14-14-1853 CBG 14201

Agreement Number

Chesapeake Bay Submerged Aquatic Vegetation (SAV): A Third Technical Synthesis

A multi-institutional effort to synthesize the state of the science regarding submerged aquatic vegetation in Chesapeake Bay

December, 2016

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Project Abstract:

Chesapeake Bay is one of the most widely studied estuaries in the world, with extensive research focused on one of the Bay's most important habitats: submerged aquatic vegetation (SAV). SAV provides a myriad of ecosystem services, from nursery grounds and habitat for ecologically and economically important fish and invertebrates, to sediment stabilization and shoreline erosion control, to carbon sequestration. While the first two SAV Technical Syntheses (published in 1992 and 2000) focused primarily on the identification, development, and refinement of five specific and measurable habitat requirements that limit SAV growth, including light attenuation, chlorophyll a, total suspended solids, dissolved inorganic nitrogen and dissolved inorganic phosphorus, this third SAV Technical Synthesis reviews advancements in our knowledge and understanding of SAV ecosystem dynamics as they relate to SAV habitat requirements, but also genetics, the effects of land-use and shoreline alterations on SAV, climate change impacts, and ecosystem services and their potential monetary value. New information and analyses are reviewed in the context of restoration and management implications and suggest that managers and policy makers must maintain or strengthen protection to SAV and must continue to improve water quality and clarity in the Chesapeake Bay in hopes of counterbalancing the impacts of climate change and increased pressures from a growing watershed population.

Below, find summary points for each chapter submitted to this third SAV Technical Synthesis.

SHIFTING PATTERNS IN SAV SPECIES DIVERSITY AND COMMUNITY STRUCTURE

- Distributions of SAV species and species richness within the Chesapeake Bay are largely controlled by salinity, with higher species richness in low salinity SAV communities.

- Comparing the periods of 1997-2013 to 1985-96, most low salinity SAV species have expanded their distributions within the Bay, whereas the distributions of medium and high salinity species have either not changed or decreased.

- Comparing the period of 1997 to 2013 with the period 1985-1996, two non-native species (*Hydrilla verticillata, Najas minor*) have increased their distributions into an additional tributary, the James River, while the distributions of two non-native species (*Myriophyllum spicatum, Potomogeton crispus*) have not been observed to spread into additional tributaries.

- For low salinity SAV communities, diversity is negatively correlated with chlorophyll a concentration, total suspended solids, and nitrogen and phosphorous concentrations.

- The proportion of natives to non-natives is higher in years with better water quality conditions.

- The dominance of the non-native *Hydrilla verticillata* increases during periods of disturbance. However, *H. verticillata* may facilitate establishment of native species in previously unvegetated areas.

- Short-time scale stressors can cause shifts in species dominance and/or loss of species. Stressors can include changes in salinity, during both abnormally wet and dry years, and summer high temperature events.

SUBMERSED AQUATIC VEGETATION AND FEEDBACK PROCESSES: IMPLICATIONS FOR RESTORATION AND RESILIENCE

- Feedback processes in SAV beds are controlled by biophysical interactions between SAV, water flow and wave height, suspended sediment concentrations, and water clarity and/or biogeochemical interactions between the plants, ambient nutrient concentrations, algal growth, and water clarity.

- Feedbacks can cause nonlinear system dynamics by stabilizing an SAV bed against changes in external conditions (e.g., nutrient or sediment loading), but only to a critical threshold in external conditions, beyond which an SAV bed suddenly disappears and the bare sediment state dominates (and vice-versa). If feedbacks are sufficiently strong, the threshold for SAV bed decline is different from the threshold for recovery (this is known as hysteresis).

- Feedbacks enhance system stability; however chronic stressors, such as nutrient loading, control resilience, or the capacity of a system to absorb disturbance.

- Positive feedback processes in SAV beds could potentially lead to discrepancies between SAV presence/absence based on predictions from the habitat requirements and actual SAV presence/absence. The habitat requirements were largely derived using data collected near existing beds. However, already established beds can, in theory, withstand worse conditions than a recovering bed because of self-stabilizing feedbacks. Therefore, recovering SAV beds may require more stringent habitat requirements than those established for existing SAV beds. Further analysis is needed to explore this possibility.

- Direct SAV plantings could also benefit from considering the role of feedbacks in stabilizing SAV beds. Large plantings of closely-spaced propagules are generally more successful due to the presence of feedbacks once a critical SAV bed size and density is surpassed.

- Mitigating nutrient loads to the system will not only facilitate SAV restoration, but also enhance SAV bed resilience.

THE ROLE OF GENETIC DIVERSITY AND CONNECTIVITY IN THE RESTORATION OF SUBMERSED AQUATIC VEGETATION BEDS

- Since publication of Technical Synthesis II, we have gained great insights into genetic variation in SAV and ecological processes that are marked by genetic patterns.

- We have more insight into past history and aspects of species biology that provides essential insight into the degree and nature of current and future threats.

- There are still important gaps in our knowledge: most studies have focused on marine species, and moreover most of those have focused on just a few species (particularly *Z. marina*).

- Recent developments, such as Single Nucleotide Polymorphisms (SNPs) and whole-genome sequencing, are bringing more tools to the realm of conservation and restoration.

- Use of fine-scale analysis of gene diversity and expression within individuals to document selection across environmental gradients is becoming increasingly feasible.

- There are three decisions to be made regarding genetics and restoration: Is active restoration necessary? Where should restoration sites be located? Where should restoration material come from?

- We see a pending quantum leap in insights into links between genetic diversity and ecological function under different environmental conditions.

- Restoration of resilient SAV beds in the Chesapeake Bay can greatly benefit from this new knowledge.

EFFECTS OF LAND USE AND SHORELINE ARMORING ON SUBMERGED AQUATIC VEGETATION

- We review the literature on relationships between submerged aquatic vegetation (SAV) and land use or shoreline armoring, focusing on Chesapeake Bay.

- SAV abundance is significantly lower in subestuaries with watersheds dominated by developed or agricultural land than in subestuaries dominated by forest.

- Human land uses release nutrient and sediments that reduce water clarity and limit light for SAV.

- Armored shorelines can deepen adjacent shallow water and reduce water clarity through sediment resuspension.

- Evidence for negative impacts of bulkheads on SAV is stronger than for riprap.

- The effects of armoring differ among salinity zones and among subestuaries with different land uses.

- Some of those differences seem counterintuitive because analyses of salinity zones lumped SAV communities with different stressor-response relationships.

- Further research is needed to understand the impacts of different living shorelines on SAV compared to riprap, bulkhead, and natural shoreline.

- Models and management plans should incorporate information on local land use, shoreline armoring, and community-specific responses to better understand SAV dynamics and to better manage SAV conservation and restoration.

21ST CENTURY CLIMATE CHANGE AND SUBMERGED AQUATIC VEGETATION IN THE CHESAPEAKE BAY

- During the 21st century three components of climate change will impact Chesapeake Bay submerged aquatic vegetation (SAV) directly: increasing temperatures, coastal zone acidification, and sea level rise.

- Current understanding of these stressors, coupled with regional climate forecasts, permits us to make basic predictions for the future of SAV in the Chesapeake Bay.

- Summer heat waves have been linked to die-offs of SAV, especially eelgrass (*Zostera marina*) in the lower Bay. Thus, future climate warming is likely to have negative impacts on SAV populations already struggling with poor water quality/light limitation in the Chesapeake Bay.

- If the current trajectory of climate change continues the Chesapeake Bay could develop some characteristics of a subtropical estuary by the next century. Predicted warming has the potential to eliminate populations of temperate eelgrass (*Zostera marina*), favoring native heat-tolerant species such as widgeon grass (*Ruppia maritima*). A variety of subtropical plants and animals are likely to become more common in the region; however colonization by tropical seagrasses is unlikely in the near future due to continued low winter temperatures and winter ice.

- The *"CO_2 fertilization effect"* of coastal acidification has the potential to stimulate photosynthesis and growth in at least some species of SAV. This may offset some of the deleterious effects of thermal stress. This may facilitate the survival of eelgrass in regions of the Chesapeake Bay.

- Sea level rise will reshape our shorelines. Where they are permitted to migrate landward, suitable SAV habitat may persist. However, where shorelines are hardened suitable SAV habitat is likely to be lost.

- The predictions are limited by a poor understanding of the indirect effects of climate change on organisms associated with seagrass die-offs, including fouling organisms, grazers, and microbes. These indirect effects may be powerful and may trigger abrupt, unforeseen changes in SAV communities.

EVALUATION OF ECOSYSTEM SERVICES OF SAV IN THE CHESAPEAKE BAY

- SAV habitats provide numerous ecosystem services to human populations, including but not limited to fishery enhancement, carbon sequestration, erosion control, and nutrient cycling.

- However, the production of services from SAV habitats has been subject to less scientific study than some other coastal habitats, such as mangroves or salt marshes, limiting the ability to quantify these services.

- We review the theory and methods supporting the measurement and monetization of ecosystem service benefits associated with SAV habitats and synthesize the current literature on ecosystem service benefits provided by SAV in the Chesapeake Bay.

SHIFTING PATTERNS IN SAV SPECIES DIVERSITY AND COMMUNITY STRUCTURE

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ABSTRACT

This chapter examines the shifting patterns in Chesapeake SAV community structure and the potential environmental variables that explain variation in species composition patterns at both long and short time periods. Bay-wide species occurrence data sets are summarized. These data show that twenty-seven or more species of SAV are found within the tidal Chesapeake Bay. Seventeen of these are common, and four of those are non-native. The distributions of these SAV species are largely controlled by salinity, resulting in species associations along salinity gradients. There is higher species richness in low salinity SAV communities compared to medium and high salinity areas, but some of the species have wide salinity tolerances and are found in more than one community type. Most low salinity SAV species have expanded their distributions within the Bay, whereas the distributions of medium and high salinity species have either not changed or decreased. Two non-native species (*Hydrilla verticillata, Najas minor*) have increased their distributions, while the distributions of two non-native species (*Myriophyllum spicatum, Potomogeton crispus*) have not been observed to spread. Factors other than salinity that affect SAV community structure include water quality conditions, water movement, sediment quality, temperature, disease, water fowl herbivory, competitive interactions, propagule availability and shading from the invasive floating aquatic vegetation, *Trapa natans*. Historic declines in SAV abundances and diversity have largely been linked to anthropogenic impacts, although disease and storms have also contributed to episodic alterations to SAV communities.

INTRODUCTION

Twenty-seven or more species of submerged aquatic vegetation are found within the tidal Chesapeake Bay. Seventeen of these are common (Orth et al. 2014), and four of those are non-native (Table 1). Several species are similar in appearance making it difficult to identify the exact number of species and misidentifications occur (Rybicki et al. 2013).The distributions of these SAV species are largely controlled by salinity (Stevenson and Conifer 1978, Moore et al. 2000, Orth et al. 2010), resulting in species associations along salinity gradients. Moore et al. (2000) recognized four species associations based on the presence and absence of dominant species, while Orth et al. (2010) divided SAV species into three community types based largely on salinity (Table 2). Their low-salinity community is generally found in tidal fresh and oligohaline regions (salinities of 0 to < 5), the medium-salinity community is generally found in mesohaline regions (salinities of 5 to < 18) and the high-salinity community is found in both mesohaline and in polyhaline regions (salinities of 18 < 30). Some of the species have wide salinity tolerances and are found in more than one community type (i.e., *P. perfoliatus, S. pectinata, Z. palustris, R. maritima, Z. marina*). The area of available habitat for the high-salinity community within the Bay is approximately double that of the other two community types (Orth et al. 2010).

Bay SAV communities have fluctuated in diversity and abundances over time. Factors other than salinity that affect SAV community structure include water quality conditions (turbidity, nutrient enrichment, hypoxia), water movement (currents, waves, storm events), sediment quality, temperature, disease, water fowl herbivory (Mjelde et al. 2012), competitive interactions (Borgnis and Boyer 2015), propagule availability and shading from the invasive floating aquatic vegetation, *Trapa natans* (Gwathmey 1945).

Historic declines in SAV abundances and diversity have largely been linked to anthropogenic impacts, although disease and storms have also contributed to episodic alterations to SAV communities (Bayley et al. 1978, Kemp et al. 1983, Orth and Moore 1984, Carter et al. 1985, Brush and Hilgartner 2000, Moore et al. 2000, Kemp et al. 2005, Orth et al. 2010, Ruhl and Rybicki 2010). This chapter examines the shifting patterns in Chesapeake SAV community structure and the potential environmental variables that explain variation in species composition pattern at both long and short time periods. Species occurrence data sets that were collected by volunteers, local, state and federal agencies working throughout the Bay are summarized. We also evaluate factors affecting SAV community structure through four regional case studies (Fig. 1).

Table 1 Common SAV in the Chesapeake Bay.

Common Native Species	Common Non-Native Species
Ceratophyllum demersum (coontail)	*Hydrilla verticillata* (hydrilla)
Elodea canadensis (common elodea)	*Myriophyllum spicatum* (Eurasian watermilfoil)
Heteranthera dubia (water stargrass)	*Najas minor* (brittle water nymph)
Najas gracillima	*Potamogeton crispus* (curly pondweed)
Najas guadalupensis (southern naiad)	
Najas flexilis	
Potamogeton perfoliatus (redhead grass)	
Potamogeton pusillus (slender pondweed)	
Ruppia maritima (widgeon grass)	
Stuckenia pectinata (sago pondweed)	
Vallisneria americana (wild celery)	
Zannichellia palustris (horned pondweed)	
Zostera marina (eelgrass)	

Table 2 SAV species found in communities as defined by Moore et al. (2000) and Orth et al. (2010). *Dominant species.

Moore et al. 2000	Orth et al. 2010
FRESHWATER MIXED Community	LOW-SALINITY Community
*Myriophyllum spicatum**	*Vallisneria americana*
*Hydrilla verticillata**	*Hydrilla verticillata*

  - *Vallisneria americana**
  - *Ceratophyllum demersum*
  - *Heteranthera dubia*
  - *Elodea canadensis*
  - *Najas guadalupensis*
  - *Najas gracillima*
  - *Najas minor*
  - *Najas* flexilis
  - *Potamogeton crispus*
  - *Potamogeton pusillus*
- POTAMOGETON Community
  - *Stuckenia pectinata**
  - *Potamogeton perfoliatus**
  - *Potamogeton crispus*
  - *Elodea canadensis*
- RUPPIA Community
  - *Ruppia maritima**
  - *Potamogeton perfoliatus*
  - *Stuckenia pectinata*
  - *Zannichellia palustris*
- ZOSTERA Community
  - *Zostera marina**
  - *Ruppia maritima*

  - *Myriophyllum spicatum*
  - *Elodea canadensis*
  - *Stuckenia pectinata*
  - *Heteranthera dubia*
  - *Najas guadalupensis*
  - *Najas minor*
  - *Potamogeton crispus*
  - *Potamogeton perfoliatus*
  - *Potamogeton pusillus*
  - *Ceratophyllum demersum*
  - *Zannichellia palustris*
- MEDIUM-SALINITY Community
  - *Ruppia maritima*
  - *Potamogeton perfoliatus*
  - *Zostera marina*
  - *Stuckenia pectinata*
  - *Zannichellia palustris*
- HIGH-SALINITY Community
  - *Zostera marina*
  - *Ruppia maritima*

CHANGES IN REGIONAL SAV COVER AND DISTRIBUTIONS

SAV species diversity in the Bay has historically been greatest in the low salinity areas, including the upper Bay and tidal fresh and oligohaline portions of the tributaries, and lowest in the mesohaline and polyhaline regions of the Bay (Table 2). Changes to SAV diversity and abundance in the Chesapeake occurred following European settlement in the watershed and accelerated in the 20th century, with abundances reaching a low point in the mid-1980s (Orth and Moore 1984, Brush and Hilgartner 2000, Orth et al. 2010). Changes in the 20th century prior to 1984 include a die-off of *Zostera marina* in the southern and more saline regions of the Bay from wasting disease in the 1930s; decline of low-salinity communities in the tidal Potomac River in the 1930s, possibly due to increased turbidity (Carter and Rybicki 1994); further reductions in the Potomac, Patuxent and other rivers in Maryland in the late 1960s (Orth and Moore, 1984); and Bay-wide reductions in the 1970s from poor water quality and high turbidity caused in part by Tropical Storm Agnes in 1972 (Kemp et al. 1983, Gurbisz and Kemp 2014). In addition, periodic invasions of several non-native species occurred in the tidal fresh to mesohaline portions between 1923 and 1982 (Carter and Rybicki 1994). In some areas SAV began to resurge prior to 1984, such as the increase in coverage of species observed in the tidal fresh Potomac in 1983, linked to upgrades in sewage plants and improved water clarity (Carter and Rybicki 1994, Rybicki and Landwehr 2007, Orth et al. 2010, Williams et al. 2010). Resurgences of SAV were also documented in the tidal fresh Susquehanna Flats, the mesohaline Tangier Sound and other localized areas of the Bay (Orth et al. 1985).

SAV coverage was monitored annually in the Chesapeake Bay beginning in 1985 (Fig. 2). SAV maximum summer biomass and area of coverage increased Bay-wide by 56% and 29% between 1985 and 1996, respectively, with the greatest increases in the ZOSTERA community (Moore et al.

2000; includes polyhaline and a portion of the mesohaline communities shown in Fig. 2). The FRESHWATER MIXED community coverage also increased, but the POTAMOGETON and RUPPIA communities fluctuated with net declines (Moore et al. 2000). Low-salinity communities of the Potomac River, although resurging between 1983 and 1987, showed a net decrease in coverage of 42% between 1985 and 1996 (Rybicki and Landwehr 2007), and abundance and coverage remained low in the Susquehanna Flats during this time period (Gurbisz and Kemp 2014).

Between 1996 and 2015, SAV coverage fluctuated with lows in 2003, 2006 and 2012 and highs in 2002, 2009 and 2012, with the most hectares of SAV recorded for 2015 since aerial surveys began in the late 1970s (Fig. 2). Most of this recent resurgence has been in the mesohaline salinity zone (Fig. 2), which includes the medium-salinity SAV community and a portion of the high-salinity community (Orth et al. 2010). In 2015, the tidal fresh and oligohaline low-salinity zone increased by 163% and 58% in comparison to 1985 and 1996, respectively. Similarly, in the mesohaline zone, the increases were 106% and 59%, respectively. However, SAV in the polyhaline zone has shown only a small increase (7%) since 1985 and a decrease (-25%) since 1996.

SAV species occurrences have been collected by various programs since 1985 and summarized annually for the Chesapeake Bay (Orth et al. 1985, Orth et al. 2013, for example). Ground observations of 16 SAV species for 21 Bay segments (selected based on the total number of observation and number of years for which there were field observations) for the years 1985-1996 and 1997-2013 are shown in Figures 3 and 4. Most of the low salinity species have increased their distributions while medium and high salinity species have not. This is reflected by recent increases in species richness and diversity in low-salinity communities (see Susquehanna Flats and Chickahominy River case studies below, Rybicki and Landwehr 2007, Ruhl and Rybicki 2010), while the medium-salinity communities are now dominated by a single species, *Ruppia maritima* (Orth et al. 2010). This species is more frequently the dominant species in high-salinity communities (see York River case study below).

Of the non-native species, *Hydrilla verticillata* and *Najas minor* expanded their distributions in the low salinity SAV communities of the James Rivers in Virginia (Figs. 3, 4, see Chickahominy River case study below).

SPECIES ASSOCIATIONS

Species associations in SAV communities are the results of complex interactions between individual species, their neighbors, and the environment. Species richness is highest in the low-salinity community as a result of limited tolerance to higher salinities by most of the species in this community. High species richness of SAV is maintained in high quality habitats by differences in morphology, growth, reproductive and nutrient uptake strategies, responses to stress and disturbance, overall competitive ability, and dispersal mechanisms (Kautsky 1988, Murphy et al. 1990, Engelhardt 2006, Ruhl and Rybicki 2010). Communities are often dominated by one or a few species (Table 2, Moore et al. 2000), and vary in area and composition with changing environmental conditions such as water quality, sediment characteristics and short-term changes in temperature and salinity (see case studies on the Chickahominy River and the York River below). Similarly, species composition can also change with season when species with the same habitat requirements have differences in phenology. For example *Zannichellia palustris* sometimes shares the same habitat as *Ruppia maritima* and *Zostera marina* and can dominate these communities in the early spring; however, *Z. palustris* is an annual that flowers in May and early June and is largely gone by July. In high-salinity and medium-salinity communities, *Z. marina* usually dominates *R. maritima*, but *Z. marina* dies-back in the mid-summer just when the more heat tolerant *R. maritima* reaches its peak biomass (Moore et al. 2000).

Some species can act as pioneers of unvegetated habitat by establishing beds in suboptimal conditions. Pioneer species are often opportunistic species that are stress tolerant with high rates of primary production and production of abundant seeds and/or vegetative propagules. Examples include the non-native *H. verticillata* in low salinity communities (Carter and Rybicki 1994, McChesney 2010, Shields et al. 2012), *Zannichellia palustris* in low and medium salinity communities (Kautsky 1988), and *Ruppia maritima* in medium and high salinity communities (Cho et al. 2009; Lopez-Calderon et al. 2010). Early colonizers may facilitate the establishment of other SAV species. For example monotypic "nursery beds" of *Ruppia maritima* may facilitate the establishment of *Potamogeton perfoliatus* when transplanted into *R. maritima* beds (Hengest et al. 2010). Transplant success of *P. perfoliatus* and density of *R. maritima* was positively correlated in a large *R. maritima* bed (>1000 m^2) but not in small patches (<10 m^2). Large SAV beds enhance habitat quality by reducing total suspended solids and nutrients, decreasing wave energy and improving water clarity (Moore 2004; De Boer 2007; Gurbisz and Kemp 2014). In smaller patches, habitat improvement may be minimal, and nursery species may out-compete rather than facilitate other species (Hengest et al. 2010).

Non-native species, such as *H. verticillata*, have dominated communities recently in the upper Potomac River (Rybicki and Landwehr 2007) and in the Bush River (Chadwell and Engelhardt 2008). In the 1960s, *M. spicatum* dominated many regions in the Chesapeake Bay (Stevenson and Confer 1978, Bayley et al. 1978) but later declined substantially possibly due to disturbance from storms and decreasing water clarity. *H. verticillata* displayed a boom and bust cycle at the Bush River with an initial invasion, fast expansion and subsequent decline (McChesney 2010). The exact mechanism for these boom-and-bust cycles is unknown. Some non-native species compete more intensely because of more rapid and synchronous growth (Wilsey et al. 2011 in Cook-Patton and Agrawal 2014). At some point during the invasion process, however, the uncontrolled growth of the non-native species provides severe limits to population growth or maintenance owing to intra-specific competition for light or depleted nutrients, disease, or sediment toxicity.

In the Chesapeake Bay, dense stands of non-natives may also improve water clarity, allowing for the recruitment/resurgence of native species (Madsen et al. 2001, Rybicki and Landwehr 2007, Ruhl and Rybicki 2010, Shields et al. 2012). For example, with improving water quality in the Potomac River, coverage of both non-natives and natives increased, and the proportion of non-natives was reduced (Rybicki and Landwehr 2007). In general, trends of increasing SAV diversity have been linked to improving water quality such as decreases in nitrogen and total suspended solids, and improving water clarity (Rybicki and Landwehr 2007, Ruhl and Rybicki 2010).

RESPONSE OF SAV COMMUNITIES TO CHANGING HABITAT QUALITY – CASE STUDIES

Low salinity communities

Susquehanna Flats. The Susquehanna Flats, located at the mouth of the Susquehanna River in the upper Chesapeake Bay (Fig. 1), has historically supported a diverse assemblage of SAV (Elser 1967, Bayley et al. 1978, Davis 1985). This tidal fresh region has been experiencing changes in water and habitat quality since colonial settlement. SAV communities in the Susquehanna Flats have been the focus of several studies, including three field investigations that analyzed SAV abundance and diversity over three time periods, 1971 to 1984 (Stevenson and Confer 1978), 1985 to 2001 (unpublished data S. Kollar and N. Rybicki), and 2007, 2008, and 2012 (unpublished data N. Rybicki), in relation to river flow and water quality variables. Water quality variables included total nitrogen (TN) and phosphorous (TP) inputs from the Susquehanna River above the fall line and in situ chlorophyll-a (CHL), total suspended sediment (TSS), dissolved inorganic nitrogen (DIN) and phosphorous (DIP) concentrations in the tidal surface water of the Susquehanna Flats. After 1985, wastewater treatment plant (WTP) TN and TP input from four WTPs on the shoreline of the Susquehanna Flats below the fall line were also analyzed for relations with species composition.

Species richness and diversity were variable over the 28 years considered in these studies (Fig. 5). Species richness was high in 1971 (8 species), low between 1974 and 1984 (1 or 2 species), and high again in later years (5 to 10 species), except in 1988 (1 species). Spearman correlation analysis showed that diversity was negatively correlated with in situ CHL, TSS, and DIP concentrations (Fig. 6) as well as TP and TN inputs from the Susquehanna River. The proportion of non-native species was positively correlated with TN inputs from the WTP while that of native species was negatively correlated with TN inputs from both the WTP and the Susquehanna River (Fig. 6). The proportion of native to non-native (invasive) species has been higher in most recent years with better water quality conditions suggesting that management efforts to improve water quality will have direct benefits for native SAV species.

Chickahominy River. Factors affecting the variation in SAV abundance and diversity in the oligohaline portion of the Bay were examined in a case study of the Chickahominy River over the period of 1998-2007 (Shields et al. 2012). Water quality data were taken monthly throughout the study to indicate differences in salinity and total suspended solids among sites and seasons. The Chickahominy River is an oligohaline tributary of the James River in Virginia (Fig. 1). Its tidal portion extends 35 kilometers upstream from the confluence with the James River to Walkers Dam, which forms a lake for the drinking water supply for Newport News, VA. Historically, SAV was absent from this river in aerial photographs taken periodically from 1937 to 1969 (Moore et al. 1999). A field and mapping survey was conducted in 1978, which documented 91 hectares of SAV (Orth et al. 1979).

SAV coverage in the Chickahominy River declined from 2001-2002, with a low of 54 ha in 2002, and then experienced a resurgence, with a maximum abundance of 297 ha in 2007 (Fig. 7). Prior to the decline, SAV was not established in the upper portion of the river, and the declines mainly occurred in the lower half. However, during the resurgence, much of the increases in abundance occurred in the very upper reaches of the river, which were areas that were not previously occupied by SAV. Between 1998 and 2007, the largest increase in coverage of available bottom occurred 32 kilometers from the mouth, where the percent of available bottom occupied by SAV increased by 92%. The introduction of *H. verticillata* did not appear to negatively affect the species that were already established (*N. minor; C. demersum*), but instead revealed a positive correlation with the spread of these species throughout the river into stretches previously unvegetated. Results over the ten-year study period indicated that the three species generally increased together over time.

The 2001-2002 declines corresponded with a historic drought that elevated salinities along the entire stretch of the river (Fig. 7). Along with elevated salinities, the lowest secchi depths of the time period were recorded. These two events combined to create a disturbance which *H. verticillata* was able to take advantage of, rapidly becoming the dominant species in the upper river by 2007, documented in monthly field surveys that year.

During 2007, eight stations were sampled monthly from May to November along the entire stretch of the tidal portion of the river. Both spatial and temporal species distribution patterns emerged with *N. minor* dominating earlier in the growing season in the lower portion of the estuary, and *H. verticillata* dominating later in the season in the upper portion (Fig. 8). Water quality data taken monthly throughout the study showed differences in salinity and total suspended solids among sites and seasons. Salinity ranged from 0 in May to 4 in November at the site nearest to the mouth of the river, while salinity at the uppermost site remained less than 1. Eighty five percent of the variability of *H. verticillata's* biomass difference between the upper and lower estuary was explained by salinity differences. Total suspended solids were at a maximum at all sites in May, and were greater at the lower river sites compared with the upper river sites. The early season decrease in light availability combined with late season salinity intrusion was likely limiting *H. verticillata* to the upper half of the estuary. *N. minor* was able to become established earlier than *H. verticillata* and was therefore able to outcompete *H. verticillata* during the early season when salinity was zero. Other studies have also found the competitive abilities of *H. verticillata* to be lessened when growing alongside another species that was able to become established earlier (Hofstra et al. 1999, Chadwell and Engelhardt 2008).

Medium and high salinity communities

Lower Potomac River. Exploring causes of seagrass transplant failure provides insight into factors affecting the variation in SAV abundance and diversity in medium salinity regions of the Bay. A small scale seagrass transplant site and a reference site, both located within the Potomac River estuary in Northumberland County, VA, (Figs. 1, 9) were monitored and sediment samples were collected in 2003 and 2004 to better understand factors affecting *Zostera marina* survival in this portion of the Bay. Water quality data were analyzed from two stations located in the mid-channel of the estuary. The transplant site was one of six SAV sites that were restored between 2000 and 2006 and that have only been marginally successful. Results indicate that low salinity affected eelgrass abundance at both transplant and reference sites. Low salinity and low concentrations of sediment nutrients contributed to the transplant failures both years (Schenk and Rybicki 2006).

In healthy *Z. marina* beds, the standing crop peaks in June or July with shoots greater than 4 inches (10 cm) throughout the growing season (Orth and Moore 1986). Between May and July 2003, *Z. marina* shoot length decreased at the transplant site while increasing at the reference site, and by October there was no live *Z. marina* at either site. In 2004, *Z. marina* length at the transplant site never exceeded 4 inches, and eelgrass was not present beyond June. At the reference site, *Z. marina* was shorter in 2004 than in 2003 but the plants survived through October. Water clarity was sufficient at both sites, with the transplant and reference sites receiving a two-year median of 25 percent and 33 percent light at a depth of one meter, respectively. Both sites were above the median 22 percent light level set as a habitat requirement for the mesohaline Chesapeake Bay.

The *Z. marina* transplant failure may have been due to above-average precipitation during both years. The increased precipitation drove the salinity below *Z. marina* tolerance limits (10 ppt) 54 percent of the time at the transplant site and 11 percent of the time at the reference site during the combined 2003 and 2004 growing seasons (Fig. 10). When the salinity was above the requirement, it was often late in the growing season (July, August, or September).

Zostera marina growth and survival could have also been limited by low sediment nutrient concentrations and poor substrate at the Virginia transplant site. In 2003, sediment ammonia concentrations were ten times lower at the transplant site than at the reference site. In 2004, sediment ammonia concentrations increased at the transplant site, but were still nearly half the concentration of the reference site. Sediments at the transplant site also contained three times less organic material than the reference site. The high (93 percent) percent sand and the low organic content (less than 0.5 percent) of the sediments could have slowed the growth and expansion of *Z. marina* at the transplant site. The low amount of nitrogen and organic matter and the high proportion of sand at the transplant site may have stunted *Z. marina* growth, making the plants vulnerable to salinity fluctuations.

Similar factors could have contributed to the failure of a large scale *Z. marina* project across the Potomac River at the mouth of the St Mary's River at Piney Point, Maryland, during the same time period (Fig. 1, Tanner et al. 2010). Despite successful test plantings in 2000 and 2001 and a median percent light level exceeding the minimum required for mesohaline SAV, the planting of 90,000 *Z. marina* shoots over three years (2003-2005) declined during the summer following planting in the fall with one-year survivals of 10%, 0% and 12% for 2003, 2004 and 2005 plantings, respectively. As with the transplant site in Virginia, sediment ammonia concentrations at the site in Maryland were significantly lower than the reference site, and salinities were below normal in 2003 through 2005, often dropping below 10 ppt. In addition, summer temperatures in the summer of 2006 reached nearly 33° C in the summer of 2006.

York River. Recent research and monitoring has documented large-scale seagrass declines due in part to elevated water temperatures related to both gradual long-term increases as well as short-term climatic extremes. In the Chesapeake Bay, two heat events in the summer of 2005 and 2010 were linked to large-scale *Z. marina* declines (Moore and Jarvis 2008; Moore et al. 2014). In the York River (Fig. 1), the 2010 decline and subsequent recovery have been monitored monthly from April – October to determine species abundance and water temperature.

In 2010, *Z. marina* experienced an almost complete die-off in the York River, as well as other areas around the lower Chesapeake Bay (Orth et al. 2011, Moore et al. 2014). This event was related in part to an extreme heat event that occurred in June, which resulted in near complete die-back of vegetation by July. Since this event, monitoring efforts have been tracking the recovery of both *Z. marina* and *R. maritima* along a fixed transect in the York River.

In 2010, integrated mean percent cover along the transect showed *Z. marina* to be the dominant species in all months (Fig. 11). Both species were at their maximum coverage in June (20% and 30% for *Z. marina* and *R. maritima*, respectively). By July, very little vegetation was found for either species, and by August, both species had a mean percent cover of less than 1%. When the data were grouped by depth, these declines occurred for both species across every depth bin (Fig. 11).

The year after this die-off event, 2011, showed a dramatic shift in dominant species along the transect. *Zostera marina* experienced only minor recovery, while *R. maritima* became the dominant species by July. By September, *Z. marina* was virtually absent from the area, experiencing a second consecutive die-off event. *R. maritima* declined as well, but remained the dominant species. In 2010, *R. maritima* was only dominant at the shallowest depths (< 25 cm above MLLW), but by 2011 was the dominant species across all depth bins (Fig. 11). In 2012, both species almost exactly mirrored each other with maximum coverage in May-June, and declines through the summer.

By 2013, *Z. marina* once again became the dominant species during all months, and by June had reached 21% mean integrated cover, similar to its maximum cover in 2010 before the die-off event

(Fig. 11). In 2014, its coverage far surpassed that of *R. maritima,* and it had expanded to levels greater than that in 2010, reaching 35% mean integrated cover in June, and nearing 100% cover in the mid-depths (30-45 cm above mean low low water) (Fig. 11).

This die-off event in 2010 has previously been related to a several-week period of extremely high water temperatures (Moore et al. 2014). The recovery years of 2013 and 2014, when *Z. marina* again became the dominant species, corresponded with cooler summer water temperatures, where the percent of time spent above 28°C was much lower than the previous 3 years.

These data show the ability of *R. maritima* to inhabit areas previously dominated by *Z. marina,* in response to *Z. marina* declines. They also show the ability of *Z. marina* to rapidly recover once conditions, such as water temperature, become more tolerable. This shift in dominant species is likely to occur again in the future as climatic events such as heat events become more frequent in the Chesapeake Bay.

CONCLUSION AND IMPLICATIONS FOR MANAGEMENT AND RESTORATION

SAV abundance and species richness continue to fluctuate in the Chesapeake Bay in response to variation in water quality and other environmental stressors such as short and long-term shifts in temperature and salinity. SAV communities in the tidal fresh and oligohaline salinity zones have seen the most improvements in SAV coverage and diversity since the beginning of aerial Bay-wide SAV surveys as water quality has improved. Non-native species within the low-salinity community persist and have spread within the Bay, but under improving water quality these species can co-exist with native species and even facilitate the resurgence of native species.

In contrast, although SAV communities in both mesohaline and polyhaline salinity zones increased in abundances periodically, they have not shown long-term sustained improvement (Fig. 2). Within the mesohaline zone, species richness in the medium-salinity community (Table 2) has declined, and this community is now dominated by *Ruppia maritima.* Within the high-salinity community *Zostera marina* is living near its physiological tolerances and is susceptible to summer heat events. Within this community *Z. marina* may be replaced by *R. maritima* or other heat tolerant SAV as the dominant species through at least part of its range as the Chesapeake Bay warms (see Chapter on climate change).

Strategies to protect and restore SAV species diversity and community structure within the Chesapeake are the same as those for expanding SAV coverage.

- Short-term and long-term increases in SAV in all salinity zones have been tied to lower nitrogen loads, so reducing nitrogen loads remains a priority for the restoration of Bay SAV. Other water quality parameters such as phosphorus loads and water clarity should also be improved as these are also important in improving SAV habitat.
- For the medium-salinity community, protecting existing beds or transplanting several species of SAV with different salinity and temperature tolerances would increase the probability of successful revegetation following extreme salinity or temperature fluctuations.

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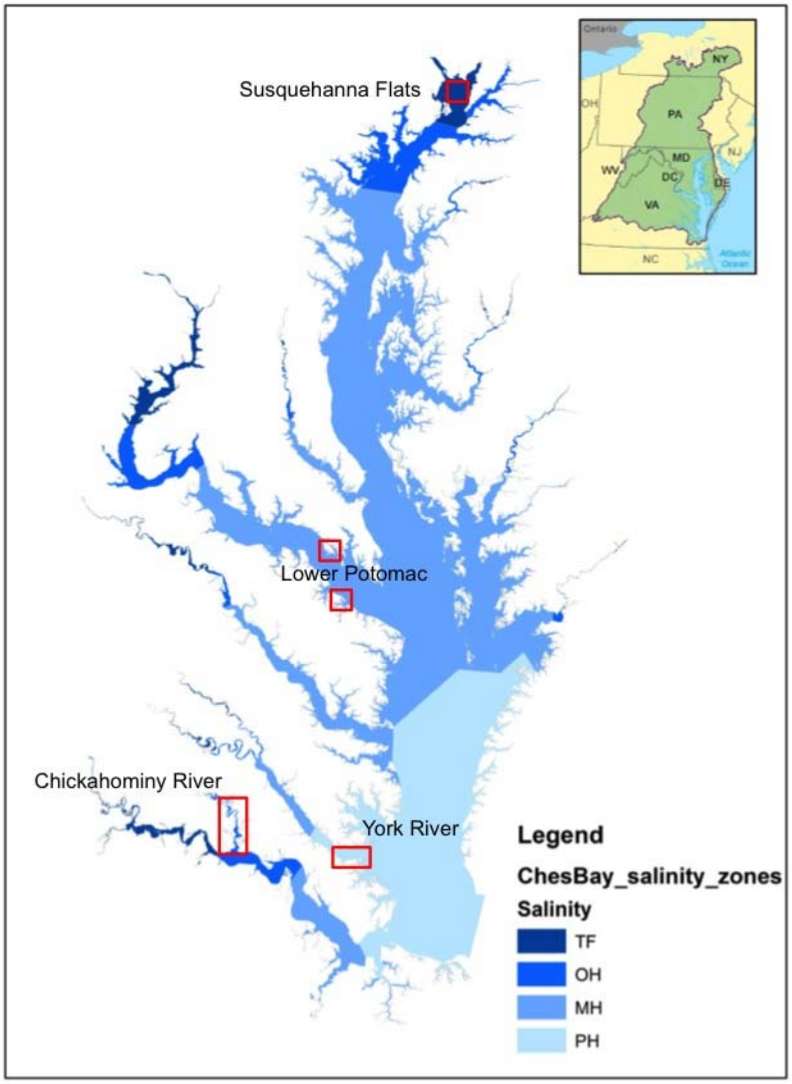


Fig. 1 Map of the Chesapeake Bay showing salinity zones and locations of highlighted studies (boxes). Red boxes are location of four case studies.

