0.4496	0.0278	
dens.percomp.change	log10(TP.spme)	0.0214	0.0457	1156	0.4684	0.6396	0.0206	
dens.percomp.change	log10(TN.spme)	−0.1007	0.042	1156	−2.3984	0.0166	−0.1057	*
dens.percomp.change	log10(Temp.spme)	−0.0701	0.1133	1156	−0.6182	0.5366	−0.0216	
dens.percomp.change	dens.percomp.y1:log10(Sal.spme)	0.6437	0.2032	1156	3.1672	0.0016	0.6882	**
dens.percomp.change	dens.percomp.y1:log10(Chla.spme)	−0.7482	0.118	1156	−6.3428	0.0000	−1.0059	***
dens.percomp.change	dens.percomp.y1:log10(TP.spme)	−0.1743	0.1724	1156	−1.0110	0.3122	−0.1678	
dens.percomp.change	dens.percomp.y1:log10(TN.spme)	0.2652	0.2086	1156	1.2711	0.2039	0.2781	
dens.percomp.change	dens.percomp.y1:log10(Temp.spme)	0.9358	0.4554	1156	2.0549	0.0401	0.2883	*
~~log10(TN.spme)	~~log10(TP.spme)	0.5607	–	1212	23.5747	0.0000	0.5607	***
~~log10(Secc.spme)	~~log10(Sal.spme)	0.1498	–	1214	5.2739	0.0000	0.1498	***
~~log10(Chla.spme)	~~log10(Sal.spme)	−0.1747	–	1214	−6.1734	0.0000	−0.1747	***
~~log10(TP.spme)	~~log10(Sal.spme)	−0.4722	–	1212	−18.6492	0.0000	−0.4722	***
~~log10(TN.spme)	~~log10(Sal.spme)	−0.7040	–	1212	−34.5128	0.0000	−0.7040	***
~~log10(Chla.spme)	~~dens.percomp.y1	0.0875	–	1214	3.0571	0.0011	0.0875	**

Supplemental Table 2b: Zostera monoculture SEM coefficient table. Global goodness-of-fit: Fisher's C = 4.63 with P-value = 0.796 and on 8 degrees of freedom

Response	Predictor	Estimate	Std.Error	DF	Crit.Value	P.Value	Std.Estimate	
log10(Chla.spme)	log10(TP.spmed)	0.2072	0.0721	605	2.8719	0.0042	0.1390	**
log10(Chla.spme)	log10(TN.spme)	1.1490	0.0722	605	15.9155	0.0000	0.7219	***
dens.percomp.change	dens.percomp.y1	−1.3138	0.6523	598	−2.0139	0.0445	−1.9222	*
dens.percomp.change	log10(Temp.sumy1med)	−1.6437	0.2828	598	−5.8121	0.0000	−0.2254	***
dens.percomp.change	log10(Sal.summed)	−0.2604	0.1576	598	−1.6521	0.0990	−0.1383	
dens.percomp.change	log10(Chla.spme)	−0.0901	0.0524	598	−1.7189	0.0861	−0.1357	
dens.percomp.change	log10(Secc.summe)	0.2908	0.0938	598	3.0993	0.0020	0.2491	**
dens.percomp.change	dens.percomp.y1:log10(Temp.spmed)	−0.4776	0.1953	598	−2.4454	0.0148	−0.6987	*
dens.percomp.change	dens.percomp.y1:log10(Sal.summed)	1.3778	0.3932	598	3.5042	0.0005	0.1889	***
dens.percomp.change	dens.percomp.y1:log10(Chla.spme)	−0.1055	0.1336	598	−0.7893	0.4302	−0.0560	
dens.percomp.change	dens.percomp.y1:log10(Secc.summe)	−0.0234	0.2051	598	−0.1143	0.9090	−0.0353	
~~log10(TN.spme)	~~log10(TP.spmed)	0.2942	−	627	7.7072	0.0000	0.2942	***
~~log10(Chla.spme)	~~log10(Sal.summed)	−0.2282	−	629	−5.8654	0.0000	−0.2282	***
~~log10(Chla.spme)	~~log10(Secc.summe)	−0.1668	−	629	−4.2322	0.0000	−0.1668	***

Supplemental Table 2c: Mixed mesohaline SEM coefficient table. Global goodness-of-fit: Fisher's C = 4.175 with P-value = 0.653 and on 6 degrees of freedom