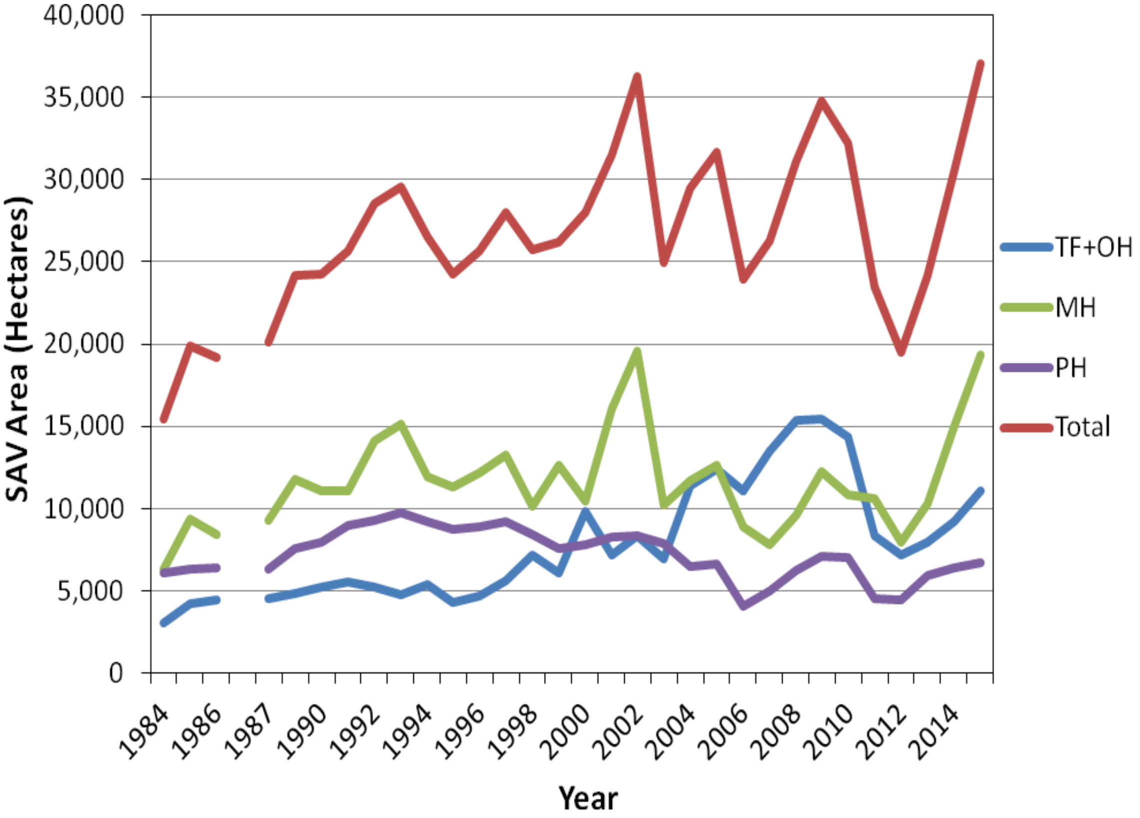
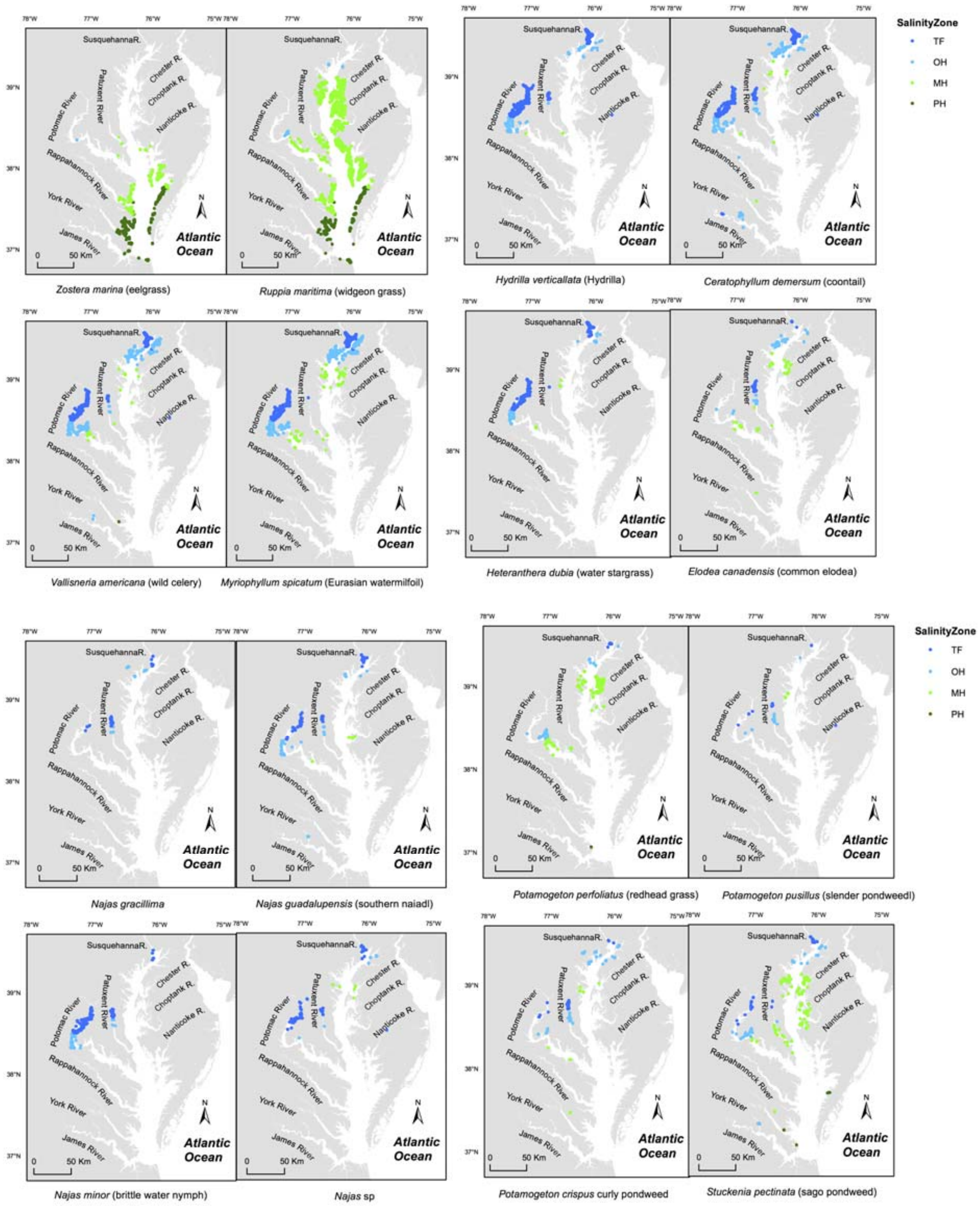


Fig. 2 SAV coverage by salinity zone for 1984 through 2015. Data from annual surveys by the Virginia Institute of Marine Sciences; http://www.vims.edu/research/topics/sav/index.php. TF = tidal fresh (salinities of 0 to < 0.5), OH = oligohaline (salinities of 0.5 to < 5), MH = mesohaline (salinities of 5 to < 18), PH = salinities of 18 < 30). Note: no data was available for 1988.



Zostera marina (eelgrass)

Ruppia maritima (widgeon grass)

Hydrilla verticallata (Hydrilla)

Ceratophyllum demersum (coontail)

Vallisneria americana (wild celery)

Myriophyllum spicatum (Eurasian watermilfoil)

Heteranthera dubia (water stargrass)

Elodea canadensis (common elodea)

Najas gracillima

Najas guadalupensis (southern naiadl)

Potamogeton perfoliatus (redhead grass)

Potamogeton pusillus (slender pondweedl)

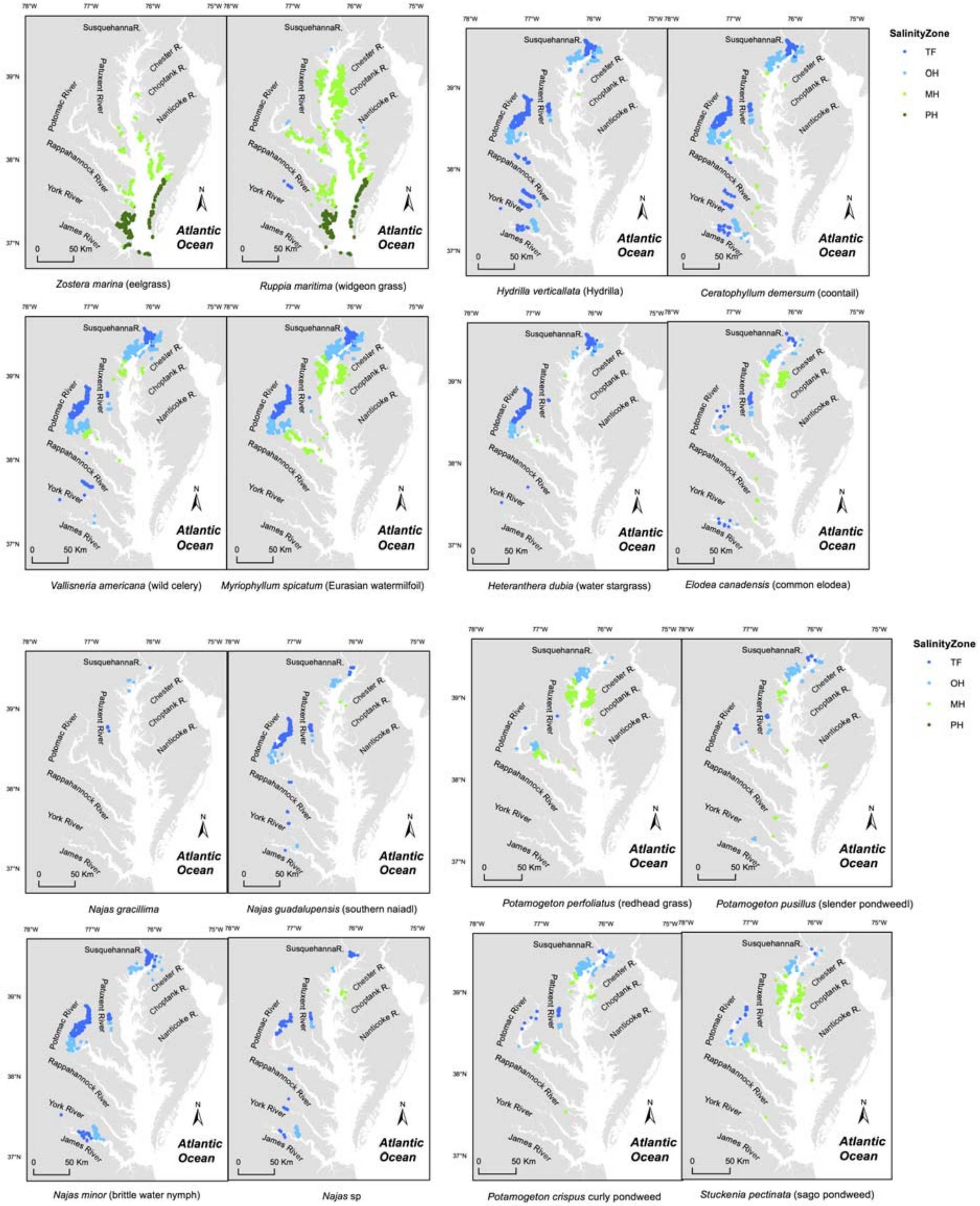
Najas minor (brittle water nymph)

Najas sp

Potamogeton crispus curly pondweed

Stuckenia pectinata (sago pondweed)

Fig. 3 Observation of common SAV species in the Chesapeake Bay between 1985 and 1996.



Zostera marina (eelgrass)

Ruppia maritima (widgeon grass)

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Najas minor (brittle water nymph)

Najas sp

Potamogeton crispus curly pondweed

Stuckenia pectinata (sago pondweed)

Fig. 4 Observation of common SAV species in the Chesapeake Bay between 1997 and 2013.

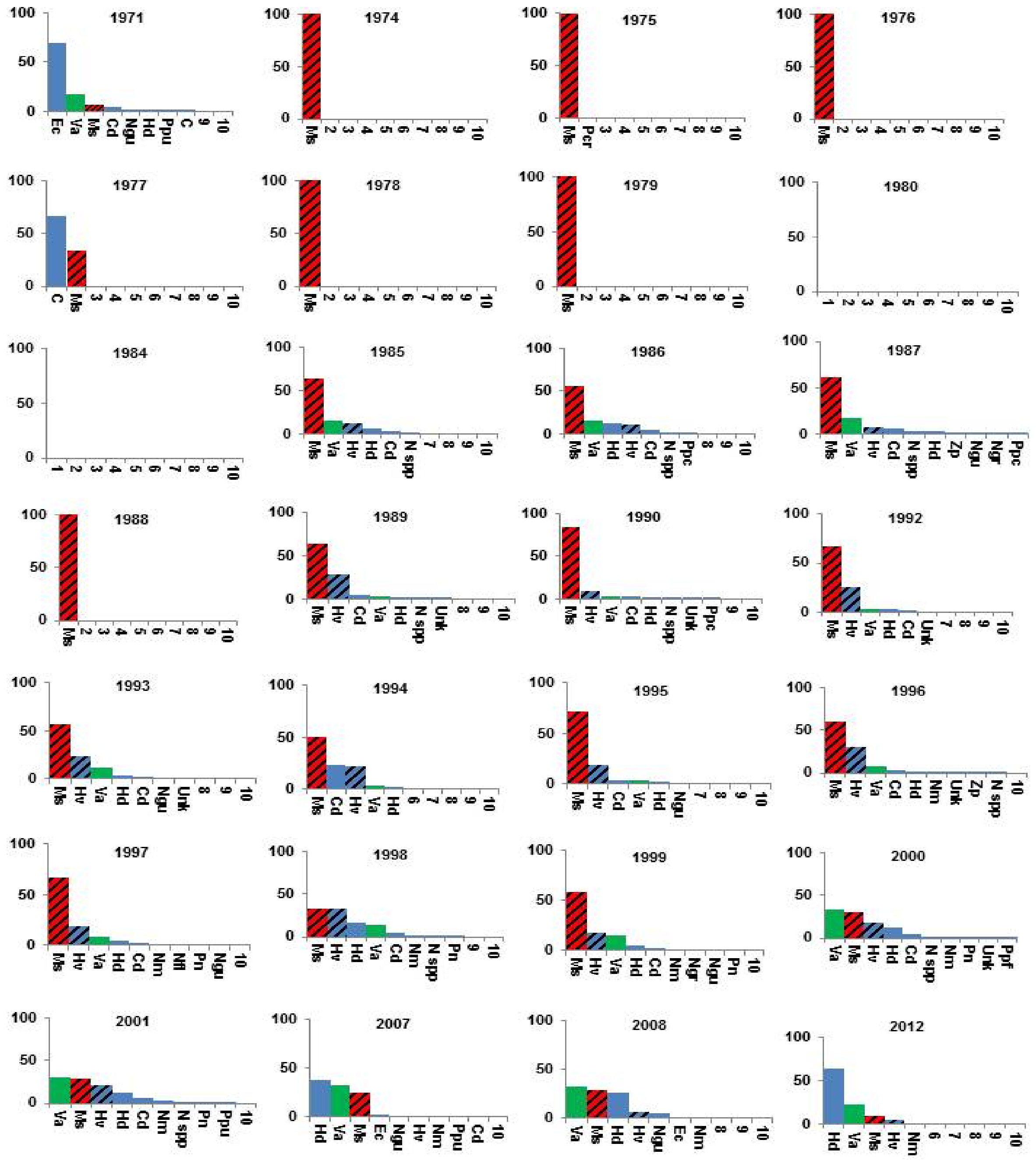

Fig. 5 Annual Susquehanna Flats SAV species abundance distribution for the 28 years species that data were available. The y axis is % SAV species, x axis is species names in order of abundance that year (rank order). Non-native species are denoted by hatch marks. Species composition included *Hydrilla verticillata* (Hv), *Potamogeton crispus* (Ppc), *Myriophyllum spicatum* (Ms), *Najas minor* (Nm), *Vallisneria americana* (Va), *Ceratophyllum demersum* (Cd), *Najas guadalupensis* (Ngu), *Najas gracillima* (Ngr), *Najas flexilis* (Nfl), *Najas minor* (Nm), *Heteranthera dubia* (Hd), *Potamogeton perfoliatus* (Ppf), *Potamogeton pusillus* (Ppu), *Potamogeton nodosus* (Pn), *Stuckenia pectinata* (Ppc), *Elodea canadensis* (Ec), *Najas spp* (N spp), *Zannichellia palustris* (Zp), Unknown species (Unk) and the macroalgae, *Chara* spp (C). Numbers indicate empty ranks of the species in that year.

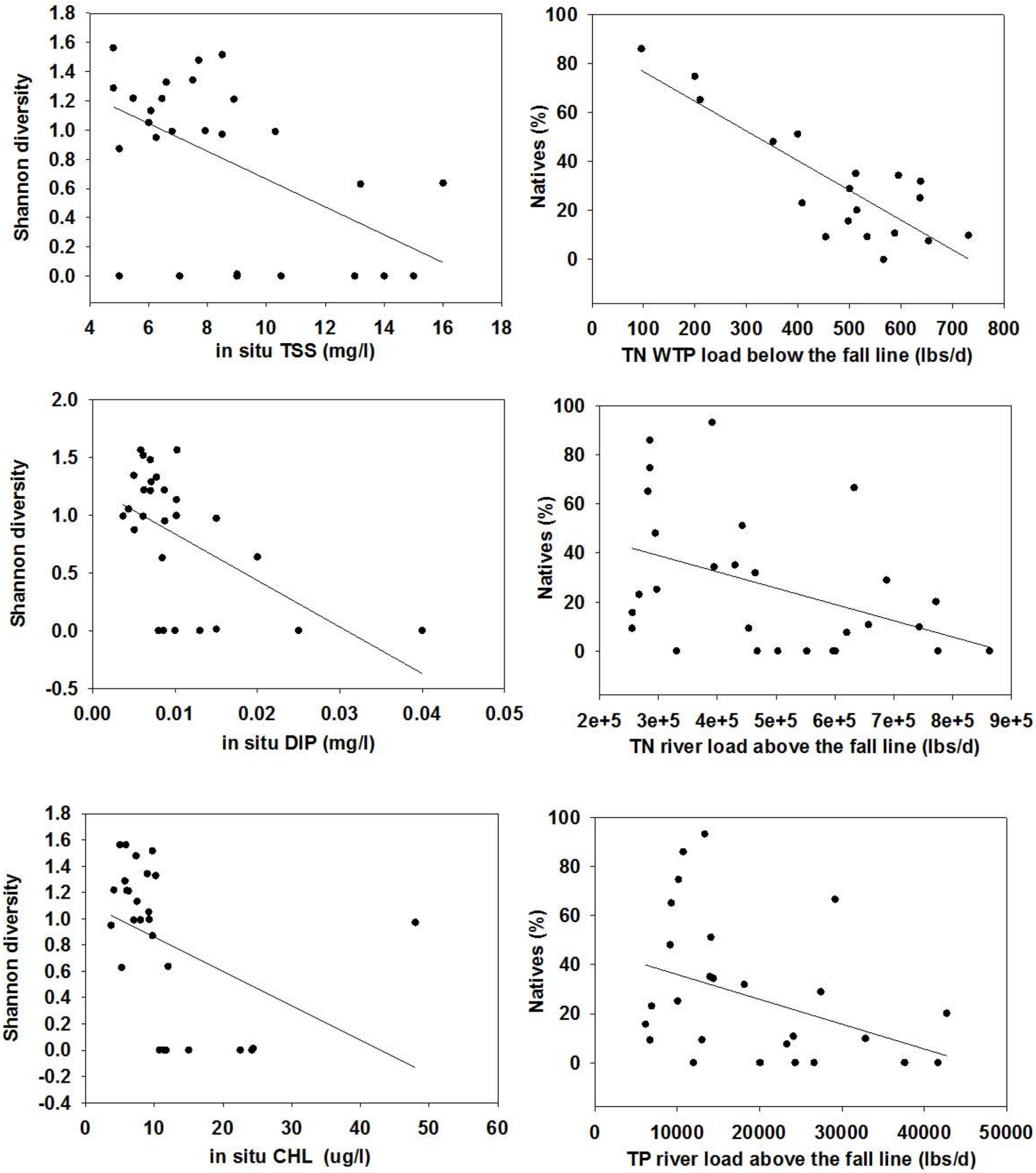

Fig. 6 Scatter plots of Shannon diversity versus in situ TSS (a), DIP (b), and CHL (c) and the percent of native species versus TN input from four WTPs on the shoreline of the Susquehanna Flats below the fall line (d), TN and TP inputs from the Susquehanna River above the fall line (e and f). Lines are only shown as visual aid, with significant Spearman-rank correlations ($p<0.05$) denoted by a solid line. "In situ" refers to Susquehanna Flats (below the fall line) surface water data.

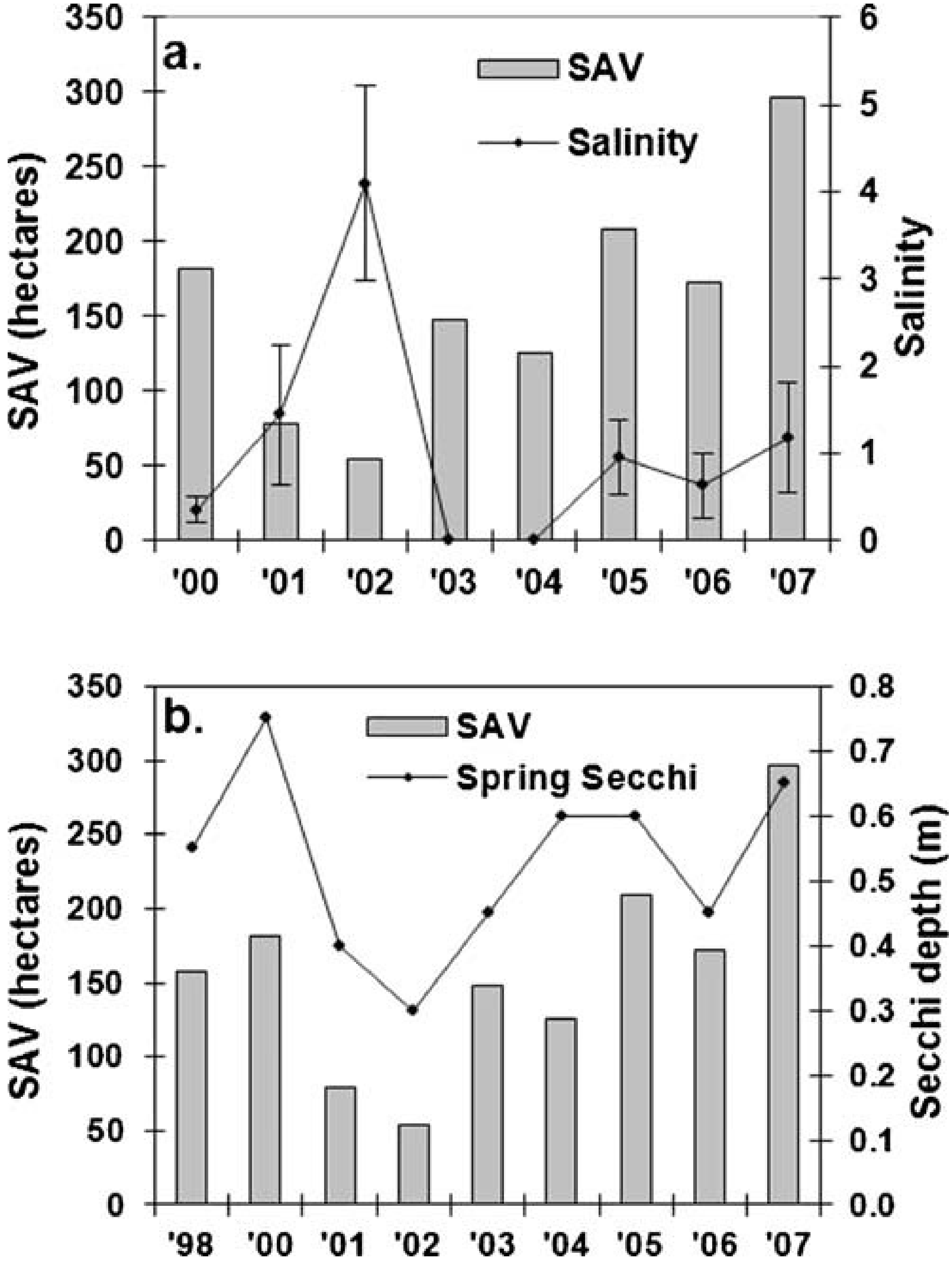

Fig. 7 a) SAV total hectares in the Chickahominy River overlayed with Chesapeake Bay Program station RET5.1A seasonal mean salinity data (± SE). 1998 is left out of the graph because several months of salinity data were missing from the CBP database. b) Total SAV hectares and yearly mean early growing season Secchi depths. The months incorporated in this analysis are the month temperatures reached 15°C and the following month. The correlation between SAV and Secchi depth was significant (Pearson correlation=0.72; $p<0.05$) (from Shields et al. 2012).

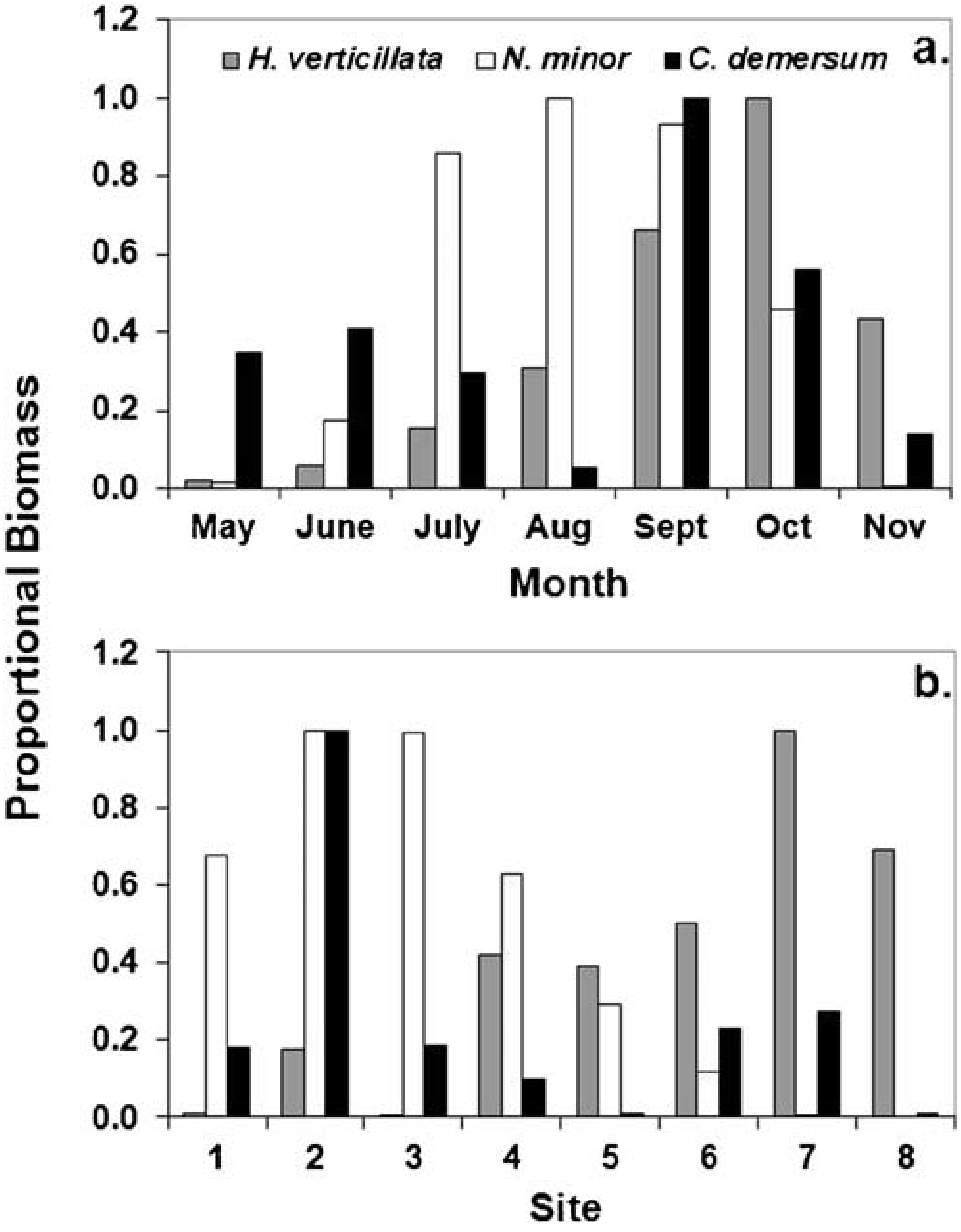

Fig. 8 a) 2007 *Hydrilla verticillata*, *Najas minor* and *Ceratophyllum demersum* biomass reported as the percent of the maximum monthly biomass for each species. b) Biomass reported as the percent of the maximum site biomass for each species. Sites 1–3 represent the lower estuary, and sites 4–8 represent the upper estuary.

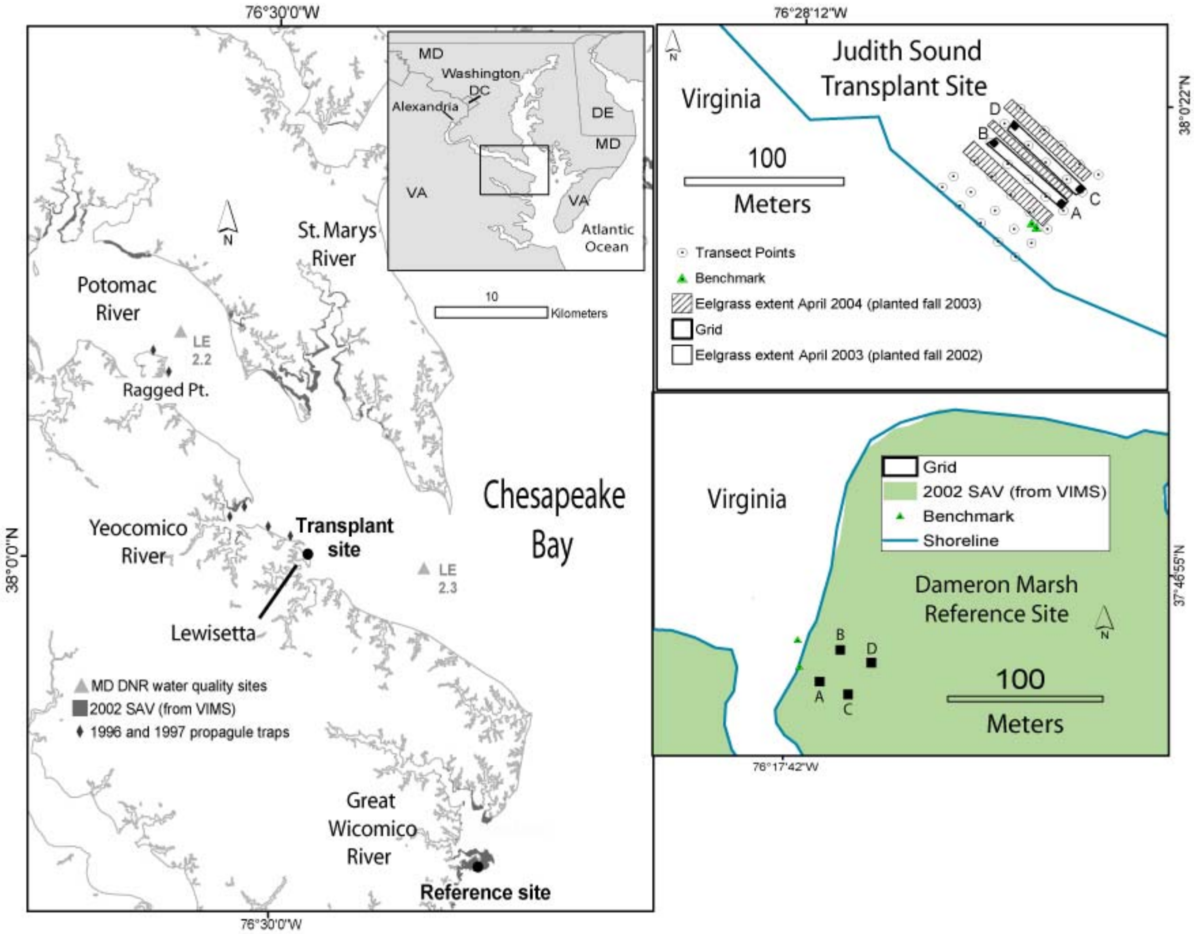

Fig. 9 Transplant and reference sites in the mesohaline portion of the estuary. (From Schenk and Rybicki 2006)

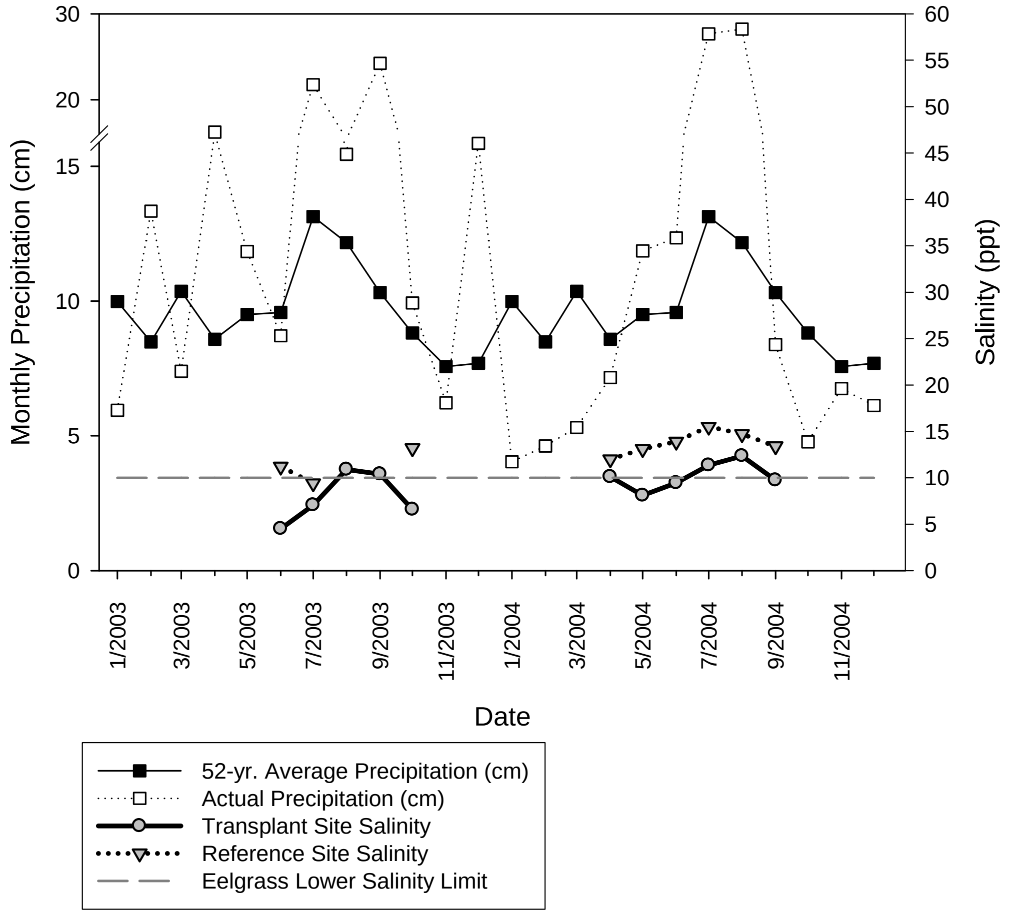

Fig. 10 Precipitation and salinity during 2003 and 2004 at the transplant site and reference site (From Schenk and Rybicki 2006). Precipitation data from Norfolk International Airport.

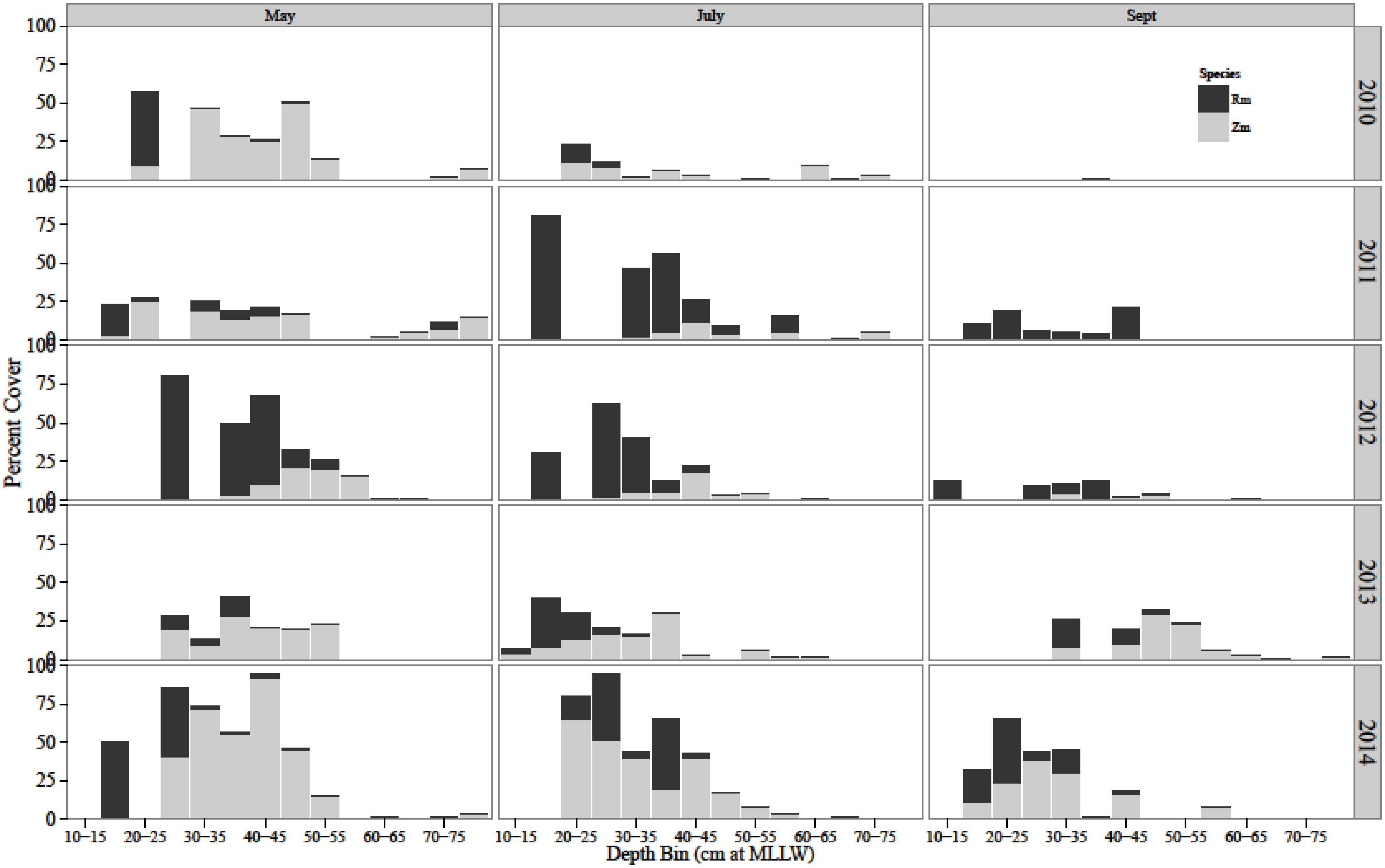

Fig. 11 Mean percent cover of *Z. marina* (gray) and *R. maritima* (black) in the York River for May, July and September from 2010-2014. Data are separated into 5-cm depth bins and reported as depth at mean lower low water (MLLW).

SUBMERSED AQUATIC VEGETATION AND FEEDBACK PROCESSES: IMPLICATIONS FOR RESTORATION AND RESILIENCE

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ABSTRACT

Submersed aquatic vegetation (SAV) has declined globally and locally in Chesapeake Bay over the past half-century primarily in association with increasing prevalence of cultural eutrophication. In an effort to bring back the valuable ecosystem services that SAV provide, federal, state, and local agencies in the Chesapeake Bay and its surrounding watershed are implementing policies aimed at restoring SAV. The primary strategy for SAV restoration is by mitigating nutrient inputs to the estuary to achieve water clarity levels that are thought necessary to sustain SAV populations. However, discrepancies between the predicted habitat thresholds and actual SAV abundance have prompted further scrutiny of these habitat requirements. We argue that positive feedback processes, whereby SAV modify ambient growing conditions in ways that enhance their own growth, could, in part account for these discrepancies. Here, we describe the mechanisms controlling feedback processes in SAV beds, review research linking plant-scale interactions with system-scale dynamics, and discuss implications for Chesapeake Bay SAV restoration and resilience. Our motivation is that this information may provide rationale and spark ideas for further refinement of the SAV habitat requirements, which, in turn, will inform restoration strategies and broaden our understanding of how SAV beds respond to chronic and acute stressors.

INTRODUCTION

Seagrasses and associated submersed aquatic vegetation (SAV) are an important component of shallow coastal and estuarine ecosystems. As foundation species, they provide food and habitat structure for a diversity of organisms, including economically valuable fisheries (Lubbers et al. 1990; Jackson et al. 2001; Duffy et al. 2015). They can also trap suspended sediment (Ward et al. 1984; Koch 2001; Madsen et al. 2001), enhance nitrogen cycling (Caffrey and Kemp 1992; An and Joye 2001), and sequester carbon and nutrients in their biomass (Risgaard-Petersen and Ottosen 2000). These functions translate to benefits not only for the broader ecosystem and society (Costanza et al. 1997; Barbier et al. 2011; Cullen-Unsworth et al. 2014), but also for the plants, themselves. For instance, low concentrations of suspended sediment and nutrients (and thus also phytoplankton and epiphytic algae) inside an SAV bed lead to more light reaching plant leaves (Fig. 1), thereby increasing plant production (Dennison 1987; Ralph et al. 2007). Suspended particle and nutrient concentrations are, thus, further reduced and water transparency is improved, further increasing SAV production, and so on. As a result of these processes, known as positive feedbacks, SAV beds have the capacity to withstand relatively poor and fluctuating environmental conditions (Carr et al. 2012; Unsworth et al. 2015).

When environmental conditions decline below a critical light threshold, however, positive feedback processes no longer effectively buffer against poor water quality and SAV are lost. Globally, SAV abundance has decreased over the past half-century (Orth, et al. 2006; Waycott et al. 2009). Their decline has been primarily attributed to cultural eutrophication linked to increasing nitrogen and phosphorous inputs to coastal waters and associated light-limited conditions. Additional localized losses have also been attributed to acute stressors such as storm events (Cabello-Pasini et al. 2002; Carlson et al. 2010; Gurbisz et al. 2016). Once SAV are lost from an area, recovery is often difficult because plant reestablishment in bare sediment may require more stringent conditions than those required to sustain an existing bed with self-stabilizing positive feedback processes (Scheffer 1990; Janse 1997; Cardoso et al. 2010).

Chesapeake Bay, the largest estuary in the USA is one example of a system that has experienced dramatic SAV declines. Once covering an area approaching 2400 km^2, bay-wide abundance began to decrease in the 1960’s as nitrogen and phosphorus inputs increased concurrently with intensified fertilizer use and urbanization in the watershed (Kemp et al. 1983; Orth and Moore 1983; Kemp et al. 2005). Extreme flooding and sediment loading during Tropical Storm Agnes in 1972 destroyed a large portion of the bay’s remaining SAV. Submersed plant abundance has generally remained low since then, although there have been some local resurgences, particularly in lower salinity regions such as the upper Potomac River and upper Chesapeake Bay (Carter and Rybicki 1986; Gurbisz and Kemp 2014).

In an effort to bring back the valuable ecosystem services that SAV provide, natural resource managers locally and globally are working to facilitate their restoration. Federal, state, and local agencies in the Chesapeake Bay region have led the way in developing and implementing cooperative strategies to restore SAV to historic abundances. Part of the restoration plan includes planting SAV seeds and propagules in appropriate high water clarity areas. However, a greater emphasis has been placed on policies centered on restoring water quality (and therefore light availability for plant growth) by placing limits on nutrient and sediment inputs from the watershed. Thresholds for the minimum light required for SAV survival (and associated maximum suspended sediment, chlorophyll *a*, and nutrient concentrations), which were established through empirical relationships between SAV presence and water quality data collected at nearby monitoring stations, currently serve as restoration targets (Dennison et al. 1993; Kemp et al. 2004).

However, discrepancies between the predicted habitat thresholds and actual SAV abundance elicit further scrutiny of these habitat requirements. For example, there are cases where SAV are present, yet water clarity at the nearest monitoring station is well below the minimum light requirement. Conversely, SAV are absent in other cases, yet water clarity is greater than the minimum light threshold (Batiuk et al. 2000). Several potential explanations could account for these discrepancies, including propagule limitation, physiological or morphological differences among plant species across sites, or an unsuitable physical environment (e.g., too much wave energy or inadequate substrate) (Koch 2001; Orth et al. 2006). However, another factor that has not been extensively considered is the role of positive feedback processes. For instance, it is theoretically possible that the minimum light requirement for a recovering or restored SAV bed may be greater than for existing or established SAV beds in which positive feedbacks improve ambient water clarity. Meanwhile, existing SAV populations may be more resistant than anticipated to fluctuating water quality conditions because positive feedback processes modify the internal bed environment sufficiently to buffer against high rates of nutrient and sediment loading and associated poor water clarity that, for instance, are typical of storm events.

The overall goal of this chapter is to help explain how feedbacks could lead to these discrepancies. In the sections that follow, we 1) provide a brief overview of the mechanisms controlling feedback processes in SAV beds, 2) review research linking plant-scale interactions with system-scale dynamics, and 3) discuss implications for Chesapeake Bay SAV restoration and resilience to extreme weather events. Our motivation is that this information may provide rationale and spark ideas for further refinement of the SAV habitat requirements (i.e., necessary environmental conditions), which, in turn, will inform restoration strategies and broaden our understanding of how SAV beds respond to chronic and acute stressors. The latter of these outcomes is particularly important in light of projected increases in the frequency and intensity of storm events and heat waves associated with global climate change (Najjar et al. 2010).

MECHANISMS CONTROLLING FEEDBACK PROCESSES IN SAV BEDS

A substantial body of literature focusing on the effects of SAV beds on local environmental conditions has accumulated over the past several decades, resulting in an in-depth understanding of the mechanisms driving feedback processes. Previous authors have comprehensively reviewed these interactions; therefore, we provide only a brief overview in the next several sections. More detailed descriptions of the biophysical and biogeochemical mechanisms controlling feedback processes can be found in Koch (2001), Havens et al. (2001), Viaroli et al. (2008), de Boer (2007), and Adams et al. (2016). A summary of feedback processes that have been measured in Chesapeake Bay is presented in Table 1.

Biophysical processes

One of the most extensively researched feedback processes in SAV beds is the sequence of regulatory interactions between plants, water movement, suspended particle concentration (SSC), and light penetration through the water column (Fig 2a). When submersed plants exert drag on moving water, their physical structure reduces current velocity and wave height within the plant bed (Fonseca et al. 1982; Gambi et al. 1990; Ackerman and Okubo 1993). As flow and wave orbital velocities fall below a critical threshold, suspended particles sink and bottom sediments are less likely to be resuspended (Ward et al. 1984; Fonseca and Fisher 1986; Gacia and Duarte 2001). As a result, water clarity inside the SAV bed (relative to outside) improves and plant production increases due to locally increased light availability (Fig. 1) (Scheffer 1990; van der Heide et al. 2011). In short, plants decrease flow, which decreases SSC, which increases light availability, which, in turn, increases plant growth. The feedback loop, then, continues as increased plant biomass further attenuates velocity, and so on.

The extent to which the plants modify flow, SSC, and light depend on a number of factors that are linked across spatial scales. At the plant scale, the effect on hydrodynamics and SSC intensifies as stem density, morphological complexity, and height relative to water depth increase (Nepf 2000; Zong and Nepf 2011). For example, dense plant beds (>40% plant cover) with a canopy extending to the water surface generally contain very clear water due to relatively high damping of water velocity and wave height. As a result, bare patches within these beds tend to quickly colonize (Luhar et al. 2008; Suykerbuyk et al. 2015). On the other hand, sufficiently sparse plant cover (<< 40%) can result in increased turbulent transfer to the sediment surface and, therefore, increased resuspension, potentially leading to a “runaway feedback” whereby turbidity increases and plants are lost (Lawson et al. 2012). At the bed scale, the length beyond which horizontal momentum dissipates is generally regulated by the proportion of the water column occupied by plants (Luhar and Nepf 2013). If this penetration scale is less than the length of a given patch, then the plant bed does not significantly alter its physical environment. This is why larger patches are generally more stable (Fig. 3) than small patches (Moore 2004; Gruber et al. 2011; Orth et al. 2012; Gurbisz et al. 2016). At the scale of a basin or reach, dense SAV beds act as flow obstructions, where flow at the leading edge of a bed is deflected and diverges around the bed (Rominger and Nepf 2011). This creates a long-range negative feedback in which higher flow velocities and associated sediment resuspension occurring in unvegetated areas adjacent to an SAV bed preclude plant establishment and growth (Bouma et al. 2009; van der Heide et al. 2010; Schoelynck et al. 2012).

Biogeochemical processes

SAV beds also affect the biogeochemical environment, as they are often considered centers of nutrient processing and removal. For example, SAV assimilate and seasonally retain nutrients (i.e., nitrogen and phosphorus) in their tissue, often at high rates and in large quantities (McGlathery et al. 2007). In some cases, SAV may also stimulate coupled nitrification-denitrification when oxygen released by plant roots oxidizes pore water ammonium to nitrate, which then diffuses to anoxic zones to fuel denitrification (Caffrey and Kemp 1992; An and Joye 2001; Eyre et al. 2010). Enhanced denitrification typically occurs when abundant nitrogen is available for both autotrophic uptake and as a terminal electron acceptor in the redox process and when sufficient organic substrate is available to serve as an electron donor (Cornwell et al. 1999; Seitzinger et al. 2006; Eyre et al. 2013). Both plant nutrient sequestration and enhanced denitrification limit water column nutrient availability for uptake by macroalgae, epiphytic algae, and phytoplankton (Havens et al. 1998; Viaroli et al. 2008), which increases light availability for SAV photosynthesis (Twilley et al. 1983; Lobelle et al. 2013). Even if water column nutrient concentrations are insufficient to support plant growth, SAV are able to meet their nutrient requirements through uptake from the sediment (Caffrey and Kemp 1992). Therefore, SAV decrease nutrient concentrations, which leads to decreased algal production, which increases light availability, which, in turn, increases SAV production (Fig. 2b).

Interactions between biophysical and biogeochemical processes

Finally, SAV bed effects on physical processes can interact with biogeochemical processes. For example, when SAV beds trap sediments, organic-rich particles may accumulate within the bed (Kenworthy et al. 1982). Decomposition of this material generates increased concentrations of dissolved nutrients in the sediment pore water (Fig. 2c), which can stimulate SAV growth (Caffrey and Kemp 1990). Although increased organic matter accumulation in the sediment can also lead to the accumulation of toxic metabolites, including hydrogen sulfide (Eldridge and Morse 2000; Terrados and Duarte 2000; Folmer et al. 2012), root exudation of oxygen can counteract this effect (Fig. 2d) by oxidizing sulfide to sulfate (Kemp and Murray 1986; Caraco et al. 2006). In addition, for large, dense SAV beds, increased water residence time due to plant interactions with flow can further enhance the depletion of water column nutrient concentrations when the rate of nutrient loss due to plant uptake and denitrification exceeds the rate of replenishment through mixing with outside water (Rybicki et al. 1997; Nepf et al. 2007; Gurbisz et al. *in review*). These findings highlight the importance of an interdisciplinary approach as research on feedbacks in coastal systems moves forward.

EFFECTS OF FEEDBACK PROCESSES ON SYSTEM DYNAMICS

Brief theoretical background

Although research investigating plant bed effects on environmental conditions has generated a wealth of knowledge about the mechanisms controlling feedbacks, linking these processes across multiple spatial and temporal scales to system dynamics can be problematic. However, the theoretical underpinnings of this idea serve as a useful guide. Whereas some systems respond to external drivers linearly (Fig. 4a), one consequence of feedbacks is that they can facilitate nonlinear dynamics. Holling (1972) and May (1977) use mathematical analysis of dynamical systems in the context of interacting natural populations to show that, in the presence of self-stabilizing feedbacks, situations arise in which there is little change in the state of the system in response to a changing external pressure until a critical threshold in that variable is crossed. Beyond the threshold, the system rapidly shifts to a different state (Fig. 4b). When feedbacks are sufficiently strong, the response curve folds over on itself because the threshold for decline is different from the threshold required for recovery (Fig. 4c). In this case, the system is "bistable," meaning it can exist within two "alternative stable states" under the same set of environmental conditions. The dynamics of such a system are said to contain "hysteresis" because the system's response to changing external conditions depends on its history and trajectory (Scheffer et al. 2001).

An application of these concepts is often illustrated with a "ball-and-cup" diagram, which shows how different sized "basins of attraction" represent varying degrees of resilience (Scheffer et al. 2001). In a system containing alternative stable states, a ball can reside within one of two valleys, or basins of attraction, representing two different system states (Fig. 5). Small perturbations push the ball up the valley, but it eventually settles back into the same basin. Although the system is not static, its fundamental structures and functions remain intact. However, a sufficiently strong perturbation can push the ball over the hill and into the other basin. "Ecological resilience" can be defined as the largest perturbation the system can withstand without moving into another basin of attraction (i.e., losing key structures and functions) and is represented by the width of a basin of attraction (Holling 1973; Gunderson 2000). An alternative definition for resilience, known as "engineering resilience," assumes that only one stable state is possible (or desirable) and can be thought of as the time required to return to that state following a disturbance (Peterson et al. 1998). Engineering resilience is represented conceptually by the steepness of the basin attraction. When the basin of attraction, or resilience, shrinks in response to increases in an external pressure, the system becomes more fragile and can easily transition to an altered state. Although perturbations, such as extreme weather events, typically push the system across the threshold to an alternate stable state, the likelihood of crossing the threshold is a function of the underlying resilience driven by chronic external pressures.

Feedback processes and natural system dynamics

The link between feedbacks and nonlinear system dynamics is difficult to show empirically because the processes involved occur at a range of very different spatial and temporal scales (Groffman et al. 2012). Lack of sufficient data, high variance in driver and response variables, and multiple stressors in natural systems further muddle the relationship between plant-scale interactions and system-scale dynamics (Knowlton 2004). However, researchers have made progress over the past several decades in addressing this question as it pertains to SAV, using theory to guide their approach.

Manipulative studies in lake systems played a key role in demonstrating the effect of feedbacks in natural aquatic systems. A classic example involves eutrophication in lakes in which major phosphorous loading reductions initially failed to reduce algal growth and improve water clarity (Meijer et al. 1994; Carpenter et al. 2001). When natural resource managers "shocked" the systems by removing planktivorous fish, eutrophication rapidly reversed. Specifically, by depleting the planktivore population, the abundance of zooplankton, which graze on phytoplankton, increased, phytoplankton abundance decreased, water clarity improved, and SAV abundance increased. Conceptually, reducing phosphorus inputs to the lake decreased the resilience of the turbid water state, while biomanipulation efforts served as the perturbation or disturbance required to shift the lake into the clear water state (Scheffer 1990; Scheffer et al. 1993; Scheffer and van Nes 2007). Once established, feedbacks facilitated by the SAV allowed some of the lakes to persist in the clear water state despite no additional decrease in nutrient loading rates, indicating bistability. This scenario serves as a reminder that "undesirable" system states can also be resilient ("perverse" resilience), and it also highlights the importance of considering the existence of alternative stable states in natural resource restoration.

A small but growing number of studies have linked SAV feedbacks to nonlinear dynamics in coastal and estuarine environments. Although mostly inferential (i.e., research approaches consist of time series analysis, correlative relationships, or numerical simulation models), the insights gained from these studies are nonetheless informative of the processes governing nonlinear system dynamics. For example, wasting disease and dam construction triggered widespread loss of eelgrass in the Dutch Wadden Sea in the 1930's, and the ensuing turbidity increase in the absence of SAV apparently precluded system recovery despite restoration attempts (van der Heide et al. 2007). Similarly, extreme weather events (a flood and a drought) prompted abrupt SAV decline and recovery in the upper Chesapeake Bay, while positive feedback processes between the plants, nutrient and suspended sediment concentrations, and light availability promoted stability within the clear and turbid water states (Fig. 6) (Gurbisz and Kemp 2014). In each of these cases, large disturbances tipped the system into a different state, whereas self-stabilizing positive feedback processes facilitated resistance to change before and after the sudden shifts. Bistable dynamics caused by feedbacks between submersed plants, SSC, and light have also been shown for seagrass populations in Moreton Bay, Australia (Maxwell et al. 2015), Western Europe (van der Heide et al. 2011), and Virginia USA (Carr et al. 2010; Carr et al. 2015; Adams et al. 2016).

Spatial patterns formed by patches of SAV and bare sediment can also indicate feedback effects on system dynamics. Although abrupt shifts in the state of a system over time often indicate nonlinearity, systems in which feedbacks are present may also contain abrupt transitions across space because local positive feedbacks are accompanied by longer range negative feedbacks (Rietkerk and van de Koppel 2008). These scale-dependent feedbacks between hydrodynamics and seagrass growth result in the formation of self-organized spatial patterns (Luhar and Nepf 2013). For example, roots and rhizomes stabilize sediment within an SAV patch, preventing uprooting and resuspension. However, aboveground plant structures also channelize flow into unvegetated spaces, enhancing scour and preventing colonization. Whereas local within-patch feedbacks facilitate SAV persistence, long-range feedbacks reinforce the bare-sediment state (Fonseca et al. 2007; van der Heide et al. 2010). It has been suggested that the nature of these patterns may indicate an impending shift in the state of a system (Rietkerk et al. 2004; Scheffer et al. 2009). In the case of SAV, as the prevalence of small, unconnected patches increases, the likelihood of increased turbidity and plant loss associated with a runaway feedback also increases (Lawson et al. 2012; Suykerbuyk et al. 2015).

Although feedback processes lead to abrupt transitions between ecosystem states and enhance stability within a given state, proximity to a state change, or resilience, is typically a function of chronic environmental stress. In coastal and estuarine systems, the rate of nitrogen and phosphorus loading is often viewed as such a pressure because associated algal growth degrades water clarity and, thus, disrupts the metabolic balance of submersed plants. As eutrophic conditions reduce light available for SAV photosynthesis, carbon fixation and available energy stores within the plant decrease, making SAV more susceptible to loss associated with light-limiting disturbances such as turbidity pulses during storm events (Moore et al. 1997; Longstaff and Dennison 1999; Yaakub et al. 2014). Heat-sensitive species, like *Zostera marina*, also become more vulnerable to loss under eutrophic conditions when exposed to high water temperatures associated with heat waves. This is because increased respiration rates at high temperatures outpace production when photosynthesis is light-limited (Carr et al. 2012; Fraser et al. 2014). Furthermore, when plants become severely depleted, their reproductive output may decrease, thus limiting renewal potential following a disturbance.

In addition, plant loss in response to nutrient loading is not always spatially uniform. Patchy plant loss and resultant increased fragmentation further degrades resilience by decreasing the extent to which feedbacks can act as a buffer against disturbance. For example, proximity to coastal effluent sources has been linked to increased SAV fragmentation in both Biscayne Bay (Florida, USA) (Santos et al. 2016) and the Mediterranean Sea (Montefalcone et al. 2010). Meanwhile, as the size of an SAV bed or patch decreases, its attenuating effect on flow and turbidity decreases and, thus, so does its capacity to absorb large disturbances (Duarte and Sand-Jensen 1990; Gruber et al. 2011; Carr et al. 2015). Therefore, nutrient loading affects SAV resilience by disrupting plant energetics and related biological processes that allow plants to withstand and recover from disturbances, and increased patchiness could be an indicator of an impending shift to the bare sediment, turbid ecosystem state.

IMPLICATIONS FOR CHESAPEAKE BAY SAV RESTORATION AND RESILIENCE

Positive feedback processes and their effect on how submersed plants respond to external environmental conditions are relevant to Chesapeake Bay SAV restoration and resilience. A key point directly related to the habitat requirements is the possibility that more light may be needed for a recovering or restored SAV bed versus an existing or established bed due to the presence of self-stabilizing feedbacks. Therefore, separate sets of habitat requirements must be developed for creating new SAV beds versus habitat requirements needed for sustaining existing SAV beds (e.g., Batiuk et al. 1992; Batiuk et al. 2000). We must devise a scheme for quantifying these parallel sets of water quality habitat requirements. Moore (2004) proposed this idea more than a decade ago, yet empirical quantitative support is still lacking. However, as monitoring data continue to pour in and more efficient and effective computing resources develop, this endeavor becomes an increasingly conceivable possibility. Future research efforts should focus on investigating whether the relationship between SAV presence and environmental conditions differs depending on SAV trajectory (recovery versus decline) and identifying thresholds for SAV decline and recovery in each salinity regime. The original set of habitat requirements were derived based on spatial differences in SAV abundance and water clarity; future analyses should incorporate the time dimension since hysteresis is time-dependent. Furthermore, as the time span encompassing monitoring datasets increases and additional shifts in SAV abundance are captured, research on detecting early warning signs for critical transitions will also become more feasible (e.g., Scheffer et al. 2009; Carpenter et al. 2011). Additional real-time in-situ monitoring sensors located both inside and adjacent to SAV beds, like those established for the Susquehanna Flats region of Chesapeake Bay (Michael et al. 2016; http://eyesonthebay.dnr.maryland.gov), could help advance research on these and related questions.

An increased emphasis on spatially explicit analyses may also be important for identifying how spatial patterns are indicative of ecosystem processes.

In addition, although restoration activities are mostly focused on water quality mitigation, there are some localized direct efforts to plant or seed SAV into presently unvegetated areas with suitable habitat. Considering the role of positive feedbacks could facilitate planting success. For example, *Potamogeton perfoliatus* and *Stuckenia pectinata* transplants placed within beds of *Ruppia maritima* in the Choptank River survived better than those planted in bare patches, supporting the idea that feedbacks in established plant beds enhance propagule survival (Hengst et al. 2010). Similarly, a global meta-analysis of seagrass plantings showed that transplant survival rate is positively related to the number of propagules initially transplanted (Fig. 7) and that a critical mass may be required to increase the chances of restoration success (van Katwijk et al. 2016). This finding implies that positive feedbacks in larger, denser planting schemes facilitate transplant persistence. Relationships between plant morphology, density, bed size, and hydrodynamic regime (e.g., Luhar et al. 2008) should be used to determine optimal planting configurations in future restoration efforts. SAV plantings could also be coordinated to exploit "windows of opportunity" during dry years, when water clarity generally improves (Scheffer and van Nes 2004; Nyström et al. 2012). Once established, a bed in which feedback processes improve the ambient environment will be more likely to persist despite a return to average external conditions in subsequent years.

Finally, given the predicted increases in the frequency and intensity of extreme weather events associated with global climate change (Najjar et al. 2010), management perspectives and strategies that focus on SAV resilience will become increasingly important. Large-scale SAV loss has been attributed to extreme weather events globally (e.g., Preen et al. 1995; Campbell and McKenzie 2004; Hanington et al. 2014) and locally (e.g., Bayley et al. 1978; Orth et al. 2010). However, the resilience perspective suggests that acute disturbance is often the "straw that breaks the camel's back" in already degrading systems. Although nutrient management plans, such as the Chesapeake Bay Total Maximum Daily Load, are aimed at restoring lost SAV populations, mitigating nutrient loads will also likely increase SAV resilience to extreme weather events and other novel perturbations by alleviating a major source of chronic stress. Recent work suggests that restored SAV beds can, in fact, be remarkably resilient. For example, a sizable portion of the newly recovered Susquehanna Flats SAV bed in upper Chesapeake Bay persisted despite high flow velocities and massive nutrient and sediment loads during a record flood in 2011, demonstrating a significant ability to absorb disturbance (Gurbisz et al. 2016).

Moving from resilience as a conceptual framework to a measurable quantity is an emerging area of research. More work is needed to identify how SAV beds of varying size exposed to a range of underlying nutrient loading scenarios respond to different levels of disturbance. Although the ubiquity of multiple spatially and temporally diverse drivers and responses complicate this type of analysis, Chesapeake Bay is an ideal system in which to pursue these questions due to the availability of over three decades of water quality and SAV monitoring data.

CONCLUSIONS

In summary, there is strong evidence that feedbacks do, indeed, facilitate nonlinear dynamics in coastal and estuarine systems by improving internal SAV bed water clarity despite changes in external habitat conditions. If feedbacks are sufficiently strong, water quality thresholds for recovery may be more stringent than those leading to SAV decline, and we may expect to see little response to nutrient load reductions until critical thresholds are crossed. The capacity for feedbacks to buffer against disturbance is, in part, a function of underlying nutrient loading trends. However, quantifying differences in thresholds for decline and recovery, as well as quantifying SAV bed resilience in relation to underlying water quality conditions remains a substantial challenge. This will be particularly difficult for large, open systems like Chesapeake Bay, which contain multiple, interacting stressors that vary across space and time. As additional monitoring data are collected and policy measures, if successful, continue to decrease nutrient inputs to Chesapeake Bay, research that focuses on unraveling these and related complexities will be crucial for developing more accurate and precise predictions of SAV distributions and responses to stressors, including those associated with climate change.

TABLES

Table 1. Summary of feedback process components measured in Chesapeake Bay SAV beds.

Authors	Year	Species	Location	Feedback process components measured
Ward	1984	*Ruppia maritima*	Choptank River	SAV beds attenuated wave energy, suppressed sediment resuspension, and enhanced sediment deposition; suspended sediment concentrations were lower inside SAV beds, but not when water level was unusually high
Caffrey and Kemp	1990	*Potamogeton perfoliatus, Zostera marina*	Experimental pond near the Choptank river	Denitrification rates were greater in vegetated versus bare sediments
Caffrey and Kemp	1992	*Potamogeton perfoliatus*	Choptank river	Denitrification rates were greater in vegetated versus bare sediments
Rybicki et al.	1997	*Hydrilla verticillata*	Potomac River	There was decreased exchange between the SAV bed and surrounding water
Schulte and Kemp	2003	*Ruppia maritima*	Honga River	Continuous, dense SAV beds were more effective in trapping fine-grained, organic rich sediments and suppressing growth of epiphytic algae
Moore	2004	*Zostera marina*	York River	Suspended sediment and inorganic nitrogen concentrations inside the SAV bed decreased when biomass > 50-100 g dry weight /m2 or plant cover > 25-50%
Gruber and Kemp	2010	*Stuckenia pectinata*	Choptank River	The plant bed attenuated waves; suspended sediment concentration and the growth rate of epiphytic algae were lower inside

				relative to outside the SAV bed; sediment organic content and pore water nutrient pools were greater inside the bed
Gruber et al.	2011	*Ruppia maritima, Stuckenia pectinata*	Missing location	The magnitude of turbidity reduction was a function of canopy height and bed size and density
Gurbisz and Kemp	2014	*Vallisneria americana, Heteranthera dubia, Hydrilla verticillata, Myriophyllum spicatum*	Upper Chesapeake Bay	Turbidity and chlorophyll were lower inside versus outside the SAV bed
Gurbisz et al.	2016	*Vallisneria americana, Heteranthera dubia, Hydrilla verticillata,Myriophyllum spicatum*	Upper Chesapeake Bay	Sediment resuspension decreased during peak SAV biomass; the SAV bed diverted and attenuated flow during a storm event
Gruber and Kemp	2010	*Stuckenia pectinata*	Choptank River	The plant bed attenuated waves; suspended sediment concentration and the growth rate of epiphytic algae were lower inside relative to outside the SAV bed; sediment organic content and pore water nutrient pools were greater inside the bed

FIGURES

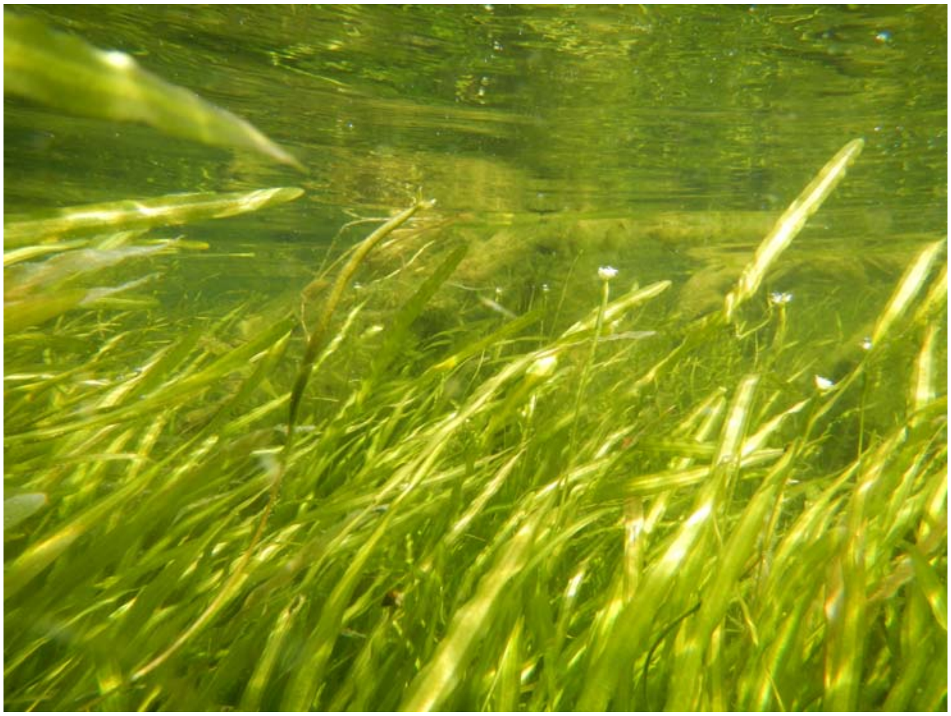

Figure 1. Example of exceptional water clarity inside the Susquehanna Flats SAV bed, which is located in the upper main stem Chesapeake Bay.

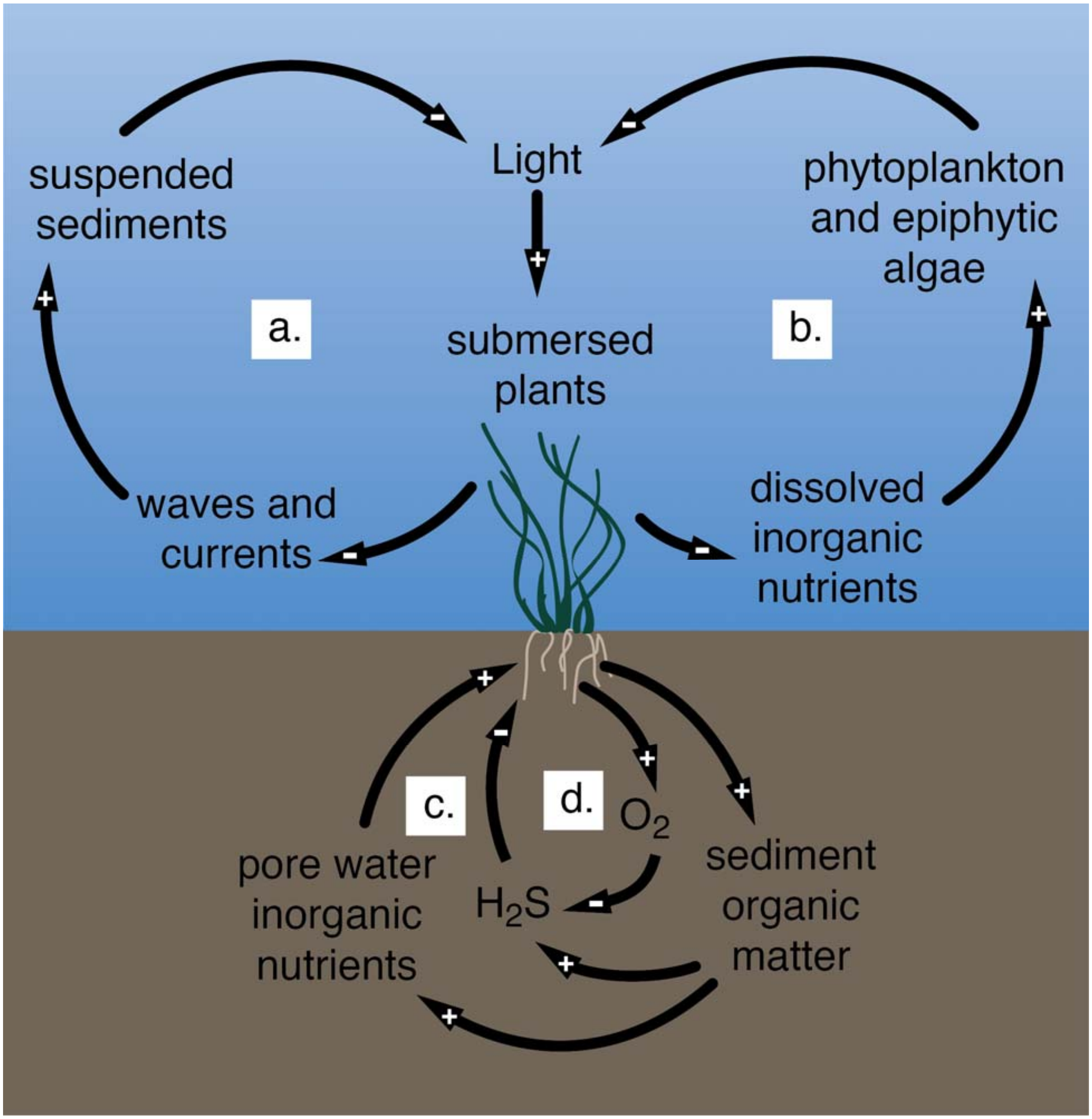

Figure 2. Sequences of regulatory interactions that drive positive feedback loops in SAV beds, including feedbacks between a) plants, hydrodynamics, suspended sediment concentration, and light, b) plants, dissolved inorganic nutrient concentration, algal growth, and light, c) plants, sediment organic matter, and sediment pore water nutrient concentration, and d) plants, oxygenation of the rhizosphere, and hydrogen sulfide concentration. Plus and minus signs indicate whether the relationship between linked elements is positive or negative.