Response	Predictor	Estimate	Std.Error	DF	Crit.Value	P.Value	Std.Estimate	
log10(Chla.summe)	log10(Temp.summe)	0.7677	0.7664	149	1.0017	0.3181	0.0727	
log10(Chla.summe)	log10(TP.summe)	0.7274	0.1317	149	5.5230	0.0000	0.5143	***
log10(Chla.summe)	log10(TN.summe)	0.2486	0.1821	149	1.3654	0.1742	0.1007	
dens.percomp.change	dens.percomp.y1	4.4376	1.7401	142	2.5501	0.0118	4.2027	*
dens.percomp.change	log10(Chla.summe)	−0.0127	0.0967	142	−0.1316	0.8955	−0.0147	
dens.percomp.change	log10(TN.summe)	0.2120	0.2031	142	1.0439	0.2983	0.0994	
dens.percomp.change	log10(TP.summe)	−0.3697	0.1619	142	−2.2831	0.0239	−0.3025	*
dens.percomp.change	log10(Temp.summin)	0.3652	0.2943	142	1.2409	0.2167	0.1085	
dens.percomp.change	dens.percomp.y1:log10(Sal.sumy1max)	−1.1092	0.5295	142	−2.0947	0.0380	−1.0505	*
dens.percomp.change	dens.percomp.y1:log10(Chla.summe)	0.3790	0.3447	142	1.0996	0.2734	0.4387	
dens.percomp.change	dens.percomp.y1:log10(TP.summe)	−0.3830	0.4903	142	−0.7811	0.4360	−0.1796	
dens.percomp.change	dens.percomp.y1:log10(TN.summe)	0.0795	0.8814	142	0.0902	0.9282	0.0651	
dens.percomp.change	dens.percomp.y1:log10(Temp.summin)	−3.8357	0.9569	142	−4.0083	0.0001	−1.1393	***
~~log10(TN.summe)	~~log10(TP.summe)	0.5546	−	159	8.4039	0.0000	0.5546	***

Supplemental Table 2d: Tidal fresh/oligohaline community SEM coefficient table. Global goodness of fit: Fisher's C = 3.969 with P-value = 0.41 and on 4 degrees of freedom

Response	Predictor	Estimate	Std.Error	DF	Crit.Value	P.Value	Std.Estimate	
log10(Chla.summe)	log10(Temp.summe)	1.9449	0.3418	1017	5.6903	0.0000	0.1403	***
log10(Chla.summe)	log10(Temp.summax)	1.6851	0.3725	1017	4.5233	0.0000	0.1060	***
log10(Chla.summe)	log10(TP.summe)	0.4188	0.0801	1017	5.2294	0.0000	0.2113	***
log10(Chla.summe)	log10(TSS.summe)	0.2945	0.0545	1017	5.4003	0.0000	0.1654	***
dens.percomp.change	dens.percomp.y1	3.0237	1.3337	1009	2.2671	0.0236	3.7976	*
dens.percomp.change	log10(Sal.summe)	-0.0287	0.0118	1009	-2.4382	0.0149	-0.1060	*
dens.percomp.change	log10(Chla.summe)	-0.0423	0.0213	1009	-1.9859	0.0473	-0.0935	*
dens.percomp.change	log10(TP.summe)	0.0882	0.0503	1009	1.7511	0.0802	0.0984	
dens.percomp.change	log10(TSS.summe)	-0.1041	0.0452	1009	-2.2996	0.0217	-0.1293	*
dens.percomp.change	log10(Temp.summe)	0.8559	0.2158	1009	3.9667	0.0001	0.1366	***
dens.percomp.change	log10(Temp.sumy1me)	0.0388	0.2755	1009	0.1409	0.8880	0.0059	
dens.percomp.change	dens.percomp.y1:log10(Sal.summe)	-0.0033	0.0398	1009	-0.0819	0.9348	-0.0041	
dens.percomp.change	dens.percomp.y1:log10(Chla.summe)	-0.1659	0.0729	1009	-2.2751	0.0231	-0.6118	*
dens.percomp.change	dens.percomp.y1:log10(TP.summe)	-0.9746	0.1687	1009	-5.7785	0.0000	-2.1563	***
dens.percomp.change	dens.percomp.y1:log10(TSS.summe)	0.1432	0.1516	1009	0.9447	0.3451	0.1598	
dens.percomp.change	dens.percomp.y1:log10(Temp.sumy1me)	-3.2239	0.9951	1009	-3.2396	0.0012	-4.0063	**
~~log10(Temp.summe)	~~log10(Temp.sumy1me)	0.5101	-	1065	19.3565	0.0000	0.5101	***
~~log10(Chla.summe)	~~log10(Temp.sumy1me)	-0.0034	-	1067	-0.1108	0.4559	-0.0034	
~~log10(Chla.summe)	~~dens.percomp.y1	-0.1052	-	1067	-3.4501	0.0003	-0.1052	***