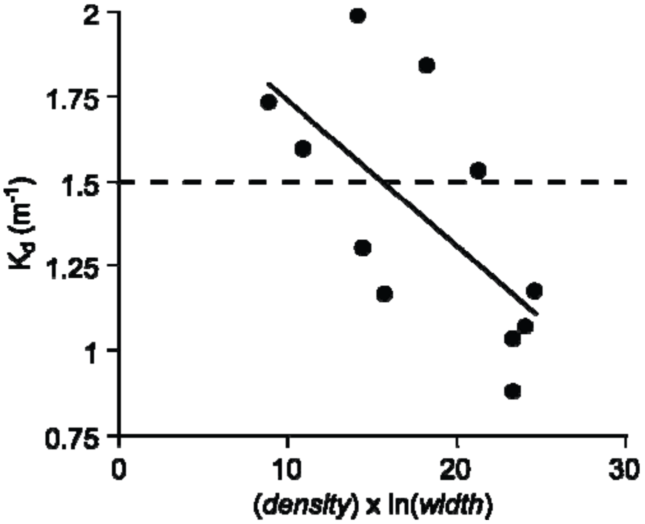

Figure 3. Negative relationship between the diffuse downwelling attenuation coefficient (K_d) and SAV bed size and density in the Choptank River. K_d represents light attenuation and is, thus, inversely related to water clarity. The dashed line indicates the maximum K_d threshold beyond which SAV cannot generally survive for an extended period of time. From Gruber et al. (2011).

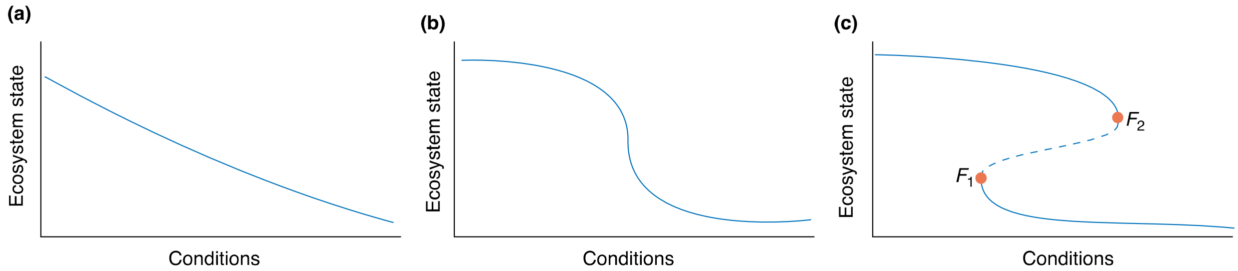

Figure 4. Possible relationships between environmental conditions and ecosystem state. The expected relationship is typically linear (a), whereby an ecological state variable responds proportionally to changing environmental conditions. However, the state variable can also rapidly shift after a threshold in conditions is passed (b). When feedbacks are sufficiently strong, the response curve folds over itself (c) because threshold for decline (F_2) is different from the threshold for recovery (F_1). In this situation, the system can exist within either of two "alternative stable states" under the same set of environmental conditions. From Scheffer and Carpenter (2003).

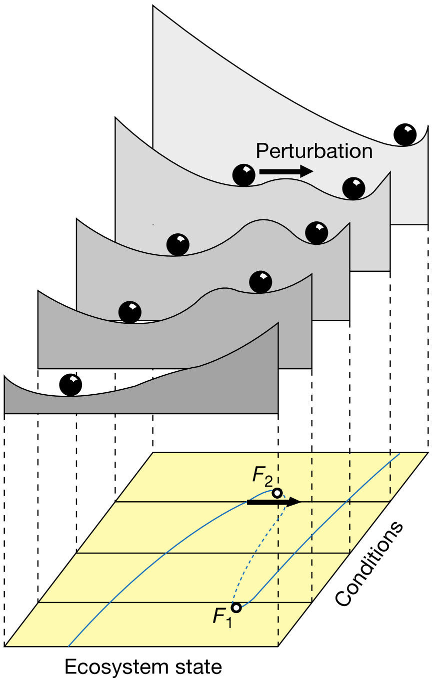

Figure 5. “Ball and cup” diagram illustrating changes in the shape of valleys, or “basins of attraction” as forcing conditions change. Decreases in basin width and steepness reflect decreased resilience of a particular system state. Scenarios containing two balls indicates that two potential ecosystem states, or “alternative stable states,” are possible for a given set of forcing conditions. From Scheffer and Carpenter (2001).

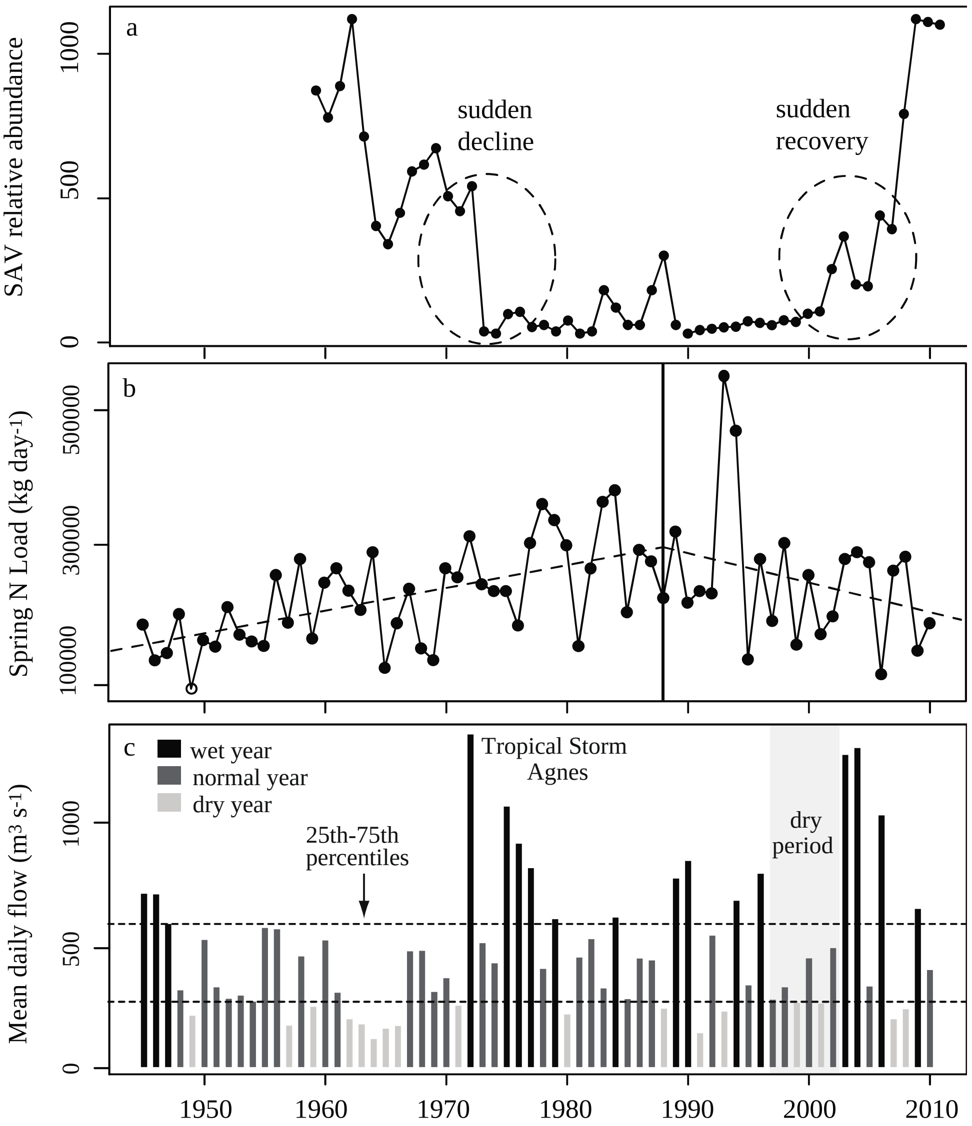

Figure 6. An abrupt SAV decline in upper Chesapeake Bay (a) coincided with long-term increases in nutrient loading (b) coupled with the largest flood event on record (Tropical Storm Agnes) (c). Meanwhile, the sudden recovery was associated with gradually decreasing nutrient loads and several consecutive dry years. These patterns support the idea that long-term changes in environmental stressors affect the resilience of a system, or its capacity to absorb a perturbation, whereas weather extremes tip the system into a new state. Adapted from Gurbisz and Kemp (2014).

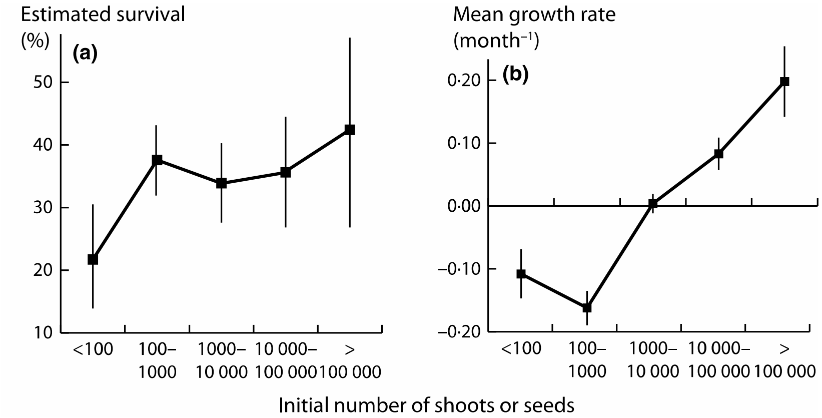

Figure 7. Relationship between initial SAV planting density and (a) survival rate and (b) log mean growth rate (log of the increase in number of shoots per month) calculated as part of a global meta-analysis of SAV restoration projects. The positive relationships suggest that feedbacks that arise in larger more dense initial plantings facilitate transplant success. From van Katwijk et al. (2016).

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THE ROLE OF GENETIC DIVERSITY AND CONNECTIVITY IN THE RESTORATION OF SUBMERSED AQUATIC VEGETATION BEDS

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ABSTRACT

Many key advances in the understanding of SAV biology since the publication of Technical Synthesis II have come from information generated by molecular genetic tools. Advances in molecular approaches have given scientists insights into deep evolution among SAV species as well as fine-scale variation in genetic diversity within and among SAV populations. This information has been increasingly applied to restoration science to assess whether, where or how to restore or conserve SAV species and populations. In this chapter we discuss how molecular data can be applied in restoration practice of SAV in the Chesapeake Bay. We synthesize publications of original population genetic data on SAV for measures of genetic diversity and gene flow at the species and population levels. We place data on genetic variation of SAV in the Chesapeake Bay within the context of genetic diversity of SAV worldwide. These insights serve as a baseline for conservation and restoration activities and identify knowledge gaps that are priorities for further research.

Three Restoration Decisions: Whether, Where, and How

If Captain John Smith traveled the Bay today, he would see vastly different ecosystems than he viewed in 1607. Most noticeable are degraded water quality, lower abundances of most native biota, and higher abundances of algae and introduced species. SAV is greatly reduced in habitat extent and bed sizes (Orth and Moore 1983), with few large and relatively persistent SAV patches, and most SAV surviving in relatively small and ephemeral patches (Lloyd et al. In press; Rybicki and Carter 2002). Sites supporting particular SAV species in the Chesapeake Bay may have always been patchily distributed due to species-specific limitations imposed by physiological tolerances to light (i.e., depth) and to salinity. In these situations, patch isolation may be less serious than it is for species that rely on large tracts of contiguous habitat. Even so, reduction in suitable and occupied habitat patches could affect overall network persistence (Hanski 1998), reducing or eliminating dispersal and recolonization, and thereby changing ecological and evolutionary processes (Fahrig 1997; Fahrig 2003; Fahrig and Merriam 1994; Merriam 1984).

To counter past losses and aid in ecosystem recovery, managers have sought to restore the acreage occupied by SAV. These efforts have included both indirect approaches through improving water quality and direct SAV plantings. Genetic data can significantly enhance the efficiency and effectiveness of these efforts by informing three main restoration decisions: whether, where, and how to restore SAV. In this chapter we discuss how genetic data can be used to inform these decisions and review what is known about genetic diversity of SAV species in the Chesapeake Bay specifically. These diversity levels are compared to genetic diversity levels reported for SAV species throughout the world.

Decision 1: Is active restoration necessary?

Active restoration involves creating or improving habitat, including introducing individuals of desired species to degraded sites. Such efforts are expensive (North et al. 2010) and failure rates are high (Duarte et al. 2015) especially when threats are not first ameliorated (van Katwijk et al. 2016). Thus, determining the need for active restoration is an important initial management decision.

In many cases, ameliorating stressors can increase regeneration to levels that meet restoration goals of increased habitat extent ('passive restoration'; Holl and Aide 2011). Improved water quality in the Chesapeake Bay has allowed recovery of SAV relative to the lowest points of abundance in the 1970's (Orth and Moore 1984). Increases of >20% coverage of SAV in most of the Bay between 2014 and 2015 (http://web.vims.edu/bio/sav/sav15/exec_summary.html) are testament to the potential for recovery with improved water clarity and lower nutrient loads. Even with observed increases, abundances and extent of SAV remain below overall targeted levels and increases in extent of the foundational species *Zostera marina* and *Vallisneria americana* that form extensive monospecific stands remain moderate (http://web.vims.edu/bio/sav/sav15/exec_summary.html), suggesting that active restoration may indeed be necessary.

The magnitude and duration of past declines generated concern that remaining SAV populations in the Chesapeake Bay may not have the genetic diversity necessary to yield high levels of fitness under current conditions or to allow acclimation or adaptation to long-term environmental changes (Chust et al. 2013; Engelhardt et al. 2014). Low fitness in populations that have been reduced in size can result from increased inbreeding. Such populations may not have the capacity for sufficient reproduction to respond demographically to recover after disturbance. Further, reduced connectivity among remaining SAV patches may preclude dispersal and gene flow among populations or to unoccupied habitat. In such situations, active restoration may be required to counteract ongoing stressors; to return species to desired abundances that are self-sustaining (Ferreira et al. 2015; Gross and Vary 2014); to improve fitness by alleviating inbreeding depression (Weeks et al. 2011); or to increase diversity to enhance potential for long-term acclimation and adaptation to novel conditions.

Even if genetic diversity is not a management target, genetic data can provide insights into population processes that otherwise are not available. Some of the most exciting insights coming from genetic studies are related to dispersal ability of species (e.g., Kendrick et al. In Press). Using genetic data to identify the source of propagules we can begin to gain insight into potential for natural recolonization. Used in concert with transport models (e.g., Jahnke et al. 2016), genetic data are drastically increasing the perceived scale of SAV dispersal.

Thus, decisions regarding the need for active restoration are best made including population-level assessments of amounts of genetic variation and levels of inbreeding, as well as among-population assessments of connectivity that give insight into recolonization potential. Active restoration may be necessary if genetic assessments indicate local populations have very low genetic diversity due to past bottlenecks, are highly inbred, or are isolated beyond regular dispersal distances.

Decision 2: Where should restoration sites be located?

If active restoration is deemed necessary, the next decision is where within the range of unoccupied habitat to place restoration sites for maximum benefit. Choices for bed placement include 1) planting adjacent to existing beds to increase their area and population size; 2) planting far from existing beds to increase the range of a species; or 3) planting in locations that would provide stepping stone connections between patches that are otherwise too far from one another for regular dispersal.

The choice of placement requires information on existing levels of diversity within populations and connectivity among SAV beds as discussed above, but goes beyond that basic information to include quantifying how connectivity could be increased by any particular placement of a restored SAV bed. Information on long-term spatial patterns of SAV beds is essential for setting goals for desirable levels of connectivity. For example, if there is little evidence of long-term connectivity between regions of the Bay, effort would be better spent increasing the size and connectedness of populations within each region rather than increasing connections between regions. By contrast, if there is evidence of a recent decrease in long-term connectivity, reestablishing those connections can be an effective means of building resilience into restoration plans. Such an analysis requires integrating information on the spatial distribution of SAV beds and genetic data on relatedness and dispersal.

Decision 3: Where should restoration material come from?

Two contradictory paradigms for selecting restoration source materials are often portrayed in the literature (Figure 1). Proponents of one extreme argue for maintaining purity of local genetic stock by using propagules collected in close proximity to a restoration site. The rationale is that local stock that is adapted to environmental conditions will flourish with no risk of outbreeding depression (Lesica and Allendorf 1999; McKay et al. 2005; Montalvo and Ellstrand 2000; Montalvo and Ellstrand 2001a). Risk of failure can be high, however, when source populations are small, have been isolated and drastically reduced in size, or have low diversity or low fitness due to inbreeding depression (Broadhurst et al. 2004; Weeks et al. 2011).

The alternative is to increase genetic diversity and counteract local inbreeding by introducing genotypes from a foreign population or mixing genotypes from multiple populations (Broadhurst et al. 2008; Fenster and Dudash 1994; Hughes et al. 2008; Lesica and Allendorf 1999; Weeks et al. 2011). Immediate negative consequences of such plantings arise if phenotypes are poorly adapted to local conditions and cannot survive and establish. Long-term consequences arise if fitness of offspring between local and foreign stock is low. Advocates of mixing propagules argue that benefits of increased diversity and reduction in inbreeding outweigh potential negative consequences of outbreeding depression (Broadhurst et al. 2008) and that risks of outbreeding depression are overstated and unsubstantiated (Frankham et al. 2011; Weeks et al. 2011).

Managed relocation, an extreme form of non-local planting, is emerging as a controversial approach to biodiversity management in the face of climate change (Schwartz et al. 2012). Managed relocation involves intentional movement of individuals from occupied areas to distant, unoccupied locations where probability of future persistence is predicted to be higher (Richardson et al. 2009). Greater understanding of the feasibility of and the risks associated with this approach is critical. Short-term negative consequences may arise if relocated individuals are poorly adapted to a new location and are not able to establish populations. Long-term negative consequences may manifest if offspring from matings between local and foreign individuals have low fitness due to outbreeding depression (Montalvo and Ellstrand 2001b). Understanding adaptive potential within and differentiation among rivers and estuaries along the Atlantic Coast of North America is necessary to evaluate the potential for local adaptation that would indicate benefits versus risks resulting from managed relocation. Of critical concern is the effect of different day lengths on photoperiodism and duration of dormancy across latitudes.

The alternative strategies discussed above form a continuum of choices regarding the spatial scale of genetic stock selection relative to target planting locations (Figure 1). There are scientific arguments for and against all points on the continuum. Ultimately choices will be normative based on the degree of risk tolerance for potential detrimental effects of genetic pollution on the one hand, versus low genotypic and allelic diversity and inbreeding on the other. Those normative choices should be made with the best estimate of the potential for each type of benefit versus risk to manifest based on the standing genetic diversity in a system and experimental evidence of performance of restoration stock.

If populations are low in genetic diversity and are highly inbred, bringing in new genetic material or combining propagules from multiple populations could be justified. Evidence of differentiation among populations from different geographic regions or ecological regions could indicate local adaptation, especially when combined with evidence of fitness consequences of crossing individuals from different regions. Where genetic diversity is high and there is no sign of inbreeding, there is no imperative for combining genetic stock from different locations and the risks associated with genetic pollution may be too high.

The clonal nature of SAV species raises a second question regarding restoration stock beyond choosing donor sites: whether to use seed or vegetative propagules for restoration. The benefit of vegetative material is higher survival of plantings. The drawback is low genetic diversity due to small numbers of propagules (Williams 2001; Williams and Davis 1996) and the potential that the propagules chosen are different shoots of the same clone. Seeds potentially overcome risks of low diversity if they are sampled from many unrelated mothers, but can have low success rates due to low germination or high seedling mortality. Some practitioners have opted to grow plants from seed and plant the resulting seedlings into the Bay. Others argue that for plantings of a scale that had potential for success (e.g., van Katwijk et al. 2016), seeds are the most feasible propagules (Orth et al. 2012).

The Genetic Measurements

Data on within-population genetic diversity, inbreeding, and gene flow can contribute to answering all of the restoration questions above. Here we briefly describe key measurements of interest and highlight their contribution to answering questions related to restoration.

Genetic markers

Measures of population genetic diversity describe how different forms of genes (called alleles) are organized in individuals, populations, and species. Individuals with two copies of the same allele for a gene (aka a locus) are homozygous whereas those with different alleles are heterozygous. Multiple techniques (termed markers) have been used to quantify genetic diversity in SAV (Figure 2a). Techniques that detect both allele copies (e.g., allozymes, microsatellites, and single nucleotide polymorphisms (SNPS)) allow identification of heterozygotes and are called codominant. Other techniques quantify only presence of a particular region of DNA which is the dominant state (randomly amplified polymorphic DNAs (RAPDs), amplified fragment length polymorphisms (AFLPs), and intersimple sequence repeats (ISSRs)) and are much more limited in their utility. Further, markers vary in the amount of variation they detect. For example, allozymes have the benefit of being codominant, but they underestimate levels of variation. Microsatellites on the other hand are short stretches of highly repetitive DNA that mutate frequently and thus can have large numbers of alleles at each locus. SNPs are most often point mutations in DNA. At any particular SNP site typically two alleles are possible. Even though variation at individual SNP loci is biallelic, this marker type is powerful in identifying variation in populations when many loci are used. Because allozymes have low ability to detect variation and SNPs have not yet been used on many species, we focus primarily on microsatellites in this chapter. However, because allozymes have been used to describe genetic diversity in *Zostera marina* in the Chesapeake, we briefly summarize what allozymes tell us about genetic diversity in this species.

Genetic diversity measures

A basic measure of diversity is the number of alleles found at each locus (*A*). The frequencies of alleles at individual loci can be summarized at the population and species levels. When samples are each measured at multiple loci, the combination of alleles present can indicate which samples are different individuals and which are replicate shoots of the same individual. The number of alleles (Reynolds et al. 2012a) and genotypes (Hughes and Lotterhos 2014; Hughes and Stachowicz 2004; Hughes and Stachowicz 2009) are known to play a role in population resilience to disturbance. The proportion of samples (*N*) that are unique genotypes (*G*) is calculated as (*G*-1)/(*N*-1). Subtracting 1 from both the numerator and denominator yields an index that ranges from 0 (all samples are the same genotype) and 1 (all samples are different genotypes). The spatial extent of individual genotypes is calculated using the location of identical samples to identify the maximum or mean linear or areal extent of individual genotypes in the whole study and within individual subpopulations. The area of influence for clones can also be quantified by comparing the spatial autocorrelation of all sampled individuals with the autocorrelation of only unique genotypes (Arnaud-Haond et al. 2007). The distance at which these two spatial autocorrelations overlap is the distance at which clones no longer influence the distribution of the genetic diversity (Alberto et al. 2005). These distances are important for determining the spatial scale of propagule collection needed to yield a genetically diverse sample.

Beyond knowing how many alleles and individuals are present, it is important to know how alleles are distributed within and among individuals. Of particular interest is the number of loci that are observed in a heterozygous (H_o) versus homozygous state. Individuals with low observed heterozygosity tend to have low individual fitness (Dudash 1990; Fenster and Dudash 1994). The expected proportion of heterozygotes (H_e) versus homozygotes for given allele frequencies is predicted by Hardy-Weinberg Equilibrium. Deviations in observed versus expected proportions indicate non-random mating. When summarized across individuals, these deviations can indicate inbreeding, genetic drift (the random loss of alleles that is common in small populations), natural selection, or gene flow. Many of the statistical tests used on genetic data determine which of these evolutionary forces is causing the deviation.

Thus, although there are many sophisticated tests applied to genetic data, they all boil down to quantifying how alleles are distributed within and among individuals or populations through space and time. Documenting how, when and where the distribution deviates from Hardy-Weinberg expectations provides insight into the evolutionary forces that have caused the deviation and therefore into the demographic history of populations. Most basically, deviations from random mating of individuals within populations is measured by the statistic F_{IS}. Positive values that are significantly different from 0 indicate heterozygote deficit (i.e., more mating among close relatives than is expected). Significant negative values indicate heterozygote excess. Although we summarize the mean and range of F_{IS} values for species, these summaries can hide key information. To assess the degree to which apparent inbreeding in populations could pose a risk, we tallied the proportion of sampled populations within species that had a significant positive F_{IS}.

Gene flow measures

Connectivity is facilitated by pollen, seed, and vegetative propagule movements among SAV beds, but these dispersal events are difficult to measure directly in nature. Further, direct observations of dispersal are biased towards short-distance dispersal events.

F_{ST} is the classic measure of genetic deviation from random mating in a population relative to all populations combined. It provides information on gene flow versus isolation and, under certain circumstances, can indicate selection in different environments. A number of analogues have been developed to correct for bias that arises when samples are small (e.g. θ; Weir 2012) and when allelic diversity is extremely high (e.g., G_{ST}', G_{ST}''; Hedrick 2005). D_{EST} developed by Jost (2008) provides a true measure of differentiation but is implemented in only a few studies of SAV. F_{ST} and analogues can be calculated for an entire set of samples (termed global F_{ST}) or for all pairs of populations (termed pairwise F_{ST}).

Data on genetic similarity among publications offer information on gene flow among populations, such as when seeds disperse long distances and establish as plants elsewhere (Pineda et al. 2007). Dispersal is often more limited in coastal systems than in terrestrial systems (Kendrick et al. 2012) such that gene flow may be low. This is manifested in high differentiation (high F_{ST}) and low migration among populations.

A large number of approaches are used to identify spatial patterns of gene flow. One of the most basic approaches is to use a Mantel test to assess whether a linear relationship exists between pairwise values of F_{ST} (typically F_{ST} /(1- F_{ST})) and pairwise geographic distances among populations. If a strong correlation exists, populations may be isolated by distance through limited dispersal distances. However, because the result of this test is simply the rate of decline over space, no detailed information is given regarding the area surrounding a planting site that would represent an appropriate gene pool for restoration.

A vast array of statistical techniques provide more comprehensive means of identifying sets of populations that are interacting through gene flow. We present results based on three such techniques that have been used on genetic data for SAV in the Chesapeake Bay. The programs Structure and Structurama (Pritchard et al. 2000) allow the genetic data to demonstrate the most likely location of breaks in gene flow among sampled locations. Individuals are assigned to groups with no reference to their origin such that deviation from Hardy-Weinberg Equilibrium is minimized. As such, individuals within groups can be interpreted as being more similar genetically than they are to individuals in other groups. The assigned groups may or may not coincide with individual sampling locations. Using Bayesian or maximum likelihood approaches and coalescent theory, the program Migrate (Beerli and Felsenstein 2001) estimates directional migration between pairs of populations. These migration rates integrate migration over time and thus confound past versus ongoing, recent migration. By contrast to Structure and Migrate that integrate over deep and shallow time, the program BayesAss (Wilson and Rannala 2003) estimates recent (<4 generations) migration rates among populations. The probabilities of each individual being an immigrant from a specific population, the offspring of an immigrant, or a non-immigrant are calculated.

A Baseline for Genetic Diversity and Gene Flow in Chesapeake Bay SAV

Our search for publications on genetic diversity in SAV yielded 154 publications providing data using 9 types of genetic markers (Figure 2a) for 38 species that occupy haline, brackish, and freshwater habitats worldwide (Figure 2b). Sixty publications provided data for 12 of the 25 species that grow in the Chesapeake Bay (Table 1). We synthesize publications that represent all data collected for natural populations sampled from the Chesapeake Bay (Table 1) for two species: *Zostera marina* (n=4; Williams and Orth 1998, Rhode and Duffy 2004, Campanella et al. 2010a, Reynolds et al. 2013) and *Vallisneria americana* (n=1; Lloyd et al. 2011). Data from restored populations are presented in one paper for *Vallisneria* (Lloyd et al. 2012). The same data for restored *Zostera* populations are presented in two papers (Reynolds 2012a, Reynolds et al. 2013). Data for natural and restored populations within papers are separated into "studies" to allow us to compare natural populations across paper. We examine the studies in detail below and place them within a context of natural variability observed worldwide. Because *Z. marina* is so well studied, we were able to compare genetic diversity of natural populations in the Chesapeake Bay to 42 studies of the same species. By contrast, few genetic data were available for *V. americana*. Thus, we compare levels of diversity in Chesapeake Bay *V. americana* populations to microsatellite-based diversity in all other SAV species.

Zostera marina

Forty-six studies of natural populations report genetic diversity of *Zostera marina* (Table 2) growing worldwide in brackish and haline portions of estuaries, sheltered bays, coastal lagoons and exposed shores. Fourteen additional studies focused on four other *Zostera* species including *Z. japonica* (n=3), *Z. muelleri* (n=1), *Z. noltii* (n=8), and *Z. pacifica* (n=2). Six marker types have been used to quantify genetic diversity in *Zostera* species including microsatellites (n=48), allozymes (n=10), RAPDs (n=1), SNPs (n=1), AFLPs (n=1) and RFLPs (n=1).

Of the four studies that report genetic data for *Z. marina* in the Chesapeake Bay region, two use allozymes (Rhode and Duffy 2004; Williams and Orth 1998) and two use microsatellites (Campanella et al. 2010a; Reynolds et al. 2012a; 2013). In 1994, Williams and Orth (1998) sampled five natural *Z. marina* populations in the Chesapeake Bay and 1 natural population in nearby Chincoteague Bay to develop baseline population data for assessing restoration efforts. Four years later in 1998, Rhode and Duffy (2004) sampled 12 natural populations within the Chesapeake Bay to examine how bed age and size contribute to variation in genetic diversity. A decade later in 2008, Campanella et al. (2010a; 2010b) broadly sampled *V. americana* populations along the Atlantic Coast including 20 individuals from a single population located at the mouth of the York River in the Chesapeake Bay. Also in 2008 and 2009, Reynolds et al. (2013; 2012b) analyzed samples from 12 natural populations distributed across haline portions of the Chesapeake Bay (n=9), Virginia coastal bays (n=2) and Chincoteague Bay (n=1) to serve as a baseline for assessing eelgrass restoration by seed. Across the 4 studies of natural *Z. marina* populations, a total of 30 natural populations in the Chesapeake Bay were sampled (n=366), with some sites sampled multiple times (e.g., Allen's Island). These were counted as separate populations in time. In addition, 2 natural populations were sampled each in the adjacent Virginia coastal bays (n=89), and in Chincoteague Bay (n=133).

Genetic diversity. Based on microsatellites, *Z. marina* of the Chesapeake Bay is high in alleles per locus compared to many populations throughout the world (Table 2, Figure 3). The other *Z. marina* populations that are as high in allelic diversity occur in the Wadden Sea and the Baltic Sea in Northern Europe (Table 2). All samples collected at ≥ 3 m sampling intervals by Reynolds et al. (2013; 2012b) were distinct genotypes, which is also high compared to other populations (Figure 3).

Likewise, 17 of the 20 samples collected ≥ 5m apart and analyzed by Campanella et al. (2010a; 2010b) were unique clones. Neither inbreeding nor bottlenecks were detected in populations. By comparison, Campanella et al. (2010a; 2010b) observed population bottlenecks in a population from Long Island and 5 populations from Barnagat Bay, New Jersey.

Results based on microsatellites contrast sharply with the early indications from allozymes that genetic diversity was low within the Chesapeake Bay (Rhode and Duffy 2004; Williams and Orth 1998). In those studies Williams and Orth (1998) identified only 68 genotypes out of 510 samples. Rhode and Duffy (2004) detected 109 genotypes out of 1199 samples, with 40 genotypes shared among more than one bed. Examination of percent polymorphic loci, allelic richness and genotypic richness showed that genetic diversity varied considerably among the 12 sampled beds (Rhode and Duffy 2004), with high inbreeding across all beds although old and small beds were on average less so.

Because allozymes underestimate diversity, we use the more recent microsatellites as the baseline for conservation and restoration activities. Based on microsatellites, *Z. marina* populations in the Chesapeake Bay are some of the most genetically diverse populations in the world despite having undergone major population declines in the past (Williams and Orth 1998). As such, there is no evidence of an urgent need to augment the natural genetic diversity that exists in *Z. marina* populations of the Chesapeake Bay.

Gene flow. Based on pairwise F_{ST} values from microsatellites, most natural Chesapeake Bay populations of *Z. marina* appeared to be relatively similar to one another ($F_{ST} < 0.1$; Reynolds et al. 2013). The low diversity Allens Island site was an exception and showed greater differences from other Chesapeake Bay sites. Another low diversity site at South South Bay in the Virginia coastal bays also had high F_{ST}, and in fact was the most distinct of all sampled locations. Slight isolation by distance was observed when all sampling populations from Woods Hole, Massachusetts to North Carolina were included in the analysis.

Structure analysis indicates that Chesapeake Bay populations were moderately distinct from Virginia coastal bay populations but that all the coastal populations from New York and Massachusetts south to North Carolina shared similarities that were inferred to reflect north-to-south gene flow (Reynolds et al. 2013). The Virginia coastal bay populations shared similarities with populations as far north as Woods Hole, Massachusetts (Reynolds et al. 2013). Likewise, Campanella et al. (2010a) showed that gene flow of a Chesapeake Bay population with other sites along the Atlantic coasts was high indicating that the Chesapeake Bay is highly connected with other coastal regions. These patterns suggest that *Z. marina* have at least historically dispersed enough over distances of 100's of kilometers to maintain population genetic diversity. Assignment tests using the program BayesAss (Rannala and Mountain 1997) indicate more localized recent migration from Chincoteague Bay into a natural population of Hog Island within Virginia coastal bays and from a variety of populations into Phillip's Island in North Carolina, and Brown's Bay and Pepper Creek in the Chesapeake Bay (Reynolds et al. 2013). Interestingly, the program indicates gene migration from restored populations into these donor populations rather than vice versa. Although migration events were documented, the relatively low diversity of three naturally recolonized sites in or at the southern end of the Virginia coastal bays indicated that gene flow might not be sufficient to restore genetically diverse populations of *Z. marina* (Reynolds et al. 2013).

An allozyme study using 13 loci (Williams and Orth 1998) observed higher F_{ST} among natural *Z. marina* populations within both the Chesapeake and Chincoteague Bays. Based on those patterns the authors suggested that gene flow among *Z. marina* populations was restricted that restoration decisions may need to take local variation into account. The conflicting results between the microsatellite and the allozyme studies are likely due to the higher resolution microsatellites. Based on the more recent microsatellite studies, dispersal is not limited within the Chesapeake Bay.

Vallisneria americana

Four publications reported genetic diversity of *V. americana*, an SAV species that occurs in freshwater to oligohaline portions of estuaries and dominates these areas in the Chesapeake Bay. Two of the studies using microsatellites focused on the Chesapeake Bay (Lloyd et al. 2011; Lloyd et al. 2012) and the other two used allozymes to characterize diversity within the Detroit River (Lokker et al. 1994) and around islands of western Lake Erie (Laushman 1993). Two additional studies focused on other species of *Vallisneria* in the middle reaches of the Yangtze River in China (Chen et al. 2007; Wang et al. 2010). The Chesapeake Bay studies were the only ones conducted within the tidal influence of an estuary. Three marker types were used to quantify genetic diversity in the genus *Vallisneria* including ISSRs (n=1), allozymes (n=3), and microsatellites (n=2) and representing 4,238 genotyped samples, 823 of which originated from the Chesapeake Bay. *Vallisneria americana* in the Chesapeake Bay cannot be compared to other *Vallisneria* studies (Table 3) because the other studies used different markers. To provide a general context for levels of genetic diversity, we compare microsatellites from *V. americana* with micr**os**atellite data from all other SAV species. Because the natural populations in Lloyd et al. (2012) were a subset of the populations included in Lloyd et al. (2011), we use only the 2011 data for comparison with other species.

Genetic diversity. Lloyd et al. (2011; Lloyd et al. 2012) sampled 26 natural *V. americana* populations in the Chesapeake Bay in 2007, 2008, and 2010 to provide a baseline for genetic diversity. Although genetic diversity was moderately high in the Chesapeake Bay as a whole, population-level genetic diversity was low compared to other SAV species (Figure 4). It was also low compared to *Z. marina* in the Chesapeake Bay (Figures 2 and 3). Specifically, the numbers of alleles per locus at the species and population levels (Table 3) were moderate to low compared to other species (Figure 4). Genotypic diversity within populations based on shoots that were collected 5 to 10 m apart varied from 0 (1 population) to 1 (2 populations) with a median genotypic richness of 0.68. Genotypic richness was less than 0.5 for 10 of 26 sampled sites. Sites with the lowest genotypic richness tended to be in the Potomac River, especially in the non-tidal reaches. The single sample site from the Mattaponi River also had few genotypes.

Low genotypic diversity is of concern because *V. americana* is dioecious and thus sexual reproduction is precluded when only one genotype and therefore one sex is present at a site. Sexual reproduction can be compromised in sites with few genotypes due to low probability of having both male and female plants and for flowering of both sexes to occur (Engelhardt et al. 2014). This degree of clonal extent contrasts with *Z. marina* in the Chesapeake Bay for which almost all individuals sampled at 3 m intervals were unique. It also contrasts with Wang et al. (2010) who found that almost all individuals of *V. natans* and *V. spiralis* sampled were different genotypes (Table 3). Of particular note were five genotypes that were shared among sites within the upper Potomac River. Two of these genotypes dominated multiple sites where they represented 53-100% of sampled shoots. Those two genotypes spanned large geographic distances covering ~160 river km 132 river km respectively. No genotypes were shared among sites within the estuarine portion of the Chesapeake Bay. No information on the spatial extent of clones within populations in the Bay has been published.

Most populations showed no signs of inbreeding. However, significant positive F_{IS} values in three populations in the tidal Potomac River indicated observed heterozygosity was lower than expected and thus there was non-random mating within these populations (Table 3). This level of non-random mating is in contrast again to *Z. marina* in the Chesapeake Bay, which showed no inbreeding based on microsatellites (Reynolds et al. 2013; Reynolds et al. 2012b). Overall, inbreeding is of minor concern because the mean F_{IS} values for *V. americana* is near mean values for all SAV species and the proportion of populations with significant F_{IS} is comparatively low (Figure 4). Further investigation is needed to determine if the source of significant F_{IS} in the tidal Potomac is due to inbreeding or to a Wahlund effect from the mixing of gene pools.

Gene flow. Overall F_{ST} (measured as θ) was moderate ($\theta = 0.114$). Pairwise θ values among all sampled populations showed the classic pattern of isolation by distance (both straight line and distance over water). Results from the program Structure also indicate potential for isolation by environment, in particular salinity. Identification of three primary genetic regions of *V. americana* that coincide with the North Bay, the Central Bay and the Potomac River (Lloyd et al. 2011) indicate dispersal limitation among these regions. A weaker but still obvious break in gene flow was evident between the tidal and non-tidal portions of the Potomac. The breaks in gene flow coincide with differences in salinity and tidal influence, but the spatial resolution of sampling was not sufficient to investigate the strength of these relationships. Pairwise θ values among sites within each of the three estuarine regions were 0.02-0.04. The median θ value among the three regions was 0.114. Isolation by distance was observed within the Potomac River region but not within the others. The low θ values and the general lack of isolation by distance indicate either extensive ongoing gene flow within the North Bay and Central Bay, or lack of genetic drift from historic conditions.

Results from the program Migrate indicated symmetrical gene flow between the tidal Potomac and the Central Bay regions and asymmetrical gene flow from both the Potomac and the Central Bay into the Northern Bay. The Migrate results are counter-intuitive in that downstream gene flow is expected. Migrate results also must be interpreted with caution because they integrate deep and recent time. The apparent gene flow may reflect shared diversity that remains from past connections. To date, assignment tests have not been used to quantify recent migration. Thus, much remains to be learned about dispersal and gene flow in *V. americana*.

Genetics and Restoration of Chesapeake Bay SAV

Of the six studies that reported baseline genetic data for Chesapeake Bay, four used genetic data to assess restoration efforts (Lloyd et al. 2012; 2013; Reynolds et al. 2012b; Williams and Orth 1998). Two papers used seeds and plants collected from the Chesapeake Bay to examine the effect of genetic diversity on ecosystem functioning and services in *Z. marina* (Reynolds et al. 2012a) and *V. americana* (Engelhardt et al. 2014). One additional paper (Marsden et al. 2013) provided information on the impact of crossing *V. americana* from the same and different genetic regions to determine the consequences on inbreeding and outbreeding on plant fitness.

Zostera marina restoration

Williams and Orth (1998) compared three restored *Z. marina* beds (Burton Point, Mumfort Island, and Gloucester Point) to compare baseline genetic data collected in five natural beds. Restoration efforts were initiated in the early 1980s using bundles of plants and seeds collected from donor beds in the lower York River, particularly Allen's Island. Allozyme analysis suggested that restored sites were not lower in genetic diversity than natural beds and that restored beds were similar to donor beds. Future restoration efforts were therefore encouraged to use multiple donor sites to conserve the natural genetic diversity of *Z. marina* in the Chesapeake Bay (Williams and Orth 1998).

Similarly, Reynolds et al. (2013; 2012b) used microsatellites to compare 5 restored *Z. marina* beds in the Virginia coastal bays to baseline data of 12 and 18 natural populations, respectively. They showed that restoration efforts using seeds can successfully restore areal coverage while also maintaining allelic diversity (Reynolds et al. 2012b). Four naturally recruited meadows, on the other hand were less diverse and showed signs of genetic drift (Reynolds et al. 2013). Although restoration efforts maintained levels of allelic richness observed in donor populations, the composition reflected a blend of donor populations which was reflected in their assignment to different groups in a Structure analysis (Reynolds et al. 2013; Reynolds et al. 2012b). The authors concluded that there was no outbreeding depression due to moving Chesapeake Bay individuals to the Virginia coastal bays. However the results were inconclusive on this point because sampling for genetic analysis was done within three years of planting and thus likely measured the original planted stock and recruits from the Chincoteague population rather than offspring of crosses between individuals from the two areas. Even if some of the samples were F1 progeny, outbreeding depression typically emerges in the F2 generation and beyond (Fenster and Dudash 1994). Further investigation is needed to assess whether crosses are occurring and whether those crosses have lower or higher fitness than the original stock.

In a field experiment Reynolds et al. (2012a) showed that allelic diversity that was related to higher density positively affected ecological performance (invertebrate density, nitrogen retention, and areal productivity). Offspring from a Virginia coastal bays donor population performed better than seeds transplanted into Virginia coastal bays from Chesapeake Bay populations (Reynolds et al. 2012b), suggesting a possible home site advantage that was not identified by the authors. Success of maintaining high levels of genetic diversity in restoration plantings is attributed to high levels of genetic diversity in donor beds, collection of seeds across a broad area, and the introduction of an adequate number of seeds (Reynolds et al. 2012b). Active restoration of the Virginia coastal bays with Chesapeake Bay stock has resulted in homogenization of the gene pools as evidenced by having some individuals that cluster with Chincoteague and others that cluster with the Chesapeake (Reynolds et al. 2012b).

V. americana restoration

Lloyd et al. (2012) compared 8 restored *V. americana* populations to 8 paired natural sites and four source repositories. Restored sites had been planted using a variety of methods and sources and had been in place for only a few weeks to 22 years. Natural and restored sites did not differ in average genetic diversity measures. However, in 5 of 8 paired comparisons, restored populations had lower clonal richness. Differences between repositories and natural populations also were not significant even though only 43% of sampled repository shoots were unique individuals. One repository from which only 4 plants were sampled had a single clone. Further, natural and restored sites did not differ in number of alleles, but restoration stock repositories supported fewer alleles than either natural or restored sites even after rarefaction to equalize sample sizes.

The only significant heterozygote deficits were found in three restored sites, whereas two natural and two restored sites had evidence of heterozygote excess. The apparent deficits could indicate inbreeding in these restored sites or they could indicate a Wahlund effect arising from planting unrelated plants from multiple sources together. An observed decline in F_{IS} with planting age is consistent with either differential survival of heterozygotes, sexual reproduction between members of divergent gene pools, of differential mortality of individuals from different gene pools over time. One natural site, one restored site, and two repositories showed evidence of population bottlenecks.

Perhaps most importantly, restored populations altered genetic composition relative to natural populations (Lloyd et al. 2012). In three cases, restored populations had a subset of the variation in the paired natural population. In four cases, the restored and natural pairs had different composition, where the restored population overlapped only a small amount with the full complement of diversity in the paired natural population. In only one case was the natural population entirely a subset of the restored population, suggestion natural recruitment in combination with restoration.

Engelhardt et al. (2014) observed genotypically based and population-based variation in growth characteristics that could affect ecosystem functioning (sensu Bolnick et al. 2003) and thus potential for acclimation and adaptation. Specifically, genotypes differed in mean values (i.e., niche optima) for phenotypic traits that affect persistence: vegetative expansion, sunlight capture, as well as timing and frequency of production of flowers and overwintering structures called turions (Engelhardt et al. 2014). Heterozygosity affected individual performance in terms of turion weight and leaf area, which affect reproduction and sunlight capture. Coefficients of variation across genotypes showed that populations differed in opportunities for selection, suggesting that populations, through their genetic diversity and phenotypic traits, may differ in their resilience to external environmental drivers.

Controlled reproductive crosses among genotypes that came from within the same versus from different genetic regions in the Chesapeake Bay indicate no strong effects of inbreeding *vs* outbreeding depression. Rather, consequences of local *vs* foreign crosses varied by population and mother (Marsden et al. 2013).

Implications for Future Chesapeake Bay Restoration Decisions

Annual distributional data from the Virginia Institute of Marine Science (VIMS), show that SAV in the CB has recovered substantially (Orth et al. 2015) from the minimum distributions observed in the 1970's (Orth et al. 2010) commensurate with improvements in water quality and extensive restoration. Despite these efforts, annual areal extent has fluctuated around 30,000 ha since the early 1990's (Orth et al. 2010), often falling far below 2010 target values (U.S. Environmental Protection Agency 2010). The total area of all SAV occupied in the Bay from 1984-2010 was 360% of the area occupied within individual years (Lloyd et al. In press). This result could indicate that marginal water quality is resulting in high turnover of patches as light conditions alternate between suitable and unsuitable in otherwise suitable habitat. Large increases in areal extent of SAV between 2014 and 2015 give hope that continued improvement of water quality will increase natural expansion of beds and resilience to future perturbation. Still, restoration of SAV continues to be a major management focus to further expand distribution and abundance and to mitigate losses. Here we synthesize what genetic data indicate for determining whether active restoration is necessary, and, if so, where and how to restore to increase SAV sustainability within the Chesapeake Bay.

Decision 1: Is restoration necessary?

Deciding whether or not active intervention is necessary requires determining whether or not 1) genetic diversity is low in existing populations, 2) existing populations and unoccupied habitat are isolated by limited dispersal such that natural recolonization is precluded, and 3) recovery rates and ecosystem functioning could be enhanced by intentionally introducing genetic diversity to restoration sites.

Despite rapid accumulation of data for SAV worldwide (Figure 2), most SAV species in the Chesapeake Bay have no genetic information (Table 1). The two keystone species with genetic data –*V. americana* and *Z. marina*– have moderate to extremely high genetic diversity, respectively, at the level of the whole Chesapeake Bay and within most populations. Most estimates of *Z. marina* genetic diversity in the Bay are among the highest diversity levels for the species in the world (Figure 3). Evidence of extensive inbreeding or bottlenecks is also low and is only found in one population of *Z. marina* and three of *V. americana*. Thus, widespread active restoration for genetic rescue is not necessary. However, some *V. americana* locations sampled in 2007-2009 had low to no genotypic variation. Full assessment of the need for genetic enhancement requires knowing the number and proximity of other patches around the sampled locations and levels of genetic diversity in those patches. If low diversity patches are isolated by long distances, supplementation could be warranted. If, rather they are in proximity of more diverse patches, there would be little justification for manipulation.

Knowledge of distances over which regular dispersal can maintain gene flow among patches and facilitate colonization of unoccupied habitat remains incomplete. Molecular techniques have provided an unparalleled means of understanding gene flow in SAV (as reivewed in Procaccini et al. 2007; Reusch 2001b) through evaluating the extent of interpatch movement of seeds and vegetative propagules. These genetic estimates are vast improvements over estimates dispersal based on observations of propagules that are known to be biased towards short distances. Conceptual models of SAV dispersal (Kendrick et al. 2012) have suggested that meadows form primarily by initial seedling recruitment (Eriksson 1993) followed by vegetative expansion of those seedlings and local recruitment of their offspring. Recurring seed dispersal into populations (Becheler 2014) has been documented and colonization via vegetative propagules (Harwell and Orth 2002; Orth et al. 2012) has been suggested. Dispersal of fruits and seeds by waterfowl, either through ingestion or through adhesion to feathers (Figuerola et al. 2003; Higgins et al. 2003; Santamaria and Klaassen 2002), are also suggested to facilitate long distance movement of genes. The relative frequency of recruitment of propagules from outside of patches and the distances over which regular recruitment occurs in the Bay, however, remain major questions. Management decisions would benefit from concerted, comprehensive efforts to understand current connectivity relative to what existed historically.

Although the picture is incomplete, multiple pieces of evidence provide clues for dispersal and gene flow in *Z. marina* and *V. americana* in the Chesapeake Bay. One piece of evidence is relatively low gene flow between *Zostera marina* beds of the Chesapeake Bay and other populations in the Virginia coastal bays and Atlantic based on F_{ST} values and clusters from Structure analysis (Reynolds et al. 2013). However, these same Structure results also show a common genetic component across all western Atlantic coastal populations. Much of the similarity appears to result from shared ancestral diversity as estimates of current gene flow were more limited (Reynolds et al. 2013). More evidence comes from the presence of individuals in restored Virginia coastal bay populations that cluster with a Chincoteague population, suggesting ongoing dispersal over distances of 70 km. Further, Harwell and Orth (2002) documented appearance of 13 naturally recolonized beds from 1 to 108 km from the nearest known beds.

Despite this potential for dispersal, arguments for active restoration have been made based on low diversity in naturally recolonized populations of *Z. marina* compared to sites that were restored using seed from multiple source populations (Reynolds et al. 2013). This recommendation to enhance diversity is based on results of a field experiment in which allelic diversity was associated with higher density of shoots and follow-on ecological function (Reynolds et al. 2012a). Thus, active restoration may enhance the rate of SAV bed recovery and functioning even when meadows have the capacity to naturally recolonize. On the other hand, *Z. marina* as well as *V. americana* show geographic substructure among natural populations that has been affected by restoration activities. More comparisons of genetic diversity associated with natural colonization at varying distances from existing beds versus active restoration is warranted to understand the distances at which genetic diversity could be compromised. In addition, small-scale preliminary field experiments may need to be used to test how the homogenization of the gene pool may affect the structure, function, and resilience of populations as opposed to keeping existing geographic substructures intact. Field trials could also determine whether an intentional planting will increase the rate of recovery of a population (as in Reynolds et al. 2012a).

Decision 2: Where should restoration sites be located?

Locations of plantings will depend on overall restoration goals. Typically, those goals focus on increasing habitat amount. If increasing connectivity is also a restoration goal, decisions regarding planting sites need to incorporate dispersal to determining where it would be beneficial to reconnect populations that are isolated. Thus, the lack of knowledge of dispersal distances for Chesapeake Bay described above limits this decision as well: it is not known whether existing distances among patches exceed dispersal capabilities and therefore preclude natural colonization nor is it known what distances would connect isolated beds.

One study (Lloyd et al. In press) assessed potential connectivity of *V. americana* using SAV from VIMS monitoring data that fell within the salinity requirements for the species. They found that connectivity varied across years as a function of the size and spatial distribution of patches in a given year. Connectivity within years was far lower than it would have been had all patches had been occupied in a single year. They also found that connectivity across the whole Bay would be unrealistic, requiring dispersal distances of at least 235 km to reach all patches. At more reasonable dispersal distances of <10 km, they found the majority of patches within tributaries and in the northern and central regions of the Bay formed connected networks. Networks that were connected at a distance ~4 km (Lloyd et al. In press) roughly coincide with genetic clusters identified by Structure (Lloyd et al. 2011). These results provide preliminary suggestion that sites within 4 km could be connected through regular dispersal and that areas that have become isolated by more than that distance due to habitat loss could benefit from increased connection. This hypothesis warrants further testing by assessing genetic diversity patterns in sites that have become isolated from other sites by >4 km relative to the historic habitat distribution.

Connectivity through seeds. It is well known that seed production in SAV is critical for dispersing individuals over long and short distances (Becheler et al. 2010) and maintaining seed banks that can replenish populations after a disturbance (Li et al. 2014). Greve et al. (2005) documented that sexual reproduction was important in *Z. marina* bed recovery in a Danish estuary after declines. Similarly, Zipperle et al. (2009a) showed that a persistent seed bank prevented extinction in *Z. noltii*, and Jarvis et al. (2014a) showed in model simulations that a *Z. marina* seed bank was important for the recovery of populations after heat induced decline. Thus, seeds generated by most SAV species may be a mechanism of recruitment from outside (Macreadie et al. 2014) as well as within patches through dormancy. Genetic data are advancing these insights by quantifying the potential for long distance dispersal.

Potential for recruitment from seeds depends fundamentally on seed longevity. Orth et al. (2000) reviewed dormancy in 42 SAV species with some period of dormancy between a few weeks to 4 years. They found dormancy for Z. *marina* may only last up to 12 months and may be primarily under environmental control. Jarvis et al. (Jarvis et al. 2014b) later showed that the viability of Z. *marina* seeds decreased after 6 months. After 15 months, no seeds from the Chesapeake Bay remained viable, and less than 5% of seeds from coastal lagoons of North Carolina remained viable. Viability was not affected by seed source, site, or sediment type. Thus, Z. *marina* produces a transient seed bank (Jarvis et al. 2014b; Orth et al. 2000) which increases susceptibility to disturbance and decreases the resilience of populations to repeated stress events. Similarly, seed density of Z. *noltii* in the North Sea was 370 to 490 seeds/m^2 (Zipperle et al. 2009b) and distribution of seeds was highly aggregated. Less than 25% of seeds germinated under lab conditions and only 12% germinated under field conditions. Z. *noltii* seeds were viable for up to 3 years, forming a relatively short term, but persistent seed bank.

Connectivity through vegetative propagules. Asexual reproduction is very common in SAV (Li et al. 2014) and can increase density and expansion of existing SAV beds (Kendrick et al. 2012) and recovery of beds that have been disturbed (Rasheed 2004). Jarvis and Moore (2010) report that asexual recolonization through rhizome growth is the dominant mechanism of recovery in Z. *marina*. At one extreme, clonal dominance may suppress gene flow by limiting the availability of sexually produced propagules for emigration, and reducing rates of immigration through pre-emption of space (Oliva et al. 2014). At the other extreme, observations of vegetative fragments floating far from their natal site (Harwell and Orth 2002; Reusch 2002; van Dijk et al. 2009) have been taken as evidence of their importance in dispersal. Evidence that fragments reestablish is limited (Diaz-Almela et al. 2008 is an exception) and some authors discount them as sources of recruitment (Ewanchuk and Williams 1996; Serra et al. 2010). Presence of large numbers of reproductive ramets as shoreline wrack (Harwell and Orth 2002; Reusch 2002) indicates that many do not land in suitable habitat and thus are questionable as a mechanism of gene flow. However, importance of vegetative dispersal in *V. americana* is demonstrated by the distribution of five genets across multiple sites in the nontidal reaches of the Potomac River. In the most extreme case, the same *V. americana* genet represented 53-100% of samples within sites spanning ~160 km of the river (Lloyd et al. 2011). Such extreme cases are rare but not isolated, e.g. one *Potamogeton pectinatus* genotype was abundant in 7 sampling locations in a nontidal river in Belgium (Triest and Fenart 2014). By contrast to the nontidal Potomac, no genotypes have been found to be shared among *V. americana* sites in the tidal Chesapeake Bay.

Worldwide, distances separating sites sharing the same genotype range from 2 km to an impressive 2,700 km. The larger distances indicate that SAV species have among the largest extents known for clonal organisms (compared with values in Table 1 of Arnaud-Haond et al. 2012). In most cases, however, genotypes are shared among sites that are more directly connected. In the case of *V. americana*, the two most widespread genotypes of *V. americana* in the nontidal Potomac River (Lloyd et al. 2011) spanned ~132 and 160 river km but sites supporting the clones were separated by <20 km and we know from unpublished data that they were found in between the sampled sites.

By contrast to the large clones we found in the non-tidal Potomac River, there is no evidence for widespread vegetative dispersal in the tidal Chesapeake. Almost all Z. *marin*a samples from the Bay represent unique genotypes, and the few identical clones were within one site (Table 1). Vegetative growth of *V. american*a is more extensive, but still is limited to within population expansion of clones in the tidal reaches of the Chesapeake Bay where no genotypes are shared among sites (Lloyd et al. 2011). This result mirrors data from Triest and Fenart (2014) who found differences in clonal dispersal of *Potomageton pectinatus* in Belgium to be more pronounced in rivers than in a pond, which they suggest is due to a greater importance of water flow than bird mediated dispersal for establishment in river sites.

Decision 3: Where should restoration material come from?

Debates over the origin of genetic stock selection relative to target planting locations (Figure 1) continue to be contentious in restoration science and management. Scientific arguments can be made for and against all points on the continuum. Ultimately choices will be normative based on the degree of risk tolerance for potential detrimental effects of genetic pollution on the one hand, versus low genetic diversity and inbreeding on the other. We argue that those normative choices should be made with the best estimate of the potential for each type of risk to manifest based on the standing genetic diversity in a system and potential for natural dispersal.

Despite increased insight into dispersal of SAV in general, information for the Bay specifically is incomplete. Moreover, the question of how local is local remains unanswered. For example, Reynolds et al. (2013) documented significant differences in *Z. marina* gene pools between the Chesapeake Bay and the Virginia coastal bays but considered them similar enough to use Chesapeake stock for restoration in the coastal bays. Similarly, *V. americana* propagules have been moved among genetic regions within the upper Chesapeake Bay. Long-term fitness consequences of these movements have not been assessed.

More precise articulation of restoration goals is necessary to develop guidance for stock selection. The most fundamental restoration goals are establishment of meadows that self-perpetuate, are robust to disturbance, and provide ecosystem benefits. As such, genetic goals are often non-existent or are secondary. However, multiple aspects of genetic diversity have been found to play roles in resilience and persistence: number of genotypes, number of alleles, and levels of heterozygosity. Degree of relatedness is also emerging as a factor for persistence. Another goal for practitioners is to represent the natural diversity in the system (Neel and Cummings 2003).

To date arguments regarding which of these goals are most important for the Chesapeake Bay have often been presented as mutually exclusive choices for either maximizing allelic or genotypic diversity or planting with relatively local stock. Given the high diversity of most populations in the Bay, this polarized thinking poses a false dichotomy. It is possible to increase diversity at sites and to do so using stock that comes from donor sites close to the planting bed. As natural recolonization proceeds, donor beds become increasingly available.

For example, we would recommend that restoration within each of the genetic regions identified by Lloyd et al. (2011) - Potomac (tidal and non-tidal), Central Bay, and North Bay - could be done with propagules from any site within the regions. All indications are that gene flow within regions is far higher than it is among regions and there is no evidence of isolation by distance within the North Bay and Central Bay regions. By contrast, moving propagules among regions should be avoided until fitness consequences can be evaluated. To date, a lack of information precludes a comparison of genetic diversity of the Bay with populations outside of the Bay. Until such information indicates sufficient similarity, using propagules from the abundance of sources in the Bay is a reasonable precautionary approach.

Regardless of the choices made, careful documentation and monitoring of restoration efforts is needed. Genetic monitoring of restoration choices would contribute to understanding the fate of planted propagules from different sources over time. For example, Reynolds et al. (2012a) planted with seed so all shoots were initially unique genotypes. Higher density of shoots in plantings with higher allelic diversity may result from complementarity or from inclusion of one or a few highly productive genotypes. Over time, some genotypes can come to dominate. Without ongoing monitoring of genotypic diversity, it is not possible to know if genotypic and allelic diversity are maintained. Another key priority is monitoring the movement and fitness effects of genes introduced into novel areas.

To date published insights for the Bay specifically come from one field restoration experiment for *Z. marina* and one greenhouse experiment for *V. americana*. More extensive rigorous experimentation is needed to test the effects of different aspects of genetic diversity.

What lies ahead?

Since publication of Technical Synthesis II, we have gained great insights into genetic variation in SAV and ecological processes that are marked by genetic patterns. We have more insight into past history and aspects of species biology that provides essential insight into the degree and nature of current and future threats. Still, there are important gaps in our knowledge. Most studies have focused on marine species (Figure 2b), and moreover most of those have focused on a few species (particularly *Z. marina*). Recent developments, such as Single Nucleotide Polymorphisms (SNPs) and whole-genome sequencing, are bringing even more exciting tools to the realm of conservation and restoration. Use of fine-scale analysis of gene diversity and expression within individuals to document selection across environmental gradients is becoming increasingly feasible. We see a pending quantum leap in insights into links between genetic diversity and ecological function under different environmental conditions (Dattolo et al. 2013; Franssen et al. 2011; Franssen et al. 2014; Maestrini et al. 2002; Procaccini et al. 2007). Restoration of resilient SAV beds in the Chesapeake Bay can greatly benefit from this new knowledge for many years to come and we envision the following trends emerging between now and the next Technical Synthesis:

1. Microsatellite markers have already surpassed allozymes and dominant markers (AFLPs, ISSRs, and RAPDs) for reliably measuring genetic variability within and among populations. Although they have been developed for many SAV species, many more species have not microsatellites developed. SNPs are emerging as an alternative to marker and will be a more common tool for assessing population genetic diversity as costs of high throughput sequencing drop and methods for focusing those sequencing methods on specific genomic regions (Ali et al. 2015). Microsatellites will continue to provide useful information but the large number of loci that can be assayed with SNPs, and the ability to choose particular parts of the genome, will provide much greater understanding of genetic diversity in SAV species. Of particular interest will be the ability to examine genes that are expected to be under natural selection in particular environments.

2. Further development and application of analytical techniques that quantify connectivity versus isolation will be especially productive. Of particular value will be approaches that identify patterns of isolation to determine 1) whether breaks/gaps in connectivity exist such that groups of “populations” form relatively cohesive genetic units that are separated by areas of no or lower dispersal, and 2) if those gaps represent long-term patterns versus recent changes in connectivity. Traditional analysis of F_{ST} alone is too imprecise to provide the spatial or temporal resolution needed. By contrast, with thoughtful application, Bayesian population identification approaches can provide valuable insights (as in two Chesapeake *Z. marina* studies

(Reynolds et al. 2012a, 2013) and one *V. americana* study (Lloyd et al. 2011)). Three other avenues of analysis will provide additional insights that will be key for restoration and management decisions.

a. To date, many landscape genetic/genomic (e.g., Manel et al. 2003) approaches that are used in terrestrial environments (e.g., Shryock et al. 2015) have not been applied to submersed aquatic macrophytes in the Chesapeake Bay. Beyond being more spatially explicit (Wasser et al. 2015), landscape genomic techniques help identify the environmental correlates of genetic isolation among populations and thus go beyond the simplistic linear model of isolation by distance. They can also distinguish when patterns of isolation across environmental gradients are related to selection versus drift to understand current and future genetic composition and adaptations to current and future climates (e.g., Fitzpatrick and Keller 2015). These and other spatially explicit genetic approaches would greatly improve understanding of the extent and nature of connectivity gaps and whether active intervention is necessary to increase connectivity.

b. Assignment tests have demonstrated great utility for separating ancient from recent changes in gene flow generally, but have been applied to the Chesapeake in only one study (Reynolds et al. 2013). Assignment tests, however, require greater sampling intensities (numbers of individuals and numbers of sites) to gain insight into among patch dispersal rates across ranges of distance. Without such intensive efforts, the identification of typical dispersal pathways along with locations where those pathways have become disconnected may not be possible.

c. Graph theoretic (a.k.a. network theoretic) approaches are also highly effective for assessing connectivity but have only rarely been applied to quantify gene flow in SAV (Rozenfeld et al. 2007) Graph theory can be used in two ways to analyze connectivity. First it can be used to analyze the spatial distribution of genotypes of a specified level of relatedness or genetic distance (e.g., Dyer & Nason 2004). Second, an analysis of which mapped habitat patches fall within specified geographic distances (e.g., Urban & Keitt 2001; Calabrese & Fagan 2004; Lloyd et al. Accepted) may be integrated with genetic data to quantify the degree to which patch networks with varying levels of connectedness share individuals with different levels of relatedness. Such an analysis could reveal key distances that are required for high levels of dispersal, and hence relatedness, and could be used to prioritize sites that would maximize potential for ongoing colonization and gene flow.

Table 1. Number of publications that provide population genetic data for common species found growing in the Chesapeake Bay. The number of publications that come from populations in the Bay versus only outside the Bay are specified separately. Species that are found in the Bay that are not in the table had no published population genetic information available as of December, 2015.

Species	Native in the Bay?	Total Worldwide Studies	Data from the Chesapeake Bay
Ceratophyllum demersum	Yes	1	0
Elodea canadensis	Yes	1	0
Hydrilla verticillata	No	1	0
Potamogeton crispus	Yes	0	0
Potamogeton nodosus	Yes	0	0
Potamogeton perfoliatus	Yes	0	0
Potamogeton pusillus	Yes	1	0
Ruppia maritima	Yes	0	0
Stuckenia pectinata	Yes	4	0
Vallisneria americana	Yes	4	2
Zannichellia palustris	Yes	1	0
Zostera marina	Yes	47	5
TOTAL for Chesapeake Bay Species		60	7

Table 2. Genetic diversity measures reported for the genus *Zostera* in 60 publications. The data are sorted first by marker type, then by species and then by alleles per locus (A). Publications that include data for the Chesapeake Bay are highlighted. Three publications include two entries because they reported data for natural (Type = N) and restored populations (Type = R). ZJ – *Zostera japonica*, ZMa = *Zostera marina*, Zmu = *Zostera muelleri*, ZN = *Zostera noltii*, ZP = *Zostera pacifica*. Data for other *Zostera* species than *Z. marina* are in light gray text. # Sites is the number of populations for which data are reported. Scale is the geographic extent that each study represents in km. n=number of samples genotyped, R = genotypic richness calculated as $(G\text{-}1)/(N\text{-}1)$ where G is the number of genotypes identified, P = proportion of markers that are polymorphic, A = number of alleles per locus, H_o = observed heterozygosity, H_e = expected heterozygosity, and F_{IS} is inbreeding coefficient. All measures are reported as the mean among all populations sampled within a study.

Author (Year)	Species	Location	Type	# Sites	Scale (km)	Marker	Loci	N	R	A	H_o	H_e	F_{IS}
Williams (2001)	ZMa	Atlantic & Pacific	N	10	4183	Allo	13	675	nr	1.0	0.013	0.019	nr
Williams and Davis (1996)	ZMa	Pacific	R	6	15	Allo	8	432	nr	1.2	0.010	0.010	-0.018
Williams and Davis (1996)	ZMa	Pacific	N	6	330	Alloe	8	916	0.036	1.2	0.027	0.027	nr
Williams and Orth (1998)	ZMa	Chesapeake Bay	N	6	140	Allo	13	510	0.125	1.3	0.036	0.043	0.144
Williams and Orth (1998)	ZMa	Chesapeake Bay	R	3	45	Allo	13	255	0.090	1.3	0.045	0.041	-0.023
Laushman (1993)	ZMa	Atlantic & Pacific	N	7	4150	Allo	5	552	0.455	1.3	nr	0.063	nr
Deheij and Nienhuis (1992)	ZMa	Atlantic	N	5	45	Allo	4	256	0.261	1.7	nr	nr	nr
Rhode and Duffy (2004)	ZMa	Chesapeake Bay	N	12	113	Allo	7	1200	0.180	2.0	0.475	0.690	0.680
Ruckelshaus (1996)	ZMa	Pacific	N	1	nr	Allo	2	na	nr	2.0	nr	nr	nr
Ruckelshaus (1998)	ZMa	Pacific	N	2	14	Allo	5	679	0.486	2.4	0.357	nr	0.057
Harrison and Durance (1992)	ZMa	Pacific	N	1	1	Allo	8	50	0.775	nr	nr	nr	nr
Araki and Kunii (2006)	ZJ	Sea of Japan	N	5	25	Allo	2	185	0.073	1.8	nr	nr	nr

Olsen et al. (2013)	ZMa	Barents Sea	N	15	208	Msat	8	644	0.889	2.9	nr	0.267	0.097
Ort et al. (2012)	ZMa	Pacific Ocean	N	6	33	Msat	7	261	0.820	3.0	0.320	0.330	0.021
Coyer et al. (2008)	ZMa	Pacific	N	15	363	Msat	9	676	0.127	3.2	nr	0.464	0.107
Olsen et al. (2004)	ZMa	Pacific & Atlantic, Europe	N	49	10838	Msat	9	2139	0.659	3.5	0.445	0.460	0.011
Gonciarz et al. (2014)	ZMa	North & Baltic Sea	N	3	1400	Msat	12	70	0.730	3.9	0.460	0.450	-0.040
Wyllie-Echeverria et al. (2010)	ZMa	Pacific	N	8	35	Msat	8	364	0.337	4.0	0.380	0.380	0.011
Oetjen et al. (2010)	ZMa	Wadden Sea	N	6	53.13	Msat	46	284	1.000	4.2	nr	0.365	nr
Becheler et al. (2014)	ZMa	Atlantic	N	26	442	Msat	9	779	0.730	4.4	0.457	0.445	0.043
Reusch et al. (2000)	ZMa	Atlantic & Pacific, Europe	N	12	10000	Msat	6	545	0.741	4.7	0.469	0.480	0.020
Reusch et al. (1999c)	ZMa	Baltic Sea, Atlantic	N	3	5164	Msat	7	na	nr	4.9	nr	nr	nr
Diekmann and Serrao (2012)	ZMa	Atlantic, North & Baltic Sea	N	20	4040	Msat	8	1315	0.565	4.9	0.458	0.435	-0.040
Olsen et al. (2014)	ZMa	Pacific	N	24	600	Msat	7	1135	0.869	5.0	nr	0.587	0.132
Becheler et al. (2010)	ZMa	Atlantic	N	7	442	Msat	9	390	0.720	5.0	0.467	0.471	0.046
Reusch et al. (1998)	ZMa	Baltic Sea	N	1	0.08	Msat	7	110	nr	5.3	nr	nr	nr
Reusch et al. (1999b)	ZMa	Baltic Sea	N	1	0.08	Msat	7	80	0.696	5.3	nr	nr	nr
Muñiz-Salazar et al. (2006)	ZMa	Pacific	N	7	22	Msat	8	146	1.000	5.3	0.520	0.539	nr
Kamel et al. (2012)	ZMa	Pacific	N	7	22.4	Msat	5	1619	0.203	5.5	0.608	0.600	-0.015
Muñiz-Salazar et al. (2005)	ZMa	Pacific	N	9	2300	Msat	9	328	0.997	5.6	0.550	0.570	nr
Tanaka et al. (2011)	ZMa	Pacific	N	12	75	Msat	5	281	0.880	5.6	0.613	0.620	0.009
Reusch (2001a)	ZMa	Baltic Sea	N	2	80	Msat	8	200	0.225	6.3	nr	nr	0.071
Campanella et al. (2010a)	ZMa	Atlantic & Pacific	N	9	5622	Msat	7	180	0.742	6.8	0.257	0.709	0.620

Reynolds et al. (2013)	ZMa	non-Chesapeake Bay	N	6	1143	Msat	7	154	1.000	6.8	0.658	0.613	-0.029
Campanella et al. (2013)	ZMa	Atlantic	R	5	22	Msat	7	173	0.975	7.4	0.348	0.596	0.408
Reusch (2000a)	ZMa	Baltic & North Sea, Atlantic	N	3	5164	Msat	5	90	1.000	7.5	0.522	0.564	nr
Peterson et al. (2013)	ZMa	Atlantic Ocean	N	4	157	Msat	8	293	0.950	7.6	0.560	0.580	0.030
Reynolds et al. (2012a)	ZMa	Chesapeake Bay	N	5	40	Msat	8	202	1.000	7.7	0.700	0.650	-0.050
Reusch (2002)	ZMa	Wadden & Baltic Sea	N	13	60	Msat	8	620	0.906	7.7	0.557	0.579	0.057
Reynolds et al. (2013)	ZMa	Chesapeake Bay	N	12	40	Msat	8	425	1	7.9	0.672	0.621	-0.070
Reusch (2000b)	ZMa	Wadden Sea	N	2	40.6	Msat	8	100	nr	9.1	nr	nr	nr
Campanella et al. (2010a)	ZMa	Atlantic and Pacific	N	11	5622	Msat	7	220	0.808	9.1	0.287	0.774	0.619
Hammerli and Reusch (2003a)	ZMa	Baltic Sea	N	4	80	Msat	9	927	0.565	9.2	0.478	nr	nr
Reynolds et al. (2013)	ZMa	Chesapeake Bay	R	4	40	Msat	8	356-428	1.000	9.7-10.7	0.750-0.779	0.700-0.712	-0.080
Campanella et al. (2010a)	ZMa	Chesapeake Bay	N	1	na	Msat	7	20	0.842	10.8	0.26	0.81	0.67
Reusch et al. (1999a)	ZMa	Baltic Sea	N	1	0.16	Msat	6	47	0.044	11.2	nr	nr	nr
Shimabukuro et al. (2012)	ZMa	East China Sea	N	5	50	Msat	7	96	nr	nr	0.378	0.398	nr
Oetjen and Reusch (2007)	ZMa	Wadden Sea	N	6	53.13	Msat	25	485	1.000	nr	nr	nr	nr

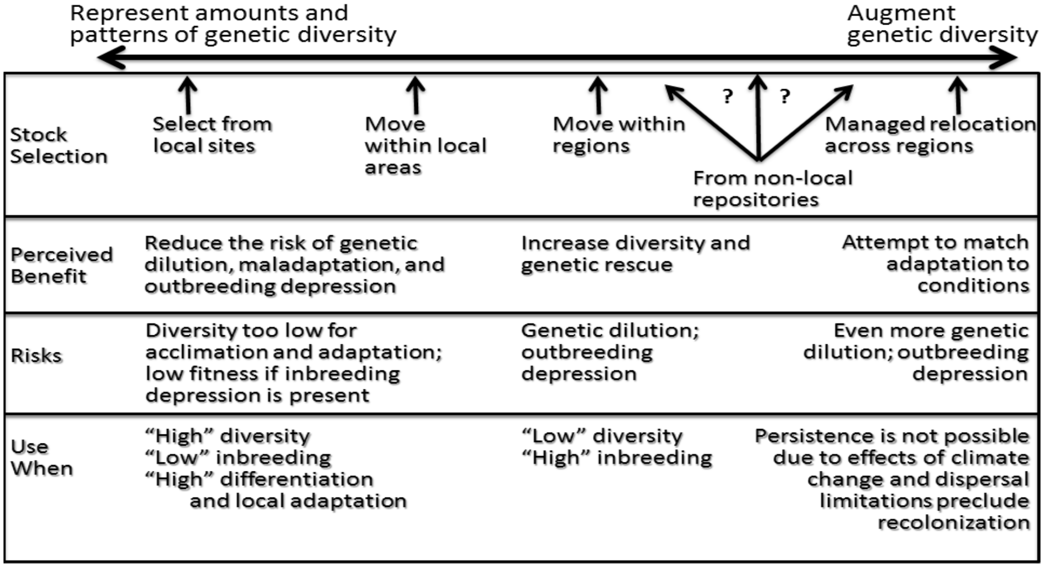
Hammerli and Reusch (2003b)	ZMa	Baltic Sea	N	4	80	Msat	9	927	0.565	nr	nr	nr	nr
Billingham et al. (2003)	ZMa	Atlantic	N	12	25	Msat	9	270	0.210	nr	0.505	0.423	-0.195
Macreadie et al. (2014)	ZMu	Tasman Sea	N	4	nr	Msat	9	477	0.348	nr	nr	nr	nr
Jahnke et al. (2015)	ZN	Mediterranean	R	2	5	Msat	9	16	0.210	2.2	0.625	0.425	-0.143
Ruggiero et al. (2005)	ZN	Mediterranean	N	1	nr	Msat	6	131	0.077	2.9	0.903	0.602	-0.254
Chust et al. (2013)	ZN	Bay of Biscay	N	9	665	Msat	7	406	0.704	4.1	0.488	0.509	0.056
Jahnke et al. (2015)	ZN	Mediterranean	N	4	30	Msat	9	178	0.968	4.8	0.531	0.531	-0.028
Coyer et al. (2004)	ZN	Atlantic	N	33	8000	Msat	9	1706	0.720	5.5	0.534	0.523	0.036
Diekmann et al. (2005)	ZN	Atlantic	N	8	990	Msat	9	372	0.620	5.7	0.563	0.570	0.054
Zipperle et al. (2009a)	ZN	Wadden Sea	N	2	0.25	Msat	9	1258	0.621	6.3	nr	nr	nr
Diekmann et al. (2010)	ZN	Atlantic	N	11	3604	Msat	9	459	0.733	6.3	nr	0.551	0.049
Zipperle et al. (2011)	ZN	Wadden Sea	N	1	0.125	Msat	9	256	0.421	nr	nr	nr	nr
Coyer et al. (2008)	ZP	Pacific	N	17	310	Msat	9	783	0.361	1.8	nr	0.239	0.090
Olsen et al. (2014)	ZP	Pacific	N	11	378	Msat	6	499	0.767	2.7	nr	0.358	-0.040
Hodoki et al. (2013)	ZJ	Sea of Japan	N	15	16	Msat	6	249	0.774	3.8	nr	nr	0.096
Li et al. (2012)	ZMa	Pacific, North Sea	N	6	9715	AFLPs	6	63	nr	26.0	nr	0.044	nr
Lee et al. (2004)	ZJ	See of Japan	N	3	400	RAPDs	45	15	nr	nr	nr	0.193	nr
Alberte et al. (1994)	ZMa	Pacific	N	3	250	RFLPs	7	59	1.000	nr	nr	nr	nr

Table 3. Genetic diversity measures reported for the genus *Vallisneria* in 6 publications. Two publications include two entries because they either reported data for natural and restored populations (Lloyd et al. 2012) or data for two species of *Vallisneria* (Wang et al. 2010). VA = *V. americana*, VS = *V. spinulosa*, VN = *V. natans*. Type indicates whether populations are natural (N) or restored (R). # sites are the number of populations for which data were reported. Scale is the geographic extent (km) over which samples were collected. N= total number of samples genotyped, *R* = species level genotypic richness calculated as (G-1)/(N-1) where *G* is the number of genotype identified, *P* = proportion of markers that are polymorphic within populations, A = number of alleles per locus, H_o = observed heterozygosity, H_e = expected heterozygosity, and F_{IS} is inbreeding coefficient. All measures are reported as the mean among all populations sampled within a study. Studies focused on the Chesapeake Bay are highlighted in gray.