Supplemental Tables 2: Predictive models ANOVA tables with conditional F test

Supplemental Table 2a: *Ruppia maritima* monoculture predictive model (Conditional R^2: 0.667, Marginal R^2: 0.248)

	F	Df	Df.res	Pr(>F)
log10(dens.weight.mean.y1)	491.77125975	1	1552.068	7.093939e-95
log10(Chla.spme)	12.81208279	1	1642.507	3.543969e-04
log10(TP.spme)	0.71274037	1	1612.007	3.986608e-01
log10(TN.spme)	34.15581859	1	1560.331	6.181978e-09
log10(Temp.spme)	3.14456978	1	1644.310	7.636516e-02
log10(dens.weight.mean.y1):log10(Sal.spme)	1.54397144	1	1655.038	2.142037e-01
log10(dens.weight.mean.y1):log10(Chla.spme)	0.02101121	1	1635.552	8.847663e-01
log10(dens.weight.mean.y1):log10(TP.spme)	0.05025041	1	1666.149	8.226556e-01
log10(dens.weight.mean.y1):log10(TN.spme)	1.89036399	1	1668.982	1.693454e-01
log10(dens.weight.mean.y1):log10(Temp.spme)	0.47838545	1	1635.203	4.892527e-01

Supplemental Table 2b: *Zostera marina* monoculture predictive model (Conditional R^2: 0.825, Marginal R^2: 0.76)

	F	Df	Df.res	Pr(>F)
log10(dens.weight.mean.y1)	1118.9665018	1	501.3083	8.461529e-130
log10(Temp.sumy1med)	0.4807117	1	759.9757	4.883119e-01
log10(Sal.summed)	1.3842263	1	640.6010	2.398196e-01
log10(Chla.spme)	9.0360002	1	749.8767	2.735472e-03
log10(Secc.summe)	3.0417422	1	538.2286	8.171967e-02
log10(dens.weight.mean.y1):log10(Temp.spmed)	3.7382555	1	751.6237	5.355515e-02
log10(dens.weight.mean.y1):log10(Sal.summed)	10.5427892	1	759.1019	1.217655e-03
log10(dens.weight.mean.y1):log10(Chla.spme)	11.7822379	1	748.9348	6.308299e-04
log10(dens.weight.mean.y1):log10(Secc.summe)	0.1155226	1	703.3070	7.340437e-01

Supplemental Table 2c: Mixed mesohaline community predictive model (Conditional R^2: 0.667, Marginal R^2: 0.248

	F	Df	Df.res	Pr(>F)
log10(dens.weight.mean.y1)	67.61860286	1	231.8138	1.418119e-14
log10(TN.summe)	0.42909478	1	233.6076	5.130780e-01
log10(Chla.summe)	2.64923011	1	232.5799	1.049540e-01
log10(TP.summe)	0.96344328	1	220.4107	3.273970e-01
log10(Temp.summin)	1.21955120	1	230.6773	2.705993e-01
log10(dens.weight.mean.y1):log10(Sal.sumy1max)	1.90279215	1	228.8684	1.691124e-01
log10(dens.weight.mean.y1):log10(Chla.summe)	6.36704765	1	229.6906	1.230230e-02
log10(dens.weight.mean.y1):log10(TP.summe)	1.24105286	1	233.9995	2.664112e-01
log10(dens.weight.mean.y1):log10(TN.summe)	4.24189397	1	234.0000	4.054467e-02
log10(dens.weight.mean.y1):log10(Temp.summin)	0.06597555	1	229.4655	7.975193e-01

Supplemental Table 2d: Freshwater community predictive model (Conditional R^2: 0.655, Marginal R^2: 0.604)

	F	Df	Df.res	Pr(>F)
log10(dens.weight.mean.y1)	1059.5536705	1	1210.6257	1.756142e-167
log10(Sal.summe)	8.9363644	1	249.6999	3.074605e-03
log10(Chla.summe)	5.2731978	1	692.6194	2.195387e-02
log10(TP.summe)	26.9181080	1	535.9022	3.015915e-07
log10(Temp.sumy1me)	0.9976869	1	1203.4505	3.180717e-01
log10(Temp.summe)	8.5611090	1	1227.4811	3.497392e-03
log10(dens.weight.mean.y1):log10(Sal.summe)	0.1393950	1	1079.6236	7.089565e-01
log10(dens.weight.mean.y1):log10(Chla.summe)	4.6090998	1	1449.1157	3.196826e-02
log10(dens.weight.mean.y1):log10(TP.summe)	6.7340018	1	1347.9138	9.561889e-03
log10(dens.weight.mean.y1):log10(Temp.sumy1me)	0.2308016	1	1465.9599	6.310017e-01