Author (Year)	Species	Location	Type	# Sites	Scale	Marker	# Loci	N	R	P	A	H_o	H_e	F_{IS}
Lloyd et al. (2011)	VA	Chesapeake Bay	N	26	226	Msat	10	675	0.570	0.85	3.9	0.540	0.530	-0.052
Lloyd et al. (2012)	VA	Chesapeake Bay	N	8	225	Msat	10	223	0.621	0.90	4.5	0.596	0.590	-0.033
Lloyd et al. (2012)	VA	Chesapeake Bay	R	8	268	Msat	10	148	0.628	0.90	4.0	0.561	0.585	0.054
Laushman (1993)	VA	Lake Erie	N	12	160	Allo	5	528	0.131	0.39	1.4	nr	0.085	nr
Lokker et al. (1994)	VA	Lake Erie	N	1	0.09	Allo	8	2094	0.081	0.71	2.0	0.242	0.334	0.030
Chen et al. (2007)	VS	Yangtze River	N	10	900	Allo	13	396	0.560	0.46	1.6	0.260	0.210	-0.240
Wang et al. (2010)	VS	Yangtze River	N	7	1400	ISSR	8	201	0.942	0.42	nr	nr	0.180	nr
Wang et al. (2010)	VN	Yangtze River	N	6	1400	ISSR	8	196	0.981	0.56	nr	nr	0.240	nr

[1] Lloyd et al. 2012 natural populations are a subset of populations sampled in Lloyd et al. 2011.

Figure 1. Perceived benefits, risks, and recommendations for use of a gradient of options for stock selection in active restoration efforts.

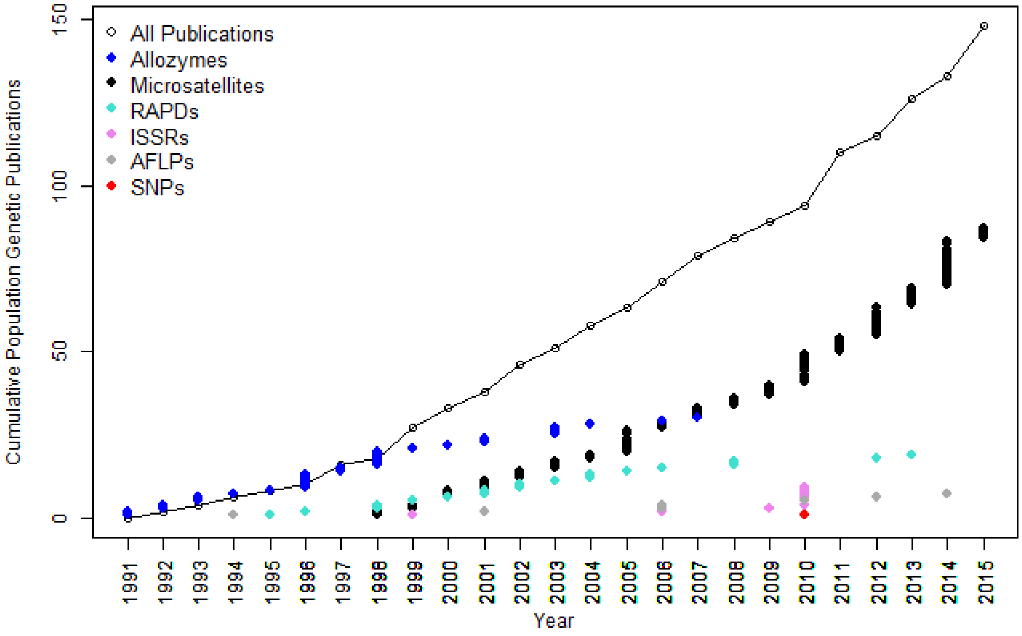


Represent amounts and patterns of genetic diversity ↔ Augment genetic diversity

Stock Selection	Select from local sites Move within local areas	Move within regions ? From non-local repositories ?	Managed relocation across regions
Perceived Benefit	Reduce the risk of genetic dilution, maladaptation, and outbreeding depression	Increase diversity and genetic rescue	Attempt to match adaptation to conditions
Risks	Diversity too low for acclimation and adaptation; low fitness if inbreeding depression is present	Genetic dilution; outbreeding depression	Even more genetic dilution; outbreeding depression
Use When	"High" diversity "Low" inbreeding "High" differentiation and local adaptation	"Low" diversity "High" inbreeding	Persistence is not possible due to effects of climate change and dispersal limitations preclude recolonization

Figure 2. Cumulative number of publications documenting population genetic diversity in SAV species worldwide from 1990 to 2015. RAPDs = Randomly Amplified Polymorphic DNAs; ISSRs = Inter-simple Sequence Repeats; AFPS = Amplified Fragment Length Polymorphisms; SNPs = Single nucleotide polymorphisms.

A) Cumulative number of population genetic publications by marker type.



B) Cumulative number or population genetic publications by salinity.

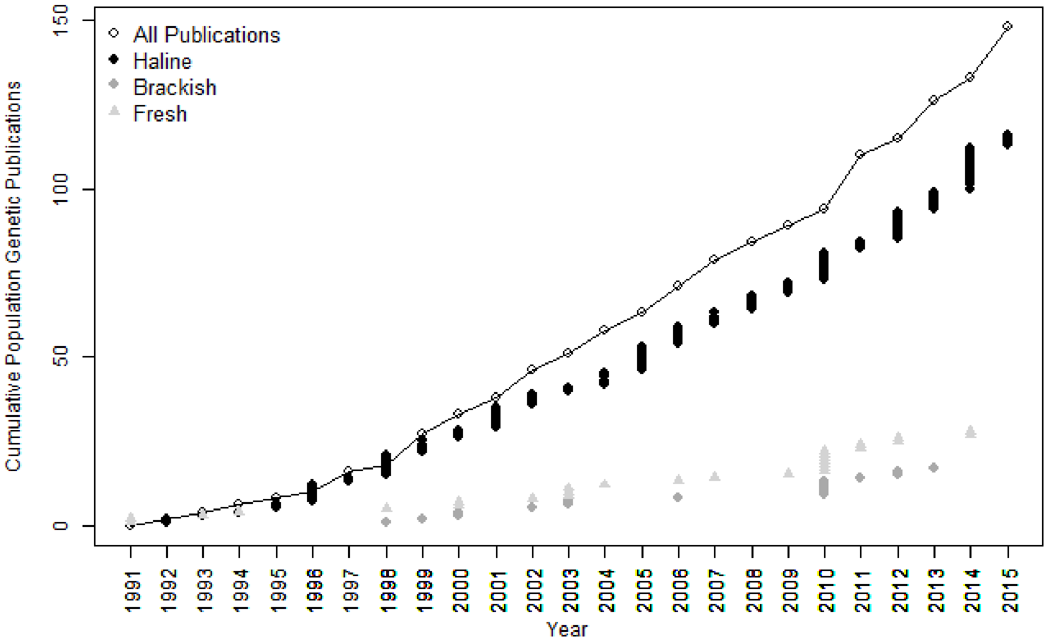


Figure 3. Distribution of measures of genetic diversity based on microsatellites from natural and restored populations of *Zostera marina* in the Chesapeake Bay and Virginia coastal bays (Campanella et al. 2010a; Reynolds et al. 2012a; Reynolds et al. 2013) <<add in Campanella 2010b and change Reynolds to 2012b>> compared with the same measures from studies of *Z. marina* world-wide. We collected the worldwide data from 42 published papers but all measures were not presented in all papers.

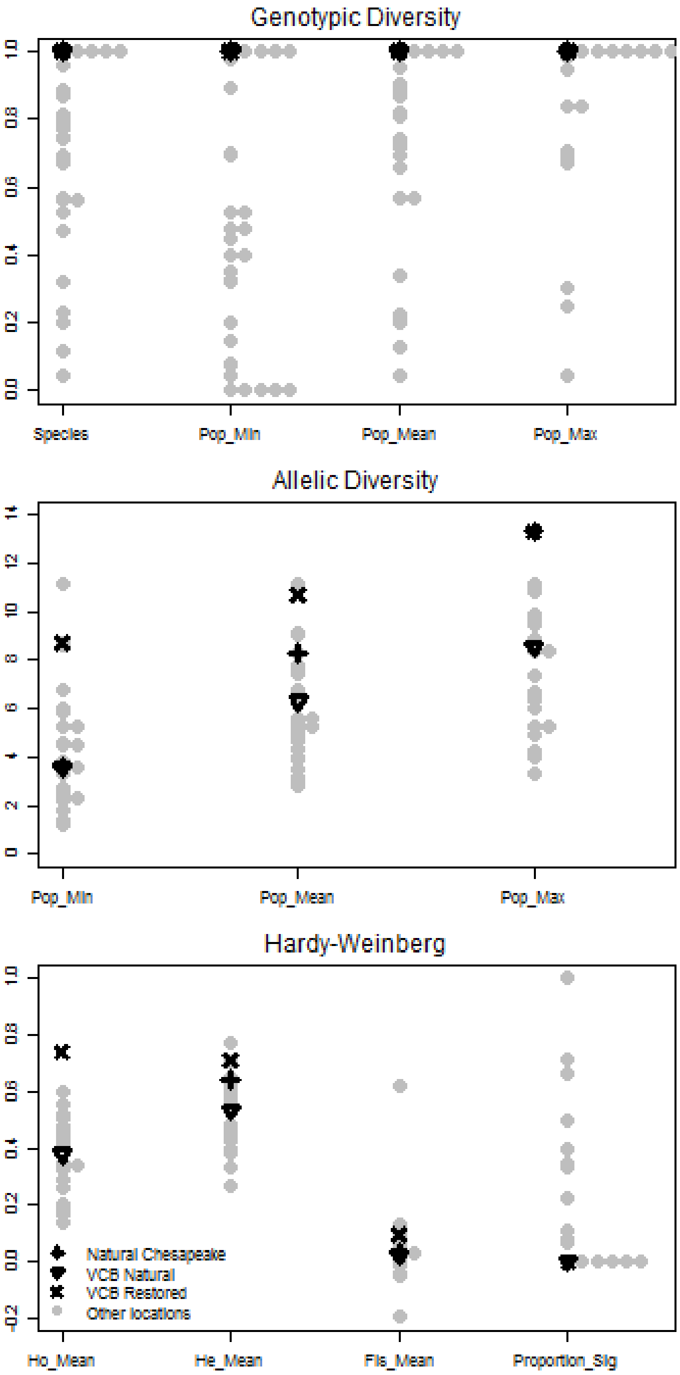
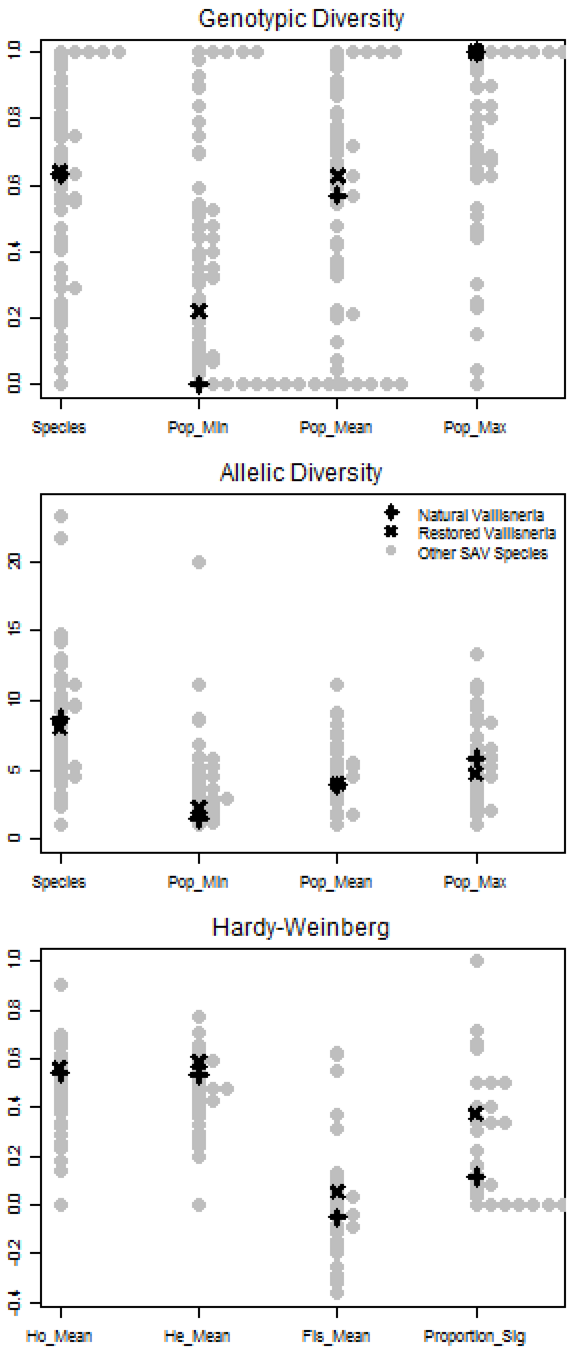


Figure 4. Measures of genetic diversity based on microsatellites from natural and restored populations of *Vallisneria americana* from the Chesapeake Bay (Lloyd et al. 2011; Lloyd et al. 2012) compared with the same measures from natural populations of all SAV species worldwide. No other *V. americana* populations have been studied and few other *Vallisneria* species have been studied to provide extensive comparison.



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EFFECTS OF LAND USE AND SHORELINE ARMORING ON SUBMERGED AQUATIC VEGETATION

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ABSTRACT

We review the literature on relationships between submerged aquatic vegetation (SAV) and land use or shoreline armoring--two stressors implicated in the worldwide decline of coastal SAV. We focus on Chesapeake Bay, where dozens of subestuaries with contrasting land uses, annual bay-wide SAV mapping, detailed maps of shoreline armoring, and intense interest in SAV restoration from scientists and managers have all fostered relevant research. SAV abundance is significantly lower in subestuaries with watersheds dominated by developed or agricultural land than in subestuaries dominated by forest. Human land uses release nutrient and sediments that reduce water clarity and limit light for SAV. Enhanced wave reflectance from armored shorelines can deepen adjacent shallow water and reduce water clarity through sediment resuspension. Evidence for negative impacts of bulkheads on SAV is stronger than for riprap, and the effects of armoring differ among salinity zones and among subestuaries with different land uses. Some of the interactions between armoring and land use seem counterintuitive, probably because analyses of entire salinity zones lumped SAV communities with different stressor-response relationships. Community and species-specific analyses are needed to improve understanding. Living shorelines (the currently preferred alternative to riprap and bulkhead) employs many different designs, materials, and construction methods. Further research is needed to understand the impacts of different living shorelines on SAV compared to riprap, bulkhead, and natural shoreline. Models and management plans should incorporate information on local land use, shoreline armoring, and community-specific responses to better understand SAV dynamics and to better manage SAV conservation and restoration.

INTRODUCTION

Submerged plants are keystone components of estuaries, providing structural habitat and a refuge from predators for invertebrates and small fish, supplying food for migratory birds, stabilizing benthic substrates, moderating shoreline erosion, playing a major role in littoral zone biogeochemical cycles, and supplying ecosystem services (Orth et al. 2006, Wainger and Kennedy in prep.). In the Chesapeake Bay, the spatial extent of submerged aquatic vegetation (SAV) is far below historic levels (Orth and Moore 1984, Orth et al. 2010), and increasing SAV coverage is a central goal of the Chesapeake Bay restoration effort (Batiuk et al. 2000; Chesapeake Bay Executive Council 2003; Chesapeake Bay Watershed Agreement 2014). The abundance of SAV is closely monitored because of the many services SAV provides. SAV abundance also provides an integrative measure of success in meeting and maintaining water quality goals because SAV requires high water clarity throughout the growing season (USEPA 2008).

Reduced water clarity is the single most important factor limiting Chesapeake Bay SAV (Kemp et al. 2004, Luckenbach et al. 2011), although other factors can impact SAV (e. g., substrate characteristics and physical energy; Koch et al. 2001). Human activities in the watershed are the primary driver of degraded water quality, and the mechanisms of the impacts on SAV are well understood (Boesch et al. 2001; Kemp et al. 2005). Sediments generated by agricultural activities, forest loss, and impervious surfaces are delivered to the estuary and reduce water clarity. Nutrient pollution (nitrogen and phosphorus) from agricultural activities, developed lands, point sources (e. g., waste-water treatment plants), and atmospheric deposition all contribute to eutrophication. Eutrophication stimulates the growth of phytoplankton in the water column and of epiphytes on SAV leaves, which together reduce the light available for SAV survival and growth. Poor water quality is the primary reason why many SAV plantings in the Chesapeake Bay have not persisted and or expanded (Luckenbach et al. 2011). Light limitation can also have sub-lethal effects on SAV. Plants stressed by low light availability become more sensitive to natural disturbances, such as hurricanes, and have reduced capacity for recovery after disturbance (Gurbisz et al. in prep.).

Although the connections of human land use to water quality and the mechanistic linkages between water clarity and SAV are both well understood, the relationships between SAV abundance and land-use distributions have only recently been quantified (Li et al. 2007; Patrick et al. 2014, 2015). Surprisingly models directly linking SAV to land use explain only part of the spatial variability in SAV abundance, suggesting that other factors besides light limitation may also be influencing the spatial distribution of SAV in Chesapeake Bay (Li et al. 2007; Orth et al. 2010; Patrick et al. 2014).

Shoreline armoring is another potential factor that may impact SAV. The practice of installing erosion-control structures; such as bulkheads, riprap, breakwaters, and living shorelines; has become one of the most pervasive human activities affecting degraded estuarine habitats worldwide (Airoldi et al. 2005; Bulleri and Chapman 2010; Gittman et al. 2015). One-third of the Chesapeake Bay shoreline (main stem and tributaries) is classified as eroding, with retreat rates up to 20-40 cm/y (CBP 2005), and these rapid erosion rates have led many property owners to armor their shorelines (Titus and Richman 2001). Seventeen percent of the Chesapeake shoreline is already armored (Patrick et al. 2015), and some subestuaries are more than 50% armored (Berman et al. 2000). Because of the strong connection between waterfront land use and armoring, locations where people live and work are more likely to be armored than undeveloped natural shorelines. Therefore, armoring is strongly correlated with other land uses, particularly the prevalence of agricultural and developed lands (Patrick et al. 2014). Shoreline armoring modifies physical and ecological processes at the land-water interface and may affect the abundance of SAV, but the ecological effects of armoring have not been extensively studied (see below). The impacts of other types of shoreline structures; such as piers, docks and living shorelines; are also poorly understood.

Here we review what is known about the impacts of land use and shoreline alteration on SAV. We draw on the general scientific literature, but focus on information from the Chesapeake Bay, especially recent studies of the effects of land use and shoreline armoring on SAV and on physical processes in the nearshore environment. Our review extends two previous syntheses of technical knowledge of Chesapeake Bay SAV (Batiuk et al. 1993; Batiuk et al. 2000) that did not explicitly consider the impacts of land use and shoreline armoring.

Land use

Recent studies have exploited the natural division of the Chesapeake Bay into dozens of subestuaries to explore and quantify the effects of nearby land use on estuarine responses, including SAV abundance. Each subestuary, an embayment at the mouth of a tributary stream, has its own local watershed with associated land use activities (Fig. 1), which makes the subestuaries especially relevant for studying land-water connections. The subestuaries can be treated as replicate study units for analyzing the effects of watershed stressors on estuarine responses, and this approach has been applied to studies of blue crab abundance, polychlorinated biphenyl (PCB) contamination of fish, bird community health, and other measures of estuarine condition (DeLuca et al. 2004; King et al. 2004, 2005). Studies of Chesapeake Bay SAV have examined stressor-response relationships across 100 subestuaries (Li et al. 2007; Patrick et al. 2014, 2015; Patrick and Weller 2015). Subestuaries differ widely in the proportions of human land uses in their local watersheds (Fig. 1). Watersheds range from having little or no forest, development, wetlands, or cropland to having as much as 79%, 77%, 51%, and 57%, of each category respectively (see Table 2 in Patrick et al. 2014). These ranges highlight how strongly land use varies near the Chesapeake Bay--some subestuaries have mostly natural land uses in their local watersheds, while others have watersheds dominated by row-crop agriculture or high-density development.

Among Chesapeake Bay subestuaries, the abundance of SAV mapped in aerial surveys is significantly related to the dominant land use in the local watershed (Li et al. 2007; Patrick et al. 2014). Generally, SAV abundance is higher in watersheds that are forested, mixed-undisturbed, or mixed-developed than in watersheds dominated by development, agriculture, or a mix of agriculture and other land uses (Fig. 2, top panel). Field measurements in 24 Chesapeake subestuaries revealed similar effects of dominant land use on SAV. SAV percent cover, bed width, and the maximum depth of SAV coverage were all lower in subestuaries with developed watersheds than in those with forested watersheds; and subestuaries with agricultural watersheds had smaller and shallower SAV beds than subestuaries with forested watersheds (Landry et al. in prep.). Minor land uses are also correlated with SAV abundance. For example, the proportion of herbaceous wetland in a local watersheds is positively correlated with SAV abundance in the receiving subestuary (Patrick et al. 2014).

Weather patterns can modify the general relationships between land cover and SAV. Compared to long-term averages, wet years (annual precipitation > 0.5 standard deviation above the mean) had higher SAV abundance in subestuaries with forested watersheds and lower SAV abundance in subestuaries with agricultural and mixed land use watersheds (Fig 2, Li et al. 2007). Agricultural impacts on SAV may be stronger in wet years when the higher runoff from agricultural lands delivers more nutrients and sediments to subestuaries. In contrast, SAV abundance in subestuaries with developed watersheds does not differ much between dry and wet years (Fig. 2), probably because urban nutrient loads are not so strongly driven by precipitation and non-point source runoff (Jordan et al. 2003).

Salinity in the receiving estuary strongly affects the relationships between land cover and SAV abundance. For example, the amount of shoreline marsh in a subestuary is negatively related with SAV abundance (Patrick et al. 2014 and Fig 3, bottom). The mechanism underlying the negative relationship is not clear. Marshes do produce colored dissolved organic matter (CDOM) that can reduce water clarity (Tzortziou et al. 2008). Marshes can also supply fine particles or peat that may create unsuitable substrates for nearby SAV (Barko and Smart 1986). The negative relationship between marshes and SAV is stronger (steeper) in the polyhaline than in other salinity zones (Fig. 3, bottom). The dominant polyhaline SAV species (*Zostera marina*) has a stronger preference for sandy substrate than the SAV species that dominate in the middle and upper Bay (Moore et al. 2000), so polyhaline SAV may be more sensitive to fine silt from eroding marshes.

Other negative land-use effects are also generally stronger in the polyhaline than in the other salinity zones (e. g., Fig. 3, top; Patrick et al. 2014; 2015). Several factors may contribute to this result. Polyhaline SAV species require more light than upper Bay species, so polyhaline species are more sensitive to stressors that reduce water clarity (Patrick et al. 2014, 2015). *Zostera* in Chesapeake Bay is near the southern limit of its geographic range, so it is susceptible to summer heat stress, which can lower its tolerance to other stressors (Orth et al. 2006; Moore and Jarvis 2008). Finally, in more diverse mesohaline and oligohaline communities, the loss of one species can be offset by increases in other species, but the potential for such compensation is limited in polyhaline SAV communities strongly dominated by *Zostera.*

Salinity itself is a stressor to some SAV species. High salinity is detrimental to freshwater SAV and to many mesohaline species, so SAV declines in dry (high salinity) years and rebounds in wet (lower salinity) years (Patrick and Weller 2015). Such rebounds may explain the positive effect of wet years on SAV in subestuaries with forested watersheds (Fig. 2), most of which are in the mesohaline zone (Fig. 1).

Land use is also an important predictor of spatial patterns in the trends of SAV recovery from past stresses (Fig. 5; Patrick et al. 2014; Patrick et al. in prep.). Recovery has been ongoing, but not uniform, since annual monitoring began in 1984 (Orth et al. 2010). The rates of recovery differ among salinity zones, with the oligohaline recovering fastest and little to no recovery in the mesohaline (Orth et al. 2010). Recent work suggests that the rates of SAV recovery are highest in subestuaries with less agriculture and development in their local watersheds (Patrick et al. in prep.).

Shoreline Armoring

Physical and Sediment Effects

Shoreline armoring strongly modifies the interactions of waves with shorelines, causing changes in shoreline structure and sediment composition. The actual effects depend on the type of armoring, wind and tidal patterns, and the type of substrate. Breakwaters and other structures may reduce physical energy at the shoreline; but seawalls, bulkheads, and riprap can increase energy at the shoreline due to wave reflection (Strayer and Findlay 2010). Increased energy can, in turn, increase nearshore scour and sediment export, resulting in deepening of the adjacent littoral zone. In Chesapeake Bay, Landry et al. (in prep.) measured deeper water and steeper bottom slopes adjacent to riprap revetment compared to natural shorelines. Strayer et al. (2012) also report that engineered shorelines were narrower, steeper, more exposed, and had coarser sediments than natural shorelines. Generally, armoring increases nearshore erosion rates and may cut off the supply of new terrestrial material to replace the lost substrate (Kraus and Pilkey 1988, Gabriel and Bodensteiner 2012; Palinkas et al. in press). This results in the loss of fine and organic particles adjacent to armored shores (Gabriel and Bodensteiner 2012; Strayer et al. 2012; Jennings et al. 2001). In the case of upland armoring, such as above sandy beaches, the upper dry zone may be lost, and the middle zone of the beach may contract (Dugan et al. 2008).

Sanford et al. (2014) recently examined changes in Chesapeake Bay shoreline characteristics associated with riprap, offshore segmented breakwaters, and living shorelines. Sediment cores were used to evaluate changes in sediment characteristics and accumulation rates, and time-series analysis of aerial photography was used to document changes to SAV type and cover (Palinkas et al. 2014). Preliminary results (Fig. 4) suggest that breakwaters are the only structure type for which mud and organic content increase after installation, likely due to sediment trapping inshore of the structure (see also Birben et al. 2007). Riprap and living shorelines seem to decrease the supply of fine sediments, likely through alteration of the land-water interface, as also reported by Gabriel and Bodensteiner (2012).

Ecosystem Effects

The ecological consequences of shoreline armoring are less well understood than the physical effects (Bulleri and Chapman 2010), but many possible negative impacts have been described. Shoreline armoring can sever the connection between terrestrial and aquatic environments, altering habitat and complexity in both the terrestrial and aquatic environment (Morley et al. 2012; Peterson et al. 2000; Romanuk and Levings 2005). Altered shorelines may have less riparian plant diversity and a higher incidence of invasive species (Strayer et al. 2012), such as the invasive strain of the common reed *Phragmites australis* (McCormick et al. 2010; Sciance et al. in review). Shoreline armoring can also create microclimates unsuitable for some native species (Rice 2006) and increase nutrient inputs to coastal systems (Groffman et al. 2004).

The severity of ecological impacts remains poorly understood (Jackson et al. 2008; Rice 2006), even as shoreline armoring continues to spread globally (Dugan et al. 2008; NRC 2006; Gittman et al. 2015). In the early 2000s, seminal work on the ecological consequences on shoreline armoring reported that structures impact coastal ecosystems by altering species assemblages at local and regional scales, but the exact impacts are largely site specific (Airoldi et al. 2005; Martin et al. 2005;

Moschella et al. 2005). In Wisconsin lakes, nearshore habitats along riprapped shorelines had coarser, more compacted sediments with lower organic matter, cooler temperatures, higher dissolved oxygen, and greater water clarity than habitats along natural shorelines (Gabriel and Bodensteiner 2012). In the Hudson River, no single shoreline type provided high values of all ecological functions, but engineered shorelines generally had less desirable biodiversity characteristics than natural shorelines (Strayer et al. 2012). Shoreline birds and beach invertebrates can be reduced alongside armored shorelines, potentially because of loss of habitat and forage (Dugan et al. 2008). Natural shorelines have been shown to have higher fish and nekton diversity than armored shorelines (Bilkovic and Roggero 2008; Gabriel and Bodensteiner 2012; Strayer et al. 2012). In Chesapeake Bay, fish food webs and size structure shifted toward more large bodied pelagic predators adjacent to riprap and bulkhead (Kornis et al. in revision). Small forage fish decline due to loss of habitat and refuge as well as increased predation pressure.

Effects on SAV

There is a small but growing body of literature the effects of shoreline condition on submerged aquatic vegetation (Gabriel and Bodensteiner 2012; Findlay et al. 2014; Patrick et al. 2014, 2015; Landry et al. in prep.). The common hypothesis is that armoring has detrimental effects on SAV through erosive habitat loss and deepening that occurs next to armored shorelines (Kraus and Pilkey 1988), as well as increased suspended sediments and bottom scour resulting from changes to near-shore wave dynamics (Findlay et al. 2014; Miles et al. 2001). These changes collectively result in lower SAV growth and survival (Moore and Jarvis 2008; Moore et al. 1997). The measured impact of shoreline armoring on SAV has varied among the few studies that have been conducted. Gabriel and Bodensteiner 2012 found that armoring had a negative effect on SAV in northern lakes, while Findlay et al. (2014) documented declines in Hudson River SAV adjacent to armoring in one period, but then no effect several years later. In Chesapeake Bay, the effects of armoring are also variable, and depend on upland land use, type of shoreline armoring, and the community of SAV species found in the littoral zone (Patrick et al. 2014; Patrick et al. 2015).

Comparisons among Chesapeake Bay subestuaries found that the abundance of SAV throughout a subestuary is negatively related to the percentage of the subestuary shoreline that is armored, and that the percentage of riprap shoreline was the strongest of 65 tested predictors of the variability in SAV abundance among subestuaries (Patrick et al. 2014). In addition, subestuaries with less than 5.4% riprapped shoreline had more SAV and more consistent SAV recovery though time than subestuaries with more than 5.4% riprap (Fig. 4, Patrick et al. 2014). However, the percentage of riprap in a subestuary may be correlated with other stressors within the subestuary (such as higher wave energy, more developed land, more boat traffic, etc.); so the negative association of riprap with SAV among subestuaries cannot be uniquely attributed to armoring (Patrick et al. 2014).

Other studies have identified more direct linkages between shoreline armoring and Chesapeake Bay SAV by focusing at a smaller scale and comparing SAV responses in beds directly adjacent to individual segments of armored or natural shoreline. In one field study, SAV beds adjacent to natural shorelines were significantly denser, less patchy, and wider (extending farther from shore) than beds adjacent to riprapped shorelines (Landry et al. in prep.). There were no significant differences in sediment type or wave height between the shoreline types, but the bottom slope was steeper adjacent to riprap shorelines (Landry et al. in prep.), supporting other reports that riprap increases wave reflectance, toe scour, and water depth (see Physical and Sediment Effects above).

Another study exploited digital maps of SAV beds and shoreline armoring throughout the Bay to quantify SAV abundance adjacent to thousands of shoreline segments (Patrick et al. 2015). Compared to natural shoreline, shoreline armoring was associated with lower adjacent SAV coverage in some settings, but the effects of armoring differed among salinity zones and among subestuaries with different dominant land uses in their local watersheds (Fig. 6, Patrick et al. 2015). Bulkhead had negative effects on SAV abundance in the polyhaline and mesohaline zones, but riprap had a statistically significant negative effect only in the polyhaline. SAV abundance was not affected by shoreline armoring in the oligohaline zone, possibly because the dominant oligohaline taxa are less sensitive to stressors than the taxa common in the other salinity zones. Shoreline armoring had a stronger negative relationship with SAV in subestuaries with less human land use in the local watershed, particularly in the polyhaline zone of the Chesapeake (Patrick et al. 2015). In highly developed or agricultural watersheds, SAV abundance was always low regardless of shoreline condition, possibly because very poor water clarity masked any possible effects of shoreline armoring (Patrick et al. 2015).

There is an important caveat in interpreting observational studies of armored shoreline effects on SAV. Armored shorelines are installed where erosion control is needed, which is likely to be in high-energy wave environments that may have limited SAV even before the armoring was installed. Manipulative experiments would resolve whether lower abundances near armored shorelines are due to armoring or to the preceding wave environments. One field study does provide strong evidence that riprap has a negative impact on SAV because riprap shorelines in the study were paired with nearby natural shorelines that had similar wave exposures (Landry et al. in prep.). The combined evidence from the field study and bay-wide analysis of thousands of shoreline segments (Patrick et al. 2015) strongly suggests that shoreline armoring adversely affects SAV in much of Chesapeake Bay.

Additional research could also better quantify how multiple stressors interact to affect SAV. Those connections can be unclear in observational studies with strong correlations among stressors. For example, watershed development, shoreline armoring, boating, dredging, all increase together as population grows. Controlled experimental manipulations of land use and shoreline armoring would be the scientific ideal, but such experiments are expensive and difficult implement where valuable private property is involved. Causal modeling frameworks, such as structural equation modeling or Bayesian hierarchical modeling, and simulation modeling may improve understanding of mechanistic linkages among stressors and between stressors and SAV responses. Better knowledge of those mechanistic connections can inform better management of SAV conservation and restoration.

Living Shorelines

Living shorelines have recently emerged as an alternative to hard structures, such as bulkheads, riprap, and seawalls. Burke et al. (2005) define living shorelines as "shoreline-management practices that provide erosion control benefits; protect, restore or enhance natural shoreline habitat; and maintain coastal processes through the strategic placement of plants, stone, sand-fill and other structural and organic materials (e. g. bio-logs, oyster reefs, etc.)". Many states, including Maryland and Virginia, have enacted regulations to encourage or require consideration of living shorelines prior to installing hard structures (Currin et al. 2010; CCRM 2010). However, there are still questions about the ecological value of living shorelines (Burke et al. 2005; Currin et al. 2010; NAS 2007). Natural shorelines (marshes and sandy beaches) seem to be preserved in many living-shoreline projects, but adjacent high-value benthic communities may suffer, especially if circulation patterns are disrupted or sand supplies to SAV beds are cut off. Significant concerns remain about the performance of living shorelines in high-energy environments and their ability to survive in the face of rapid sea level rise. A recent study of eight hybrid living shorelines (Burke et al. 2005) concluded that living shorelines designed with erosion control as a primary goal and habitat creation as a secondary goal had the most long-term habitat stability and maintenance. Bilkovic and Mitchell (2013) found that there was a demonstrative benefit in constructing a living shoreline, instead of riprap, in terms of the presence of diverse intertidal infauna. They suggest that living shorelines may be beneficial when the only alternative is traditional armoring, colonization by filter-feeding epifauna is likely, or impacts of installation can be minimized and shallow subtidal habitat can be maintained. They suggest that living shorelines may be detrimental when they unnecessarily or extensively replace existing habitat. For example, if there are healthy SAV beds near an existing armored shoreline, it may be better to leave the shoreline alone rather than risk disturbing the SAV through removal and replacement.

Living shoreline and riprap seem to decrease the supply of fine sediments, likely through alteration of the land-water interface (e. g., Gabriel and Bodensteiner 2012). Thus, those SAV species that prefer sediments with <35% mud and <5% organic content (Barko and Smart 1986, see Requirements and Stressor Responses Differ among SAV Communities and Species below) could potentially benefit from riprap or living shorelines, through decreased supply of mud and organic material from adjacent shorelines (but see overall negative effects of rip rap above). Breakwaters appear to be detrimental to SAV, unless sand layers are applied during installation, because sediment is trapped landward of the structure. Changes in sedimentation rates are more variable among structure types, and the impact of these changes to SAV is unclear. If rates are too fast, seeds could become buried; if rates are too slow, seeds could be lost to erosion and/or predation (Palinkas and Koch 2012).

Further research is needed to better quantify the effects of living shorelines on SAV. Past research has been limited by available information on the locations and types of existing living shoreline installations. For example, existing bay-wide maps of shoreline armoring (www.ccrm.vims) do not resolve living shorelines, which are instead categorized as either natural or riprap shorelines. The wide variety in construction methods, materials, designs, and pre-installation conditions among living shoreline installations also confounds efforts to understand their impacts on adjacent SAV and its habitat.

Docks and Piers

Increasing coastal populations also lead to more docks and piers (Kelty and Bliven 2003), which have individual and cumulative effects on SAV by lowering light availability via shading (Kenworthy and Fonseca 1996; Czerny and Dunton 1995). Experimental shading of SAV generally induces stress responses and reduces productivity (Dean and Durako 2007), and shading by docks has been shown to reduce productivity in several SAV species (Shafer 1999; Beal and Schmidt 2000; Landry et al. 2008; Loflin 1995; Burdick and Short 1999). Besides shading, docks and piers can also impact SAV through impacts during construction, and subsequent boat activity can damage SAV both directly and by further reducing light from sediment resuspension. Multiple docks in one area may also promote fragmentation of SAV beds that further reduces resilience to these impacts. The density of docks in Chesapeake Bay ranges between 0 and 242 per km (a dock every 16 m in the densest areas), and the median density is 16 per km (Patrick et al. 2015). Light is significantly reduced underneath piers, and the density of *Zostera marina* vegetative and flowering shoots directly under docks in Chesapeake Bay has been shown to be significantly lower than the density of shoots just a few meters away from the structure (Johnson et al. 2015). It is unknown how docks and piers may directly affect other species of submerged aquatic vegetation in this region, however, there is a weak negative relationship between dock density and SAV abundance throughout Chesapeake Bay (Patrick et al. 2014). The fragmenting and shading effects of docks may be particularly important in the Chesapeake Bay where SAV are already challenged by reduced clarity caused by other stressors.

Requirements and Stressor Responses Differ among SAV Communities and Species

Many studies have reported that the relationships between stressors and SAV differ among salinity zones (Patrick et al. 2014; Patrick et al. 2015; Landry et al. in prep.). Those studies used salinity zones as a proxy for different SAV communities because salinity is a strong environmental filter (*sensu* Tonn 1990; Poff et al. 1997) that controls which species of submerged plants can thrive in a given location (Moore et al. 2000). SAV species also differ in other habitat preferences and in stressor sensitivities (Fig 7, Moore et al. 2000; Patrick and Weller 2015). In the lower Bay, SAV communities are primarily composed of *Zostera marina*, *Ruppia maritima,* and macroalgae. *Zostera* and *Ruppia* have higher light needs and stronger preference for sandy substrate than upper Bay species (Fig. 7). In the upper bay, species richness is higher both within beds and among subestuaries, and SAV communities can include invasive species that benefit from some disturbances and canopy-forming species that deploy leaves at the water surface where water clarity is much less limiting (Fig. 7). The mesohaline zone, which contains 63% of the potential SAV habitat in Chesapeake Bay (Patrick and Weller 2015), encompasses many SAV communities (Moore et al. 2000), and mesohaline SAV can be quite sensitive to the year-to-year variations in salinity (Orth et al. 2010). Given the variety of SAV communities within the Bay, "one size fits all" approaches to modeling and managing SAV are not adequate. Optimizing conservation and restoration will require models and management strategies that consider the differences in composition, environmental requirements, and stressor sensitives among SAV communities. Additional research on the requirements and sensitivities of SAV species could provide better knowledge to inform those models and strategies.

Interacting Effects of Future Development and Climate Change

Future population growth, land development, and shoreline armoring will likely further stress Chesapeake Bay SAV. The population of the bay's watershed has increased from 13.5 million to 17.9 million since 1950 and is projected to grow to 20 million by 2030 (www.cbf.org). Forty percent of current US residents live in coastal shoreline counties (www.stateofthecoast.noaa.gov), and future population growth in the Chesapeake Bay watershed is likely to drive new land development near the Bay (Claggett et al. 2004) and associated shoreline armoring (Dugan et al. 2008; Gittman et al. 2015). SAV in the Chesapeake Bay and other coastal systems is already stressed and degraded by human activities (see above), and our review suggest that more land development and more shoreline armoring (as well as docks, piers, and marinas) will further reduce SAV habitat and abundance.

Population growth and land development will play out in the broader global context of global climate change, which will impose further stress on SAV. Global climate change is driving rising sea level, which is expected to increase 80 to 130 cm by 2100 in Chesapeake Bay, and the frequency and intensity of storms (and associated erosion) are also expected to increase (Arnold et al. in prep.). These changes will likely accelerate shoreline armoring to protect property from erosion and flooding. Along a low-relief natural shoreline, shallow coastal ecosystems might migrate landward as the shoreline erodes and sea level rise floods adjacent land. However, armoring fixes the shoreline position, prevents that migration, and maroons SAV in continuously deepening water where more intense storms may generate stronger waves. Thus, rising sea level and shoreline armoring may together eliminate large swaths of the shallow water habitat of SAV.

On the other hand, SAV can help moderate the impact of anthropogenic carbon emissions on climate change. Coastal wetlands and seagrass meadows can absorb and store large amounts of carbon from the atmosphere (so called "blue carbon"). One study estimates that seagrass beds store as much carbon per unit area as terrestrial forests; however, much of that carbon can return to the atmosphere as CO_2 when the seagrasses are lost (Fourqurean et al. 2012). Managing land use and shoreline armoring to limit negative impacts on SAV will maximize the potential for SAV to persist in the changing climate and to help reduce atmospheric CO_2 and associated climate change.

Conclusion

Land use and shoreline armoring are significant stressors on submerged aquatic vegetation (SAV), which is also impacted by rising sea level and changes in weather patterns from global climate change. Land use impacts, especially from agriculture and developed land, have contributed to lower SAV abundance throughout the Chesapeake Bay, primarily by supplying nutrients and sediments that reduce water clarity and light availability. Shoreline armoring can also reduce SAV habitat by promoting deeper water and reduced water clarity; but the reported effects of armoring differ among salinity zones and among subestuaries with watersheds dominated by different land uses. The strongest negative impact of armoring has been reported in polyhaline zone, where SAV is dominated by two species of marine seagrasses. Also in the polyhaline, armoring has clear negative effects on SAV in subestuaries with mostly forested watersheds, but little impact in subestuaries where highly agricultural or developed land use limits SAV regardless of armoring. The effects of armoring and its interaction with land use are more complex in the mesohaline and fresher parts of the bay. These salinity zones include many SAV communities that should not be lumped together because they have different stressor-response relationships. New research that quantifies the responses of particular SAV species and communities together with new research that confirms mechanisms linking stressors to responses may clarify patterns that are presently unclear or counterintuitive. That work would inform improvements in the models used to predict future conditions, compare the like consequences of different management scenarios, and guide management decisions throughout the bay.

Acknowledgements This work is part of the project *Chesapeake Bay Submerged Aquatic Vegetation (SAV) Habitat Requirements and Restoration Targets: A Third Technical Synthesis* which was funded by a 2013 award from the U.S. Environmental Protection Agency through a Chesapeake Bay Implementation Grant authorized by section 117 of the Clean Water Act. We thank Lee Karrh and Ken Moore for organizing and editing the technical synthesis volume, and we thank the other synthesis participants for their ideas and helpful comments.

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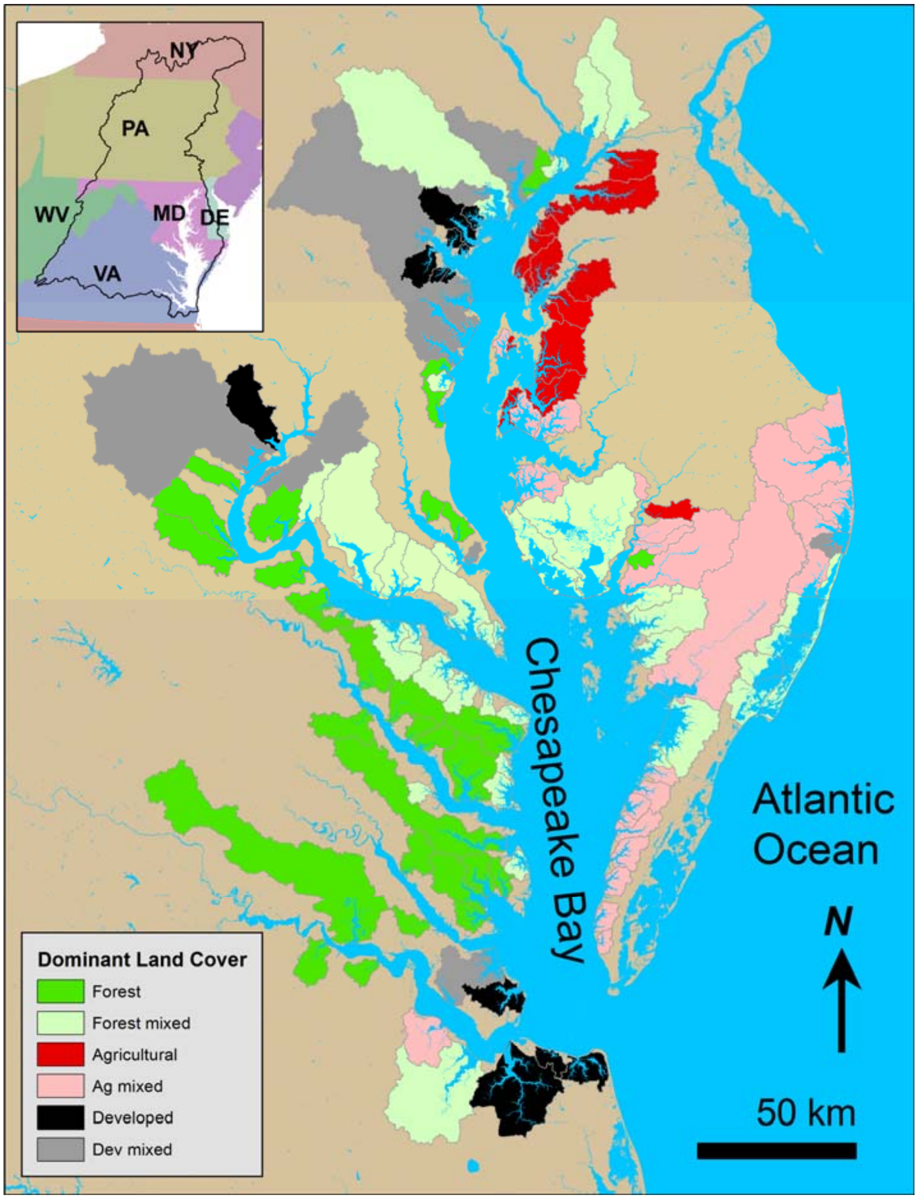

Fig. 1 Subestuaries of the Chesapeake Bay colored by dominant land cover in their local watersheds (Li et al. 2007). The map includes 100 Chesapeake Bay subestuaries and 14 Coastal Bay systems along the Atlantic coast (Patrick et al. 2014)

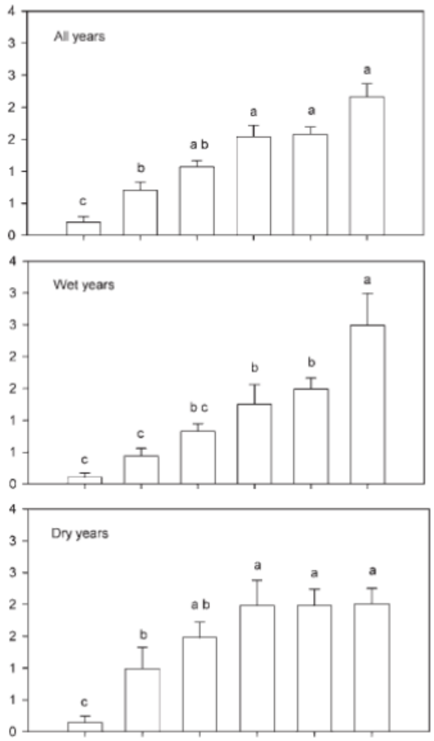

Fig. 2 SAV abundances with standard errors for different dominant land covers for all years and for dry years and wet years only (Li et al. 2007)

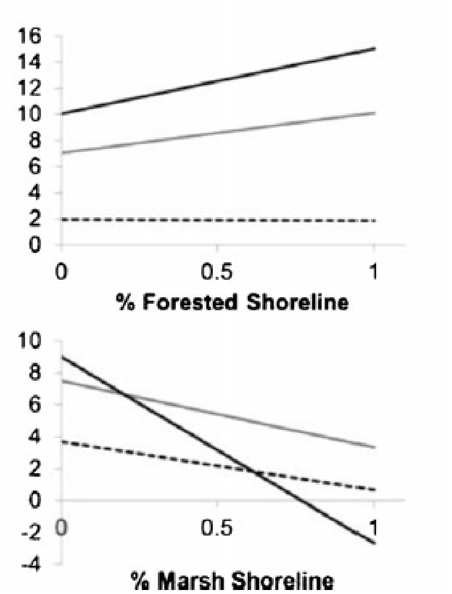

Fig. 3 The relationships between SAV abundance and the fraction of shoreline occupied by forest (top) or marsh (bottom) vary among salinity zones (solid line polyhaline, dashed line mesohaline, and oligohaline gray line) with the strongest effects in the polyhaline zone (Patrick et al. 2014)

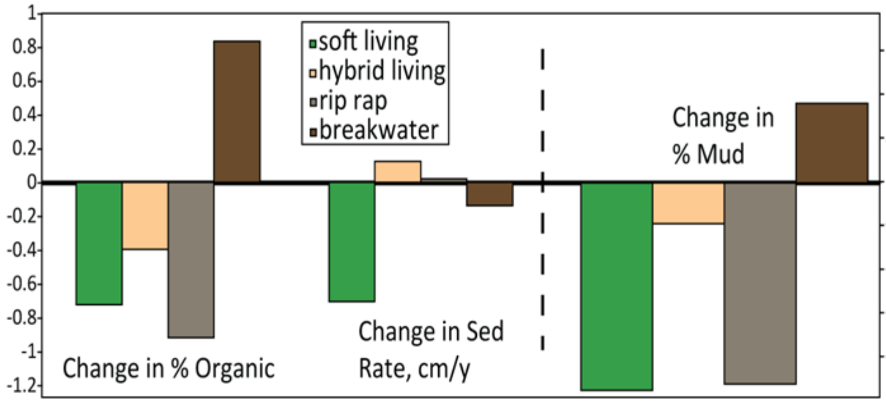

Fig. 4 Average changes in organic content (%), sedimentation rate (cm/yr), and mud content (%) adjacent to shorelines with four types of shoreline armoring structures (Palinkas et al. (2014). In this study, soft living shorelines use only vegetation to control erosion, and hybrid living shorelines combine vegetation with hard materials, such as breakwater or rip rap.

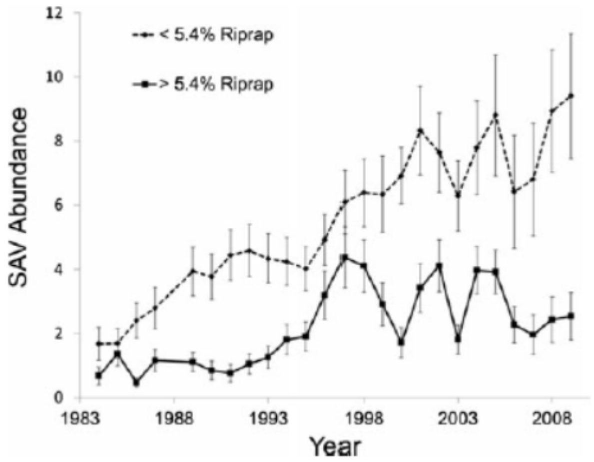

Fig. 5 Subestuaries with little riprap (dashed lines) have significantly greater SAV abundance and have showed continued recovery since 1984. In contrast, subestuaries with more riprap (>5.4% of the shoreline) have lower abundance and little recovery since 1995 (Patrick et al. 2014). The 5.4% breakpoint was the first split in a classification tree analysis of 65 potential predictors of SAV abundance (Patrick et al. 2014)

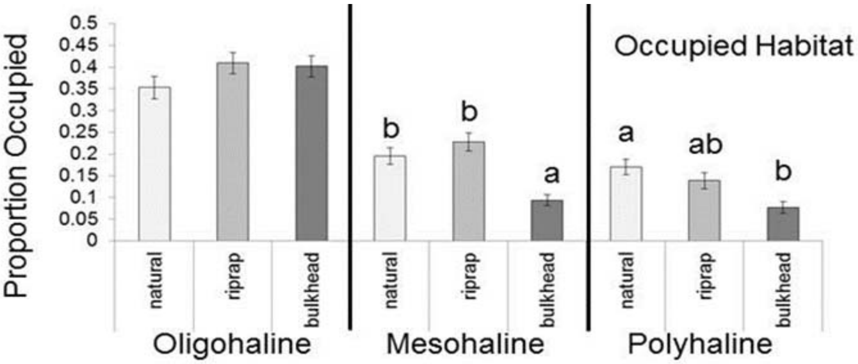

Fig. 6 SAV abundance directly adjacent to individual shoreline segments (natural, riprap, or bulkhead) in three salinity zones. Letters indicate that abundances that are not significantly different in a two way ANOVA of SAV abundance versus shoreline type and salinity. There was no significant effect of shoreline condition in the oligohaline zone (Patrick et al. 2015)

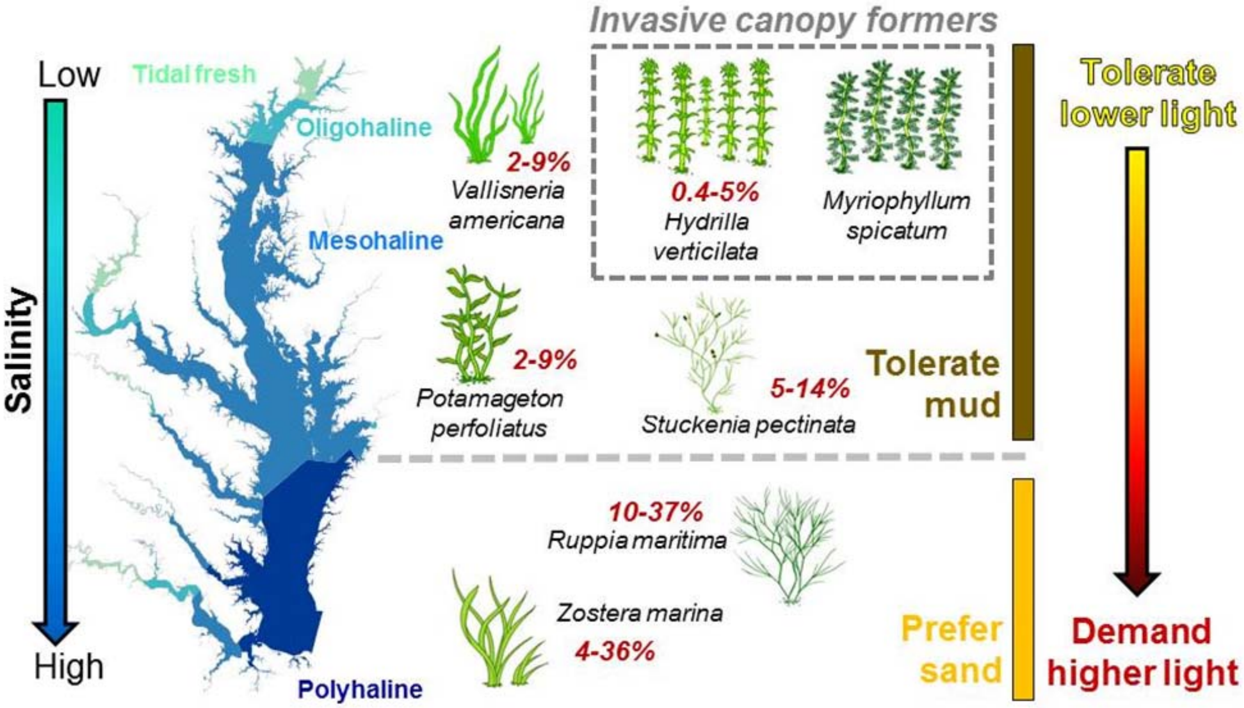

Fig. 7 Salinity controls the SAV species that can occur in each salinity zone. The species have different light penetration requirements (red numbers) and substrate requirements, and some oligohaline species are invasive canopy formers that can overcome turbid water by deploying leaves at the surface. These species differences lead to communities with very different stressor tolerance (Patrick and Weller 2015)

21^{ST} CENTURY CLIMATE CHANGE AND SUBMERGED AQUATIC VEGETATION IN THE CHESAPEAKE BAY

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ABSTRACT

The Chesapeake Bay was once renowned for expansive meadows of marine and freshwater submerged aquatic vegetation. However, like many estuaries, the Chesapeake has suffered substantial loses of SAV and today only 10% of the original meadows survive. In the 21st century, restoration efforts will be complicated by new stressors associated with accelerating climate change. In the Chesapeake Bay these are: a mean temperature increase of 2-6°C, a 50-160% increase in CO_2 concentrations, and sea-level rise of 0.7-1.6m. Warming alone has the potential to eliminate eelgrass (*Zostera marina)*, the dominant seagrass, from the Chesapeake. Already high summer temperatures cause mass die-offs of this cool-water species, which lives near its thermal limits. During this century warming will continue and the Chesapeake will begin to exhibit characteristics of a subtropical estuary, with summer heat waves becoming more severe. This will favor native heat-tolerant species such as widgeon grass (*Ruppia maritima*) and certain ecotypes of freshwater SAV, and may facilitate colonization by subtropical seagrasses (e.g., *Halodule* spp.). Intensifying human activities will also fuel biological processes, such as eutrophication, that drive coastal zone acidification. The resulting high CO_2 / low pH conditions, shaped by diurnal, tidal, and seasonal cycles, may benefit SAV. The *"CO_2 fertilization effect"* has the potential to stimulate photosynthesis and growth in at least some species of SAV and this may offset the effects of thermal stress, facilitating the continued survival of eelgrass at some locations. This equipoise between two forces - thermal stress and acidification - may ultimately determine the fate of cool-water plants in warming estuaries such as the Chesapeake Bay. Finally, sea level rise will reshape the shorelines of estuaries, especially the Chesapeake Bay where land subsidence is significant. Where waters are permitted to migrate landward, suitable habitat may persist; however, where shorelines are hardened SAV may be lost. Our understanding of SAV responses to these three stressors have greatly improved in recent years and allow us to make basic, testable predictions regarding the future of SAV in estuaries. However, the indirect effects of climate change on associated organisms, including fouling organisms, grazers, and microbes, are poorly understood. These indirect effects are likely to prevent smooth transitions, triggering abrupt phase changes in estuarine and freshwater SAV communities subjected to a changing climate.

THE NEW CHESAPEAKE

The Chesapeake Bay is entering a period of new challenges. During this century, climate forces will transform it from a temperate estuary to a subtropical one, unless carbon emission trajectories change dramatically. Such a transition will have profound implications for submerged aquatic vegetation (SAV), which have been a defining characteristic of the Chesapeake ecosystem for centuries. To manage the health of Chesapeake Bay SAV we must now address the old challenges of the 20th century in the new context of accelerating global climate change.

In the current century, the familiar challenges of increased sedimentation, eutrophication, turbidity, anoxia and hypoxia, habitat destruction, and the introduction of invasive species (Kennish et al. 2014) will persist for freshwater, estuarine and marine ecosystems. Coastal ecosystems will also be increasingly impacted by a changing climate, including ocean warming, sea-level rise, and the increasing "acidification" of coastal waters. Such scenarios of human disturbances are common for U.S. estuaries (Sillimen et al. 2009; Lotze 2010). They follow a predictable sequence of events: human expansion, overfishing, pollution, mechanical destruction of habitat, and the introduction of invasive species introductions (Jackson et al. 2001). Climate change, the most recent environmental impact, threatens current and future efforts to restore SAV in the Chesapeake Bay (e.g., Carr et al. 2012).

THE CHESAPEAKE IN THE 20th CENTURY

The Chesapeake Bay was once renowned for expansive meadows of marine and freshwater SAV, including eelgrass (*Zostera marina*), widgeon grass (*Ruppia maritima)*, American wild celery (*Vallisneria americana*), coontail (*Ceratophyllum demersum*), common waterweed (*Elodea canadensis*), horned pondweed (*Zannichellia palustris*), water stargrass (*Heteranthera dubia*), and various pondweeds (*Stuckenia pectinata* and other *Potamogeton* spp.). Historically, these species covered an estimated 250,000 ha in the bay, or about 20% of the bottom area. Today, only 10% of the original Chesapeake Bay SAV meadows survive, covering about 2% of the bay floor at depths < 2 m (Moore et al. 2000; Orth et al. 2010). Some of these vegetated areas are dominated or threatened by invasive species, including Eurasian water milfoil (*Myriophyllum spicatum*), waterthyme (*Hydrilla verticillata*) and Brazilian waterweed (*Egeria densa*).

The first signs of ecological degradation, including the loss of SAV meadows, coincided with European colonization in the early 1700s (Jackson et al. 2001; Yasuhara et al. 2012). In the 1930s, mass die-offs were triggered by an outbreak of the wasting disease pathogen, *Labyrinthula* spp., and a destructive hurricane (Orth and Moore 1983, 1984, 1986; Moore et al. 2000; Orth et al. 2006). These were followed by a period of some recovery from 1940 - 1960. Subsequent declines were associated with poor water quality, specifically increasing eutrophication and hypoxia, and Hurricane Agnes in 1972, one of the most damaging storms to hit the Chesapeake Bay (Orth and Moore 1983; Kemp et al. 2005; Stevenson and Kearney 2005, Wazniak et al. 2007; Yasuhara et al. 2012). By the late 1970s and early 1980s, SAV abundances were at all-time lows and nutrient pollution was identified as the primary cause of the decline (Orth et al. 2010). Modest gains were made in the 1990s but these were offset by the failure of several natural and restored eelgrass beds in the mid-bay from 2005 to 2010 (Orth et al. 2010; Moore et al. 2012). Recently, encouraging recoveries of aquatic vegetation in certain areas have been documented. For instance, freshwater SAV has significantly increased in cover, in part due to the recovery of aquatic grasses in the upper-Bay along the Susquehanna flats. In addition, reseeding efforts in the cooler, less eutrophic and higher salinity waters of the Virginia coastal bays have been successful, resulting in the expansion of restored eelgrass populations at rates of ~66% per year for a decade (Orth et al. 2010; Moore et al. 2012). However, these gains have been restricted to specific localities. Overall, populations of eelgrass, historically the dominant submerged plant in the polyhaline portion of Chesapeake Bay, have not recovered.

For nearly half a century, coalitions of federal, state, and local agencies have sought to restore Chesapeake Bay SAV to "*reflect 1930s abundance*" (e.g., 2000 Bay goal). Later, a more specific goal was established to restore 185,000 acres (75,000 ha) of SAV by 2010. However, SAV currently covers less than 100,000 acres (40,500 ha) in the Chesapeake, falling well short of these goals. Restoration efforts have been impeded by a growing coastal population and intensifying agricultural impacts on water quality, especially transparency, in the Chesapeake Bay.

Similar SAV declines have been reported in nearby estuaries, including the inland bays of North Carolina (Micheli et al. 2008). Indeed, the loss of marine and estuarine flowering plants in the Mid-Atlantic reflects a world-wide trend. Globally, approximately 60 species of seagrasses inhabit the coastal margins of every continent except Antarctica, covering an area of approximately 177,000 km^2 of marine and brackish habitat (Waycott et al. 2009). Freshwater species inhabiting freshwater and oligohaline portions of estuaries substantially add to this global diversity of submerged aquatic plants. Continued coastal development, however, threatens seagrasses communities (Orth et al. 2006, 2009); abundances have declined 29% globally since 1879 and for the last several decades seagrasses have been disappearing at a rate of 110 km^2 yr^{-1} (Lotze et al. 2006; Micheli et al. 2008; Waycott et al. 2009; Hughes et al. 2009). At current rates, 30–40% of world seagrasses could be lost in the next 100 years.

CURRENT VALUE OF CHESAPEAKE BAY SAV

Aquatic plants are a critical component of a healthy Chesapeake and, as such, have been used as bio-indicators of bay health. Their roles have been well-described: they form dense meadows, baffle currents, filter water, absorb nutrients, and accelerate the settlement of marine larvae. They are key primary producers, often called foundation species, with rates of productivity "*matching or exceeding the most productive terrestrial systems*" (e.g., Worm et al. 2005; Orth et al. 2006; Waycott et al. 2009). SAV production nourishes coastal food webs (e.g., Harrison and Mann 1975; Fenchel 1977; Thayer et al. 1977). In the Chesapeake Bay, SAV are grazed by migrating waterfowl (Stevenson 1988), from which the plants sometimes derive their common names (e.g. "redhead grass", "widgeon grass"). SAV also serve as habitat for fish, crustaceans, and shellfish, including species supporting commercial and recreational fisheries (Peterson 1979; Heck and Thoman 1984; Orth et al. 1984; Beck et al. 2001; Heck et al. 2003; Larkum et al. 2006; Jones 2014).

The value of SAV can be quantified in terms of these ecosystem services, estimated at approximately \$1.9 trillion per year, globally. Waycott et al. (2009) estimated the value of healthy SAV communities at as much as \$28,916 ha^{-1} yr^{-1} (also see Costanza et al. 2014). By this measure, the estimated value of Chesapeake Bay SAV beds would exceed \$2.9 billion yr^{-1}. Dewsbury et al. (2016) recently suggested that such indirect estimates may actually underestimate the true value of SAV communities. It is clear, however, that the "value" reaches well beyond SAV communities themselves: trophic interactions extend the benefits to other nearby communities, including salt marshes, and to coastal fisheries in general (Duarte 2000; Stevenson et al. 2002; Jones 2014).

An additional service of seagrass meadows has emerged recently: the capture and long-term storage of "blue carbon". Globally, underwater meadows can act as effective carbon sinks, which sequester approximately 10% of oceanic organic carbon, an estimated 27.4 Tg carbon yr^{-1}. In total they may store as much as 19.9 Pg of this "blue carbon" in the form of anaerobic, organic-rich loams for thousands of years (Duarte et al. 2010; Fourqurean et al. 2012). The protection and, to a lesser extent, restoration of coastal seagrass populations is likely to be a viable strategy for long-term carbon capture and storage (Irving et al. 2011; Fourqurean et al., 2012; Greiner et al. 2013). This process of carbon capture may also counteract ocean acidification, sheltering vulnerable organisms in and near SAV communities from the full effects of high CO_2 / low pH conditions, at least during the daytime. The fact that carbon capture and storage has traditionally not been included in ecosystem service valuations of seagrasses, and SAV in general, implies that the true value of these communities remains underestimated.

THE CHESAPEAKE IN THE 21st CENTURY

Any attempt to predict the future of SAV in the Chesapeake Bay must consider the impacts of accelerating climate change (reviewed by Short et al. 1999 and Duarte 2002). By the end of the century, the Chesapeake region will be subject to a mean temperature increase of 2-6°C, 0.7-1.6m of sea-level rise, and a 50-160% increase in CO_2 concentrations (Najjar et al. 2010). These changes will alter the distribution, health, and survival of submerged aquatic plants.

Some impacts of climate change will effect SAV directly. Others, such as changes in rainfall and the frequency and intensity of storms, will be indirect (Day et al. 2011; Statham 2012). Both will interact to modify the effects of other stressors, including those associated with water quality (Porter et al. 2013; Kennish et al. 2014). **Here we consider three aspects of climate change that will directly impact seagrass physiology, productivity, health, reproduction, and survival in future decades: increasing temperatures, ocean acidification, and sea level rise.**

1. TEMPERATURE

Chesapeake Bay waters are predicted to warm by 2 to 6° C, on average, during this century. This is similar to global forecasts for surface air temperatures and ocean surface temperatures, which are predicted to increase 1.1 to 6.4° C and 3 to 4 ° C, respectively (Levitus et al. 2001; Meehl et al. 2007; Intergovernmental Panel on Climate Change [IPCC] 2007, 2014). These increases in temperature would be in addition to the 0.8 °C increase in mean global surface temperatures that has already occurred, as a result of atmospheric CO_2 exceeding 400 ppm. There are direct, first-order relationships between atmospheric carbon dioxide levels, air temperatures, and Chesapeake Bay water temperatures (Wood et al. 2002). In some areas of the Bay, such as the main stem of the Bay and the Potomac estuary, water temperatures are increasing faster than air temperatures (Ding and Elmore 2015). Unless there is a drastic change in the prevailing "business-as-usual" scenario whereby CO_2 levels continue to rise, exceeding 1000 ppm in the atmosphere over the next century, observed warming of Chesapeake Bay waters will continue in the future. In this case the Chesapeake Bay is likely to develop characteristics of a subtropical estuary by the next century.

Although average temperature projections represent a useful window into climate change, they provide an incomplete picture of the thermal environment, particularly in the near-term when the most devastating temperature effects may result from an increased in the frequency, duration, and amplitude of periodic summer heat waves (IPCC 2014). Furthermore, warming of the Chesapeake Bay will not occur uniformly. Local water temperatures will continue to depend upon circulation patterns that affect ocean mixing, precipitation, and other factors, all of which are impacted by climate change. The greatest and most inconsistent warming will almost certainly occur in shallow waters, the habitats of submerged vegetation, as well as in areas affected by urbanization, such as the Patapsco River in Baltimore (Ding and Elmore 2015).

For Chesapeake Bay SAV, which can live close to their thermal limits, even moderate warming is problematic (Somero 2002; Hughes et al. 2003). Most Bay species are considered to be "temperate" species, with an optimal growth temperature of 11.5° C to 26° C. In general, increasing temperatures alter rates of photosynthesis and respiration, interfere with life-cycles, trigger disease outbreaks and algal blooms, and cause increased seagrass mortality e.g., (Campbell et al. 2006). The ability of SAV to tolerate warming will however be species-specific (McMahon 2005; Campbell et al. 2006; Walker et al. 2006).

Eelgrass. General consensus supports the prediction that increased temperatures will adversely impact eelgrass populations during this century (Najjar et al. 2010). *Zostera marina* is a temperate species with an optimal water temperature of approximately 10-20° C, with 16-17° C being an optimal range for seedling growth (Niu et al. 2012). Colder temperatures are tolerated and plants remain healthy at 5° C. At these colder temperatures growth is slowed (Nejrup and Pedersen, 2008) but photosynthesis:respiration ratios are maximized (Marsh et al. 1986; Zimmerman et al. 1989). Eelgrass growth rates increase linearly from 5 to 25° C (Kaldy 2014). Beyond this temperature, however, deleterious effects emerge. High temperatures of 25-30° C depress rates of photosynthesis and growth (Zimmerman et al. 1989; Niu et al. 2012) and dramatically increase mortality. Marsh et al. (1986) determined that above 30°C, *Zostera marina* has a negative net carbon balance, photosynthesis becomes overwhelmed by increasing rates of respiration, and plants decline rapidly. The impact of elevated temperatures can be worse in low light. Kaldy (2014) showed the temperature-induced increase in eelgrass respiration can be problematic even at temperatures between 10-20° C when light is limiting photosynthesis (also see Ewers 2013; Jarvis et al. 2014). In theory, eelgrass could escape deleterious temperatures by retreating to deeper, cooler waters (McKee et al. 2002; York et al. 2013). Increasing colonization depth, however, is not likely to be a successful strategy for adapting to future climate change, as the lower depth of eelgrass is restricted by light penetration and climate change is likely to cause further deterioration of water clarity in the Chesapeake (Thayer et al. 1984; McKee et al. 2002; York et al. 2013). The poor tolerance of elevated temperatures suggests a bleak future for eelgrass in the Chesapeake Bay.

The impacts of thermal stress have already been observed in the Chesapeake and neighboring coastal bays in Delaware, Maryland and Virginia. Extended warm periods, such as those occurring in the 1980s and 1990s, have been linked to population declines of eelgrass in the eastern Atlantic (Glmarec 1997). Acute warming from summertime heat waves has triggered shoot mortality and population declines. Eelgrass diebacks in the Godwin Islands and York River Chesapeake Bay National Estuarine Research Reserve in Virginia during 2005 were attributed to a greater frequency and duration of water temperatures above 30°C (Moore and Jarvis 2008; Moore et al. 2014). These authors noted a tipping point at 23° C; changing eelgrass cover from 2004 to 2011 was linked with temperatures below and above 23° C, respectively. Although a variety of other factors influence the thermal tolerance of Z. *marina*, it is clear that temperatures above 25°C or, more generally, increases of 1-5°C above normal summertime temperatures, can trigger large-scale die-off of eelgrass in the Chesapeake Bay (Jarvis et al. 2012; Moore et al. 2012, 2014; Jarvis et al. 2014). For example, these authors predicted that: (1) short-term exposures to summer temperatures 4-5° C above normal will *"result in widespread diebacks that may lead to* Z. marina *extirpation from historically vegetated areas, with the potential replacement by other species"* (Moore et al. 2014); (2) longer-term average temperature increases of 1-4° C are predicted to "*severely reduce or eliminate" Zostera marina* from the Chesapeake Bay (Moore et al. 2012, 2014); and "*an increase in the frequency of days when summer water temperature exceeds 30°C will cause more frequent summer die-offs*" and is likely to trigger a phase change from which *"recovery is not possible"* (Carr et al. 2012).

Similar losses have been predicted in neighboring regions, e.g. for the Bogue Sound-Back Sound in North Carolina (Micheli et al., 2008). Restored eelgrass meadows are also vulnerable as higher temperatures (at or above 30° C) are associated with summer die-offs and failures of these new meadows (Tanner et al. 2010; Carr et al. 2012). Similarly, successful SAV restoration in the neighboring coastal bays has been attributed to cooler temperatures (Orth et al. 2010, 2012; Moore et al. 2012) and more favorable water quality resulting in a better light environment (Zimmerman et al. 2015).

Widgeongrass. *Ruppia maritima* tolerates a wider range of temperature and salinity conditions than does eelgrass (Stevenson 1988). It ranges along the eastern coastline of North America from Florida to Nova Scotia and is distributed within meso- and polyhaline portions of the Chesapeake Bay, though populations are patchy and ephemeral (Stevenson et al. 1993). Although biomass does not approach that of eelgrass in the lower polyhaline region of the Bay, it can be the dominant SAV species in the meso- and polyhaline regions of the central Bay, even in intertidal flats when temperatures are moderate in spring and fall (Staver et al. 1996). Unlike eelgrass, *Ruppia* tolerates a wide range of water temperatures ranging from 7 to 40° C. Ideal growth conditions are have been reported to range from 20 to 25° C or even 18 to 30° (see Pulich 1985; Lazzar and Dawes 1991; Moore et al. 2014). Anderson (1969) sampled SAV from a thermal plume at the Chalk Point Power Plant on the Patuxent River and found that the lethal temperature was 45°C. Although *Ruppia* tolerates these conditions, higher temperatures have a negative influence on photosynthesis beyond 25°C. For instance, Evans et al. (1986) observed that the maximum photosynthetic rate (P_{max}) increased with temperatures up to 23°C before becoming inhibited (compared to 19°C for *Z. marina* in the same study).

Ruppia sp. reproduction is also impacted by temperature. Optimal seed germination occurs at 15-20°C. In Europe, seed germination was observed to occur at temperatures beginning at 16°C but only after a period of cold stratification at 2-4°C (Van Vierson et al. 1984). If the Chesapeake becomes more subtropical, it may not eventually be cold enough for presently adapted *Ruppia* plants to reproduce by seed, reducing overall population resilience. Temperature changes may have other subtle effects on future population cycles; for example, plants germinated at low temperatures reproduce much more quickly than plants germinated at higher temperatures.

Ruppia's very wide temperature tolerance may make it a "winner" in a warmer climate, replacing eelgrass in much of the lower Bay. This has already been observed in some locations, at least temporarily (Stevenson et al. 1993), when unusually high summer temperatures caused die-offs of eelgrass. For example, *Zostera*-to-*Ruppia* transitions occurred in San Diego Bay following the 1997-8 El Niño Southern Oscillation (ENSO), leading Johnson et al. (2003) to predict that a warming of 1.5 to 2.5° C would result in *"a permanent shift in the local seagrass vegetation from eelgrass to widgeongrass"* in this bay.

Freshwater species. Lower salinity regions of the Chesapeake and its tributaries are also experiencing significant warming (Seekell and Pace 2011; Ding and Elmore 2015; Rice and Jastram 2015). Warming may decrease photosynthesis and increase respiration (Ryan 1991), thereby impacting the distribution, modes of reproduction, germination, growth, and dormancy of freshwater SAV (Welch 1952; Barko and Smart 1981; Lacoul and Freedman 2006).

The response of freshwater aquatic plants to climate warming is often species-specific, and may vary even for locally-adapted "biotypes" of a single species (Haller et al. 1976; Haag and Gorham 1977; Madsen and Adams 1988; Barko and Smart 1981; Pip 1989; Svensson and Wigren-Svensson 1992; Spencer and Ksander 1992; Santamaria and Van Vierssen 1997; Rooney and Kalff 2000; Sala et al. 2000; Lacoul and Freedman 2006; Amano et al. 2012). Some species exhibit earlier germination and increased productivity, while others do not (McKee et al. 2002; Lacoul and Freedman 2006). Most submerged freshwater plants require temperatures above 10°C during the growing season, exhibit optimal growth between 10° and 20° C, but do not survive temperatures above 45°C (Anderson 1969; Lacoul and Freedman 2006).

Myriophyllum spicatum, a non-native species, also has a broad temperature range with optimal photosynthesis between 30 to 35°C (Barko and Smart 1981; Nichols and Shaw 1986). Similarly, net photosynthesis of *Potamogeton crispus*, another non-native species, is also highest around 30° C (Nichols and Shaw 1986). *Stuckenia pectinata* prefers 23 to 30° C for early growth (Spencer 1986) and can tolerate 35° C (Anderson 1969). Perhaps the most temperate sensitive species that occurs in freshwater areas of the Bay is *Elodea canadensis* with a reported range of 27 to- 35° C (Santamaria and van Vierssen 1997; Olesen and Madsen 2000). In complementary growth chamber experiments, *Elodea canadensis* from the Chesapeake Bay performed best at 28°C but were stressed at higher temperatures that are commonly experienced in the thermal plume (32°C) of C. P. Crane Power Station (Beser 2007). However, population of the same species may vary widely in their adaptation to warm temperatures. For example, *Vallisneria americana*, the most dominant freshwater SAV species in the Chesapeake Bay, is reported to grow best between 33 and 36° C (Korschgen and Green 1988). However, Beser (2007) observed that *Vallisneria* from the Chesapeake Bay were able to survive 36°C over a six-week period whereas plants from Wisconsin could not, suggesting that conspecific plants are acclimated or are adapted to different temperatures through phenotypic plasticity and genetic diversity.

Warming may also impact the reproduction of freshwater SAV. Germination for many species requires cold stratification. However, warmer conditions and an extended growing season, now increasing at a rate of over 1 day per year (Kari Plough et al. in prep.), cause species such as *Potamogeton* spp., *Stuckenia pectinata* and *Vallisneria americana* to germinate more quickly, grow deeper, become more productive, and yield more biomass (Hay et al. 2008; Jarvis and Moore 2008; Yin et al. 2013; Bartleson et al. 2014). Cao et al. (2014) observed that temperature also increases growth of periphyton on aquatic macrophytes (an effect that was dependent upon the presence or absence of periphyton grazers). Periphyton overgrowth is a major problem for the survival of *Potamogeton perfoliatus* in the upper portion of Chesapeake Bay where grazers are not effective in cleaning leaves, leading to a decline of light availability (Kemp et al. 1983; Staver 1984).

Unlike marine seagrass beds that are often monotypic, freshwater beds often consist of a diversity of SAV species (Crow 1993) with different niche requirements. These differences provide some insurance against changes in the environment - as one species declines due to unfavorable conditions, another may compensate and increase in abundance. Thus, it has been suggested that increasing temperatures may have neutral effects on communities or even enhance species diversity within temperate freshwater aquatic plant communities (Grace and Tilley 1976; Haag 1983; Rooney and Kalff 2000; Heino 2002; Lacoul and Freedman 2006). However, warming may eventually compromise and weaken diversity. For example, observations of the SAV community within and outside the thermal effluent of the power generating station C. P. Crane located along Dundee and Saltpeter Creeks of the Gunpowder River, MD, (Beser 2007) show that SAV cover and diversity are both generally lower inside the thermal plume and that temperature is an important environmental gradient. SAV diversity is also impacted when warming boosts the productivity of non-native species such as *Hydrilla verticillata*, which invaded the tidal freshwater regions of the Chesapeake Bay from further south in the 1980s. This invasive species possesses a variety of physiological adaptations that allow it to competitively exclude native species (e.g. *Vallisneria americana*) in freshwater (Haller and Sutton 1975; Staver and Stevenson 1995).

It is worth noting that freshwater SAV habitats have been among the most highly-altered ecosystems, impacted by human activity and invasive species, motivating new insights and approaches to resource management in the 21st century. Restoring freshwater SAV communities to *"an earlier condition or stable state"* is often no longer possible (Moyle 2014). This realization spawned the new field of "reconciliation ecology", described by Rosenzweig (2003) as the *"science of inventing, establishing, and maintaining new habitats to conserve species diversity in places where people live, work, and play"* and by Moyle (2014) as *"a practical approach to living with the new reality"* where resource managers take *"an active approach to guiding ecosystem change to favor desired species"* (see Hershner and Havens, 2008). Within the context of climate change, our poor understanding of how warming impacts freshwater SAV limits this type of "active management". To manage the impacts of climate warming on freshwater aquatic plants, we require not only a better understanding of thermal tolerance of dominant plant species, but also their interactions with grazers and microbiota, which can be symbiotic or pathogenic (e.g. fungi, bacteria, archaea, viruses, phages and etc.)

Comparison to other regions. Thermal stress impacts seagrasses inhibiting other coastal ecosystems beyond the Chesapeake. For example, it is well-established that changing climate conditions have impacted populations of *Posidonia oceanica* in the Mediterranean (between 1967 and 1992; Marba and Duarte 1997). More recently, Olsen et al. (2012) documented reduced growth rates, leaf formation rates and leaf biomass per shoot in response to warming from 25-32°C on *Posidonia oceanica* and *Cymodocea nodosa* from the Mediterranean Sea. Climate-induced thermal stress is a concern for Australian seagrasses as well, where *Zostera muelleri* was deemed *"sensitive to temperatures predicted under future climate change scenarios"* (York et al. 2013). *Z. muelleri* from southeast Australia has a thermal tolerance similar to *Z. marina* in the Chesapeake: it "grows optimally at 27° C, shows signs of thermal stress at 30°C, and exhibits shoot mortality at 32° C" (York et al. 2013). A modest warming of 2° C is believed to be responsible for a loss of *Z. muelleri* and a transition to the smaller, more tolerant *Halophila ovalis*, a shift that has persisted at one site for 33 years. Thomson et al. (2015) reported the >90% die-back of the temperate seagrass, *Amphibolis antarctica*, in Shark Bay, Australia, following an extreme heat event in 2010-11. These, and other studies, strongly suggest that climate warming could lead to the local extinction of seagrasses with low thermal tolerance in regions beyond the Chesapeake (Short and Neckles 1999).

WARMING IMPACTS: COMPLICATING FACTORS

Climate warming will alter the diversity, composition, and functioning of SAV, grazers, fouling organisms, and pathogens (Blake and Duffy 2010; Blake et al. 2012). Some of the community-level changes that are likely to be triggered by warming include: increased eutrophication and poorer light penetration; proliferation of epiphytes that grow on the leaves of SAV; increases in harmful sediment sulfide levels (Goodman et al. 1995; Garcia et al. 2013); and increases in outbreaks of the seagrass wasting disease caused by the microbial pathogen *Labyrinthula* spp. (Kaldy 2014, but see

Olsen and Duarte 2015 and Olsen et al. 2015). These interacting forces are likely to trigger episodic events, pass ecological thresholds, trigger tipping points, and induce phase changes so as to make it more difficult to predict the future of SAV communities. Wood et al. (2002) surmised that *"While it is likely that a prolonged warming will lead to a shift in the ecosystem favoring subtropical species over temperature species, physical or ecological factors other than temperature may preclude a smooth transition to a balanced <subtropical> ecosystem."*

CONCLUSION

Logically, nutrients and light have received the majority of attention for influencing SAV growth rates and survival in the Chesapeake Bay. However, long-term observations and research have also shown that temperature is an important environmental factor that controls the germination, growth, reproduction and mortality of SAV. These effects will become even more important in the future with global climate change and the continued development and urbanization of coastal zones. The direct impacts of warming on most marine seagrasses are relatively well-understood. An abundance of evidence suggests that the outlook is poor for eelgrass (*Z. marina*), a cool-water species, in a steadily warming Chesapeake. The indirect impacts of warming on SAV species are more complex and difficult to predict and are likely to trigger relatively sudden, unpredictable changes, including increased abundances of thermo-tolerant species and the introduction of subtropical species, particularly *Halodule wrightii*, which currently persists in Back Sound, North Carolina (Kenworthy 1981). In contrast, it is difficult to accurately forecast the impacts of climate warming on SAV in the freshwater regions of the Chesapeake Bay, where temperature effects on plant metabolism may significantly interact with other environmental changes such as salinity and eutrophication (Ryan 1991).

2. COASTAL ZONE ACIDIFICATION

Since the industrial revolution, atmospheric carbon dioxide levels have increased 40% from 280 to 400 ppm (parts per million), the highest levels occurring on our planet in 800,000 years (Sabine et al. 2004; Doney et al. 2009). Approximately one-third of the CO_2 emitted from human activities has been absorbed by the oceans, slowing the rate of global warming. However, the oceanic CO_2 loading generates significant climate stress for marine ecosystems through a process commonly referred to as "ocean acidification". Ocean acidification decreases the total alkalinity and carbonate saturation state of the water, which can have significant deleterious effects on organisms that precipitate calcium carbonate (Doney et al. 2009). In the past 150 years, the oceans have become net CO_2 sinks and the average ocean pH has dropped from 8.21 to 8.10 (Royal Society 2005). By the end of the century, it is expected to fall another 0.3 to 0.4 units (Orr et al. 2005; Doney et al. 2009). This shift in ocean chemistry represents a 150% increase in the concentration of hydrogen ions and a 50% decrease in the concentration of carbonate ions (CO_3^{2-}) (Orr et al. 2005; Doney et al. 2009). Ocean acidification lowers the availability of CO_3^{2-}, and therefore the seawater saturation states (Ω) with respect to several carbonate minerals, so that the formation and deposition of new $CaCO_3$ minerals is reduced, and the dissolution of existing minerals is enhanced. This can disrupt the growth of many calcifying organisms, including important species of shellfish, plankton, and corals, which struggle to form $CaCO_3$ shells, skeletons, and tests.

Within the Chesapeake Bay, and other estuaries, the process is more complex. Coastal zone acidification is driven primarily by biological processes, fueled by organic carbon inputs from the land. Estuaries are surrounded by terrestrial and intertidal environments, which export massive amounts of organic carbon to the oceans *via* the *"land–ocean continuum"* (Jiang 2010; Herrmann et al. 2015). This organic carbon is subsequently converted to dissolved inorganic carbon (DIC, includes CO_2) *via* biological processes, e.g., respiration and decomposition (i.e., heterotrophy), generating high CO_2 / low pH conditions *in situ*. Other factors contribute coastal zone acidification in the Chesapeake, including acid sulfate soils, larger-scale processes such as ocean mixing or coastal upwelling, and the atmospheric deposition of NOx and SOx combustion products. Combustion products can acidify estuarine waters directly and some (e.g., NOx) also drive acidification by stimulating eutrophication. Indeed, eutrophication is a common cause of acidification in estuaries: nutrient enrichment stimulates the production of algal DOC, which fuels microbial respiration in anoxic bottom waters, generating high levels of CO_2 (Cai et al. 2011; Melzner et al. 2013; Wallace et al. 2014). Sunda and Cai (2012) surmised that "*we should expect that eutrophication of Chesapeake Bay, and the subsequent release of CO_2 by the decomposition of algal blooms, will generate acidified conditions in bottom waters*". These authors predicted, using biogeochemical models tested in other estuaries, that eutrophication alone could decrease local pH values by ~1 pH unit (Sunda and Cai 2012).

Estuarine waters generate massive amounts of DIC and release a fraction to the atmosphere as CO_2. Globally, estuaries are an important net source of CO_2 to the atmosphere with a global efflux of 0.25 ± 0.25 Pg C y^{-1} (Jiang 2010). Estuaries also sequester and store some carbon and export the rest directly as organic carbon to the oceans.

Estuarine waters are unusually sensitive to acidification. High CO_2 levels reduce the pH, CO_3^{2-} levels, and $CaCO_3$ mineral saturation states of coastal waters, just as in the open ocean. However, the precise relationships between excess CO_2 and these parameters can be complicated by the changing chemical properties of coastal waters – their fluctuating salinities, temperatures, and nutrient compositions, in particular. Further, much of the excess CO_2 / acidity observed in estuarine waters results from *in situ* respiration of imported terrestrial and marine organic carbon, rather than the direct absorption of atmospheric $CO_{2.}$ In general, estuarine waters are more susceptible to CO_2-induced acidification due to their reduced buffing capacity from alkalinity, which is lower than in seawater (Miller et al. 2009; Hu and Cai 2013). Furthermore, not all estuaries or regions of estuaries are equally sensitive; some mid-salinity estuarine waters have particularly low buffering capacities and are especially vulnerable to acid stress (Hu and Cai 2013). In fact, the presence of a mid-salinity minimum buffer zone (MBZ), areas especially prone to acidification, has been proposed for several of these estuaries, including the Chesapeake Bay (Hu and Cai 2013).

As a result of these combined biological, chemical and physical factors, the pCO_2 / pH conditions of estuaries are highly variable. Within the Chesapeake, its tributaries, and outer bays, pCO_2 concentrations commonly fluctuate from less than 100 to greater than 3,000 ppm, as determined by time of day, winds, waves, tides, stratification, and patterns of circulation, as well as the presence or absence of periodic algal blooms or anoxic zones. For example, tidal wetlands generate high pCO_2 "hot spots" with pCO_2 levels >10,000 ppm (A.W. Miller, unpublished; Baumann et al. 2015). Plumes of high CO_2/low pH waters have been observed during ebbing tides in Chesapeake and elsewhere. On the other hand, high rates of estuarine primary production during the daytime can strip dissolved inorganic carbon from estuarine waters. For example, photosynthesis in spring algal blooms and healthy seagrass meadows can draw down pCO_2 levels to <100ppm during the daytime, with an increase in pH of ~1-2 units (Miller and Arnold, unpublished). Diurnal fluctuations of 2 pH units are common, and such variation is nearly an order of magnitude greater than the projected global effects of ocean acidification. In terms of pCO_2 concentrations, the natural fluctuations occurring in the Chesapeake Bay each day are approximately ***fifty times*** greater than those that have been occurring in the open oceans during the past century. This is similar to observations made for other estuaries, in the US and elsewhere (Raymond et al. 1997, Cai & Wang 1998, Frankignoulle et al. 1998, Borges 2005, Borges et al. 2006; Akhand et al. 2012).

Coastal acidification is likely to intensify during this century. Human activities have increased the conversion of forests to agriculture, the loss of wetlands, patterns of precipitation, and the intensity of storm events, which all *"increase rates of sediment runoff and [OC] transport towards the oceans"* (Schlesinger, 1997). Flooding from intense storm events can mobilize "aged" carbon, stored for hundreds of years on land, into the rivers and estuaries (e.g., Tittel et al. 2013). In short, in the future, the Chesapeake will receive substantial and *increasing* inputs of carbon from many directions, resulting in additional changes to the estuarine carbonate system. Furthermore, the climate change is likely to stimulate biological remineralization/decomposition of DOC to DIC and foster high CO_2 and low pH conditions. Warmer temperatures generally increase rates of respiration and decomposition, while decreasing the efficiency of photosynthesis. In the future, climate change is likely to push the "noisy baseline" of coastal acidification even higher.

Can we observe acidification in the Chesapeake? There is an abundance of evidence to show that the absorption of excess CO_2 from the atmosphere is driving a steady acidification of the open oceans. However, in the Chesapeake this climate shift is less recognizable, for two reasons: (1) no coordinated long-term effort has been implemented to monitor carbonate system parameters using reliable, modern methods and (2) the anthropogenic signal tends to be obscured by the typical variation in the estuarine carbonate system.

Nonetheless, attempts have been made to reconstruct historical pCO_2 and/or pH values in the Chesapeake Bay. For example, Waldbusser et al. (2011) used water quality data from the Chesapeake Bay Program's Data Hub (http://www.chesapeakebay.net/dataandtools.aspx) from 1985-2008 to identify significant declines in "*seasonally averaged daytime pH*" in polyhaline surface waters that were great enough to impact calcification in the Eastern Oyster (*Crassostrea virginica*). In fact, this observed rate of change is significantly greater than that for the open ocean during this same time period (González-Dávila et al. 2007; Hu and Cai 2013). Interestingly, they also noted pH *increases* in mesohaline regions. The authors hypothesized that the transport and remineralization of organic carbon through the Chesapeake Bay and towards the ocean may account for this observation. In their view, eutrophication triggered primary production (and a rise in pH associated with photosynthesis) at mesohaline sites. The resulting organic carbon subsequently drifted southward, triggering CO_2 production *via* heterotrophy in the polyhaline (with a corresponding decrease in pH). This view highlights some of the challenges involved in studying acidification in estuaries, where significant lateral transport of organic carbon (both DOC and POC) is to be expected.

SAV AND COASTAL ACIDIFICATION

SAV has a unique place at the center of the estuarine carbonate system. Submerged aquatic plants are directly impacted by high CO_2 / low pH conditions. At the same time, they have the potential to modify the pH conditions in their local environmental *via* photosynthesis (counteracting acidification) and respiration (accelerating acidification).

High CO_2 conditions may benefit SAV photosynthesis, which is often CO_2-limited. Many species of SAV struggle to obtain adequate inorganic carbon because they lack effective carbon-concentrating mechanisms for photosynthetic exploitation of bicarbonate (HCO_3^-). This is unlike many other marine photosynthetic organisms, which have the ability to utilize HCO_3^- as an additional source of inorganic carbon, especially when CO_2 is limiting. For example, most marine algae derive 90% or more of their photosynthetic carbon requirements from HCO_3^-, but marine seagrasses manage to satisfy only ≤50% of their carbon requirements in this way (Zimmerman et al. 1995, 1996; Beer & Koch 1996; Beer & Rehnberg 1997; Zimmerman et al. 1997; Invers et al. 2001; Bjork et al. 2997; Jiang et al. 2010). In addition, some freshwater SAV species are almost totally reliant on dissolved aqueous CO_2, and light-saturated photosynthesis is typically CO_2-limited in low alkalinity water (Lloyd et al. 1977). As a result, a high CO_2/low pH world may release SAV from CO_2 limitation, making them more productive (e.g., Bjork et al. 1997; Ow et al. 2015; Zimmerman et al. 2015; Takahashi et al. 2016). This has been termed the "*CO_2 fertilization effect*". Such conditions also benefit SAV by reducing photorespiration (Buapet et al. 2013). For this reason seagrasses have been called "winners" in a high CO_2 / low pH world (Fabricius et al. 2011; also see Palacios and Zimmerman 2007; Hall-Spencer et al. 2008; Zimmerman et al. 2015). Some have suggested the term *"coastal carbonation"* to more accurately describe this process (e.g., Zimmerman et al. 2015).

SAV may also create temporary refuges from acidification because the photosynthetic removal of CO_2 from the water increases pH. In healthy seagrass meadows, photosynthesis normally draws down CO_2 within seagrass beds significantly, *increasing* pH to levels as high as a pH of 9, creating a zone of *low* CO_2/*high* pH conditions during the daytime (Bjork and Beer, 2009; Baupet et al. 2013b; Hendriks et al. 2014). As a result, daytime seawater chemistry in seagrass beds may be sheltered from acidification (Bjork and Beer 2009). This has been observed in South Bay, Virginia, where pCO_2 concentrations drop dramatically, from 600 to <100ppm, as coastal waters enters eelgrass meadows during the daytime (A.W. Miller, unpublished; Miller and Arnold, *in prep*.). However, it is important to note that this is a temporary phenomenon. During the night seagrass community respiration will contribute to acidification, generating CO_2 and creating wild swings in CO_2/pH on a diurnal cycle.

We are beginning to accumulate enough data to understand seagrass responses to acidification, alone or in concert with other environmental factors such as warming and light availability.

Eelgrass. For *Zostera* high CO_2 / low pH conditions are often beneficial. Photosynthetic carbon assimilation is increased and photorespiration, which can reduce photosynthetic capacity of eelgrass by 40%, is decreased (e.g., Thom 1996; Zimmerman et al. 1997; Palacios and Zimmerman 2007; Alexandre et al. 2012; Buapet et al. 2013). The most convincing evidence has been provided by Zimmerman and coworkers who have simulated coastal acidification in manipulative experiments with eelgrass for nearly two decades. First they compared the performance of *Z. marina* under ambient (pH: 8.2, total CO_2: 2074 μmol kg^{-1}) and CO_2 enriched (pH: 6.2, total CO_2: 3673 μmol kg^{-1}) conditions and found a rapid 3x increase in photosynthetic rates, which allowed enriched plants to maintain a "positive whole-plant C balance" with only <3h of saturating irradiance per day, compared to the normal 7 h for control plants (Zimmerman et al. (1997). Later, Palacios and Zimmerman (2007) examined the impact of four levels of CO_2-enrichment (pH range: 8.1 to 6.4, total CO_2 range: 2225 to 3610 μM) over a period of 1 year. Here, the combination of CO_2 enrichment and high-light yielded a significantly higher reproductive output and an increase in below-ground biomass (which exhibited higher levels of carbohydrate reserves) and the proliferation of new shoots.

Zimmerman et al. (in review) recently conducted a long term (18 month) experiment with eelgrass from Virginia growing in outdoor aquaria exposed to the natural seasonal cycles in irradiance and water temperature. They demonstrated that tolerance of high summer water temperatures increased linearly with CO_2 availability, resulting in increased rates of plant survival and vegetative growth, plant size, accumulation of internal carbon reserves (sugar) and flowering shoot production the following spring. Formulations resulting from these experiments enabled Zimmerman et al. (2015) to model the combined impacts of acidification, warming, and irradiance on eelgrass. As with the experimental results, model calculations revealed that high CO_2 conditions projected for the end of the 21st century can alleviate the deleterious impacts of warming on eelgrass. For example, they observed that eelgrass required 5h of light-saturated photosynthesis to balance its "respiratory load" in cool waters (10°C) compared to 9h in warm waters (30°C), demonstrating the peril of climate warming for eelgrass in the Chesapeake Bay. However, they also showed that under acidified conditions, corresponding to CO_2 concentrations predicted for the end of century, eelgrass was able to balance its respiratory load in only 4.8 hours, even at 30°C. The *GrassLight* model predicted that pCO_2 levels of 600ppm – predicted to occur at mid-century – nearly compensated for the negative effects of 30°C thermal stress. Thus, estuarine acidification should stimulate eelgrass photosynthesis sufficiently to offset the deleterious effects of thermal-stress, "*facilitating the survival of eelgrass in Chesapeake Bay despite a warmer climate*."

Other species. High CO_2/low pH conditions may be beneficial for other species of SAV. For example, such conditions promote gross photosynthesis and decrease photorespiration in widgeon grass, *Ruppia maritima* (Buapet et al. 2013). Similar results have also been observed for species not native to the Chesapeake. For example, in early lab experiments, Durako (1993) found that a pH shift of 1.5 units resulted in an 85% change in photosynthesis of tropical *Thalassia* spp., even when overall DIC concentrations were unchanged. Bjork et al. (1997) found similar results for a related species, *T. hemprichii*, in field experiments (also see Campbell and Fourqurean, 2013). Increased productivity was observed for *Cymodocea serrulata, Halodule uninervis, and T. hemprichii* exposed to pCO_2 levels ranging from 442-1204 ppm for two weeks in the lab (Ow et al. 2015). Higher seagrass productivity has also been observed for natural populations near high CO_2 vents (Hall-Spencer et al. 2008; Fabricius et al. 2011; Russel et al. 2013; Takahasi et al. 2016).

Fewer studies have been conducted in low salinity and freshwater systems, and therefore the impacts of acidification on freshwater SAV are poorly understood. These systems are especially vulnerable to pH changes as the carbonate system of fresher waters is not well-buffered against perturbation. Thus, both low and high pH conditions are fairly common. In the tidal fresh regions of the Bay, daytime pH can rise dramatically to exceed pH 10 in SAV beds due to the vigorous photosynthetic uptake of inorganic carbon by dense SAV communities, e.g., in the upper Potomac River and at the head of the Chesapeake where above-ground biomass reaches 500 to 1,000 g DW (Carter et al. 1987; Staver & Stevenson 1994). The impacts of such fluctuations on freshwater species are poorly characterized. For instance, some freshwater species, including native *Stuckenia pectinata* and non-native *Hydrilla*, have carbon concentration mechanisms that seagrasses do not, and they can therefore use bicarbonate ions effectively for photosynthesis when other carbon sources are depleted (Holaday & Bowes 1980), assuming bicarbonate is available. In short, the "*CO_2 fertilization effect*" seems to be common, at least for seagrasses if not freshwater SAV. It is important to note, however, that some seagrass species benefit more than others from elevated CO_2 and, as a result, continued acidification may contribute to shifts in benthic species composition (e.g., Ow et al. 2015).

Indirect and community-level effects of acidification. The indirect effects of acidification can be at least as important as the direct effects (Duarte et al. 2016), and are more difficult to predict (Kroeker et al. 2013).

In the Chesapeake we must consider the impacts of coastal acidification on the competitive balance between submerged vegetation and competing macroalgae and epiphytes. On one hand, acidification may inhibit the growth of calcifying epiphytes and coralline macroalgae, benefiting seagrasses (Newcomb et al. 2015; Johnson et al. 2014; but see Johnson et al. 2012). On the other hand, these same conditions may fuel the overgrowth of other fouling organisms. For example, acidification can boost the growth of epiphytic diatoms and cyanobacteria (Martínez-Crego et al. 2014). In a 6-week mesocosm experiment these authors observed rapid epiphyte overgrowth, which suppressed the expected benefits of elevated pCO_2 (800ppm), on *Zostera noltii* under both low and high-nutrient conditions. Acidification is also likely to benefit macroalgae, especially those without effective carbon-concentrating mechanisms. It often increases rates of photosynthesis, nutrient assimilation, growth, and reproduction of fleshy seaweed species (Koch et al. 2012; Baggini et al. 2014; Burnell et al. 2014; Johnson et al. 2014; Duarte et al. 2016; Kubler and Dudgeon 2016). Kroeker et al. (2013) noted that in acidified conditions, fleshy seaweeds can rapidly overgrow other species, dominate ecosystems, and cause phase-changes "*leading indirectly to profound ecosystem changes in an acidified ocean*". It is important to note that the dramatic overgrowth of fouling organisms observed in some studies and attributed to CO_2 might be due, in part, to the difficulty of maintaining realistic levels of micrograzing in mesocosm experiments. Regardless, when considering the future of Chesapeake Bay, we need to consider the possibility that the "*CO_2 fertilization effect*" may benefit fleshy macroalgae more than submerged vascular plants, allowing them to overwhelm the slower-growing plants under future climate conditions. In addition, acidification may also allow non-native fleshy seaweeds to invade new areas, especially when combined with higher temperatures (Kubler and Dudgeon 2016).

High CO_2 / low pH conditions may also influence grazing rates on seagrasses and co-occurring macroalgae (Tomas et al. 2015). Arnold et al. (2014) observed that rates of fish grazing on *Zostera* sp. from high CO_2 / low pH waters near an acid spring in Australia were dramatically increased, perhaps in response to the loss of soluble phenolic substances in these plants. A similar result was reported by Duarte et al. (2016) who found that ocean acidification altered the nutritional composition of the brown alga *Durvillaea antarctica*, inducing increased compensatory grazing by a co-occurring amphipod. The impact of acidification will also depend on the diversity of herbivores. A diverse assemblage of grazers, which includes some that are resistant to high CO_2 / low pH conditions, may help to maintain community structure, e.g., by protecting communities from the overgrowth of fleshy seaweeds (Baggini et al. 2015; Ghedini et al. 2015).

Finally, future acidification, alone or in concert with other factors, may alter the susceptibility of seagrasses to disease outbreaks. High CO_2 / low pH conditions cause the loss of antimicrobial phenolics in *Ruppia maritima* and *Potamogeton* sp from the Chesapeake, as well as *Cymodocea nodosum* from the Mediterranean and *Zostera* sp. from Australia (Arnold et al. 2012; Arnold et al. 2014). Specific phenolic acids known to inhibit the growth of the seagrass wasting disease pathogen, *Layrinthula* spp., were reduced by as much as ~95% as these plants accumulated insoluble lignins instead. Martínez-Crego et al. (2014) observed a similar decrease in leaf phenolics in *Zostera noltii.* Such decreases in protective phenolic compounds have been linked to wasting disease outbreaks and seagrass mortality (e.g., Vergeer and Develi 1997; Buchsbaum et al. 1990; Vergeer et al. 1995). Interestingly, acidification also reduces the concentration of bioactive polyphenols in brown algae (e.g., Korbee 2014; Gamze and Sukran, 2015) despite the fact that these similar substances are synthesized via a different metabolic pathway.

CONCLUSION

High CO_2 / low pH conditions generated by continuing coastal acidification can stimulate SAV photosynthesis *via* the "*CO_2 fertilization effect*". This can boost seagrass productivity and, at least for eelgrass, it can offset some of the deleterious effects of climate warming. Thus, acidification may actually improve the prognosis for eelgrass in the Chesapeake, allowing for its survival in the region. However, acidification may also have indirect effects by benefitting competitors and decreasing disease resistance.

It is worth emphasizing that water transparency, the most influential environmental factor regulating the distribution and abundance of SAV in the Chesapeake Bay (Batiuk et al. 1992; Dennison et al. 1993; Carter et al. 2000), can alter the responses of SAV to the other factors we have discussed here. For instance, light levels can directly impact the ability of SAV to withstand elevated temperatures by impacting the photosynthetic machinery or altering the photosynthesis:respiration balance. Poor water transparency can prevent SAV from retreating to deeper, cooler waters (Thayer et al. 1984; McKee et al. 2002; York et al. 2013). In addition, adequate sunlight is required to drive the assimilation of carbon and, thus, can determine the magnitude of the beneficial "*CO_2 fertilization effect*" of acidification. Poor Chesapeake Bay health affects both the quantity and quality of penetrating light. Of course, when total benthic light levels are low in turbid waters, SAV health declines. Growth is also limited when high concentrations of phytoplankton, suspended particulate matter, and colored dissolved organic matter lead to green-dominated underwater light fields, which are not efficient at driving photosynthesis. In addition, past SAV losses may exacerbate the problem by destabilizing shallow sediments, resulting in very high levels of turbidity, particularly in the mesohaline and freshwater reaches of the Bay. Eutrophication can reduce overall water column productivity and increase the potential for local anoxia, especially at very shallow depths (< 2 m). Further, the nature of suspended particulate matter in the Chesapeake Bay appears to be changing, and this is likely to alter light penetration. All these factors may trigger additional losses of SAV, and make restoration efforts more difficult. They highlight the need to meet water quality targets, by managing nutrient and sediment loadings that ultimately drive concentrations of phytoplankton and suspended particulate matter in the Bay (Gallegos 2001), in order to protect and restore SAV resources in the future (Gallegos et al. 2011).

3. SEA LEVEL RISE

The Chesapeake region has been deemed *"more vulnerable than many other coastal regions to sea-level rise"* (Eggleston and Campbell 2013). Local rates of seal level rise are reported as 3.2 to as high as 11mm year^{-1}, exceeding global rates estimated at 1.7 to 3.2 mm year^{-1} (Ezer and Corlett 2012). Because SAV habitat represents the shallow-most fringe of the Bay, sea level rise threatens to decrease SAV distributions unless populations are allowed to migrate shoreward with the rising sea level. Sea level rise also threatens the alteration of the coastal landscape, drowning islands and mainland promontories, and eroding shoals etc. that protect existing sites from wind and swell, and/or alter sediment geochemistry (Kearny and Stevenson 1991; Koch 2001).

Over geologic time scales, sea levels within the Chesapeake Bay have fluctuated significantly. During glacial periods, sea levels were 120-125 meters below current levels and the Bay was merely an extension of the Susquehanna River Basin. The last interglacial period produced sea levels 5-6 meters above current values (Colman and Mixon 1988; Colman et al. 1990; Bratton et al. 2003; Cronin et al. 2007). However, during the past 3,000 years of extraordinary climate stability, and until the mid-19th century, sea levels and the general shape of the Chesapeake Bay have been relatively stable (Williams 2013).

Global sea level rise driven by the increasing ocean volume resulting from continental ice melt and thermal expansion from increasing ocean temperatures (Meier et al 2007; Cogley 2009; Rignot et al. 2008; Rignot et al. 2008). Sea level rise in the Chesapeake region is also impacted by land subsidence caused by isostatic rebound and groundwater pumping resulting in aquifer system compaction, which can rival rates of global sea-level rise. For example, in the lower Bay along sections of the Virginia coastline, subsidence alone accounts for 1.5 and 3.7 mm/yr of apparent sea-level rise for the periods of 1979–95 and 1982–95, respectively (Pope and Burbey, 2004). Future sea-level rise is notoriously difficult to predict; however, there is a general consensus that rates of sea-level rise will accelerate to 9 to 14 mm year^{-1}, leading to a rise of about 80 to 130 cm during this century (Grinsted et al. 2010). Williams (2013) recommends "*adaptation planning on local, state and national scales for projected sea-level rise of 0.5-2 m by A.D. 2100*". Rates of land subsidence are also difficult to predict, and could be slowed by improved groundwater management practices in coastal communities.

CONCLUSION

With rising water levels, coastal communities will experience increased flooding. Shoreline hardening or "armoring", and other adaptive practices, are likely to become more prevalent. These practices can negatively impact SAV in the Chesapeake (Patrick et al. 2016). Natural habitats may experience greater hydrological stress (Varnell 2014), increased turbidity, altered salinities, and greater impacts from storms. Communities such as tidal marshes and wetlands may migrate landward (Kirwan and Tammerrman 2009; Drake 2014) or be lost entirely when migration is not possible, (Stevenson and Kearney 2009). Near-shore benthic communities, including SAV meadows, would be altered in terms of their ranges, species richness, and composition (Drake 2014; Watson et al. 2014).

OUTLOOK AND SYNTHESIS

In the next century the Chesapeake Bay will be subject to the continued challenges of the last century, as well as new challenges related to accelerating climate change. The Chesapeake Bay will become warmer and may begin to exhibit some of the characteristics of a subtropical estuary. Coastal acidification is likely to increase, in both absolute terms and in terms of variability. The shape and nature of the shoreline will change due to sea level rise. Many of the direct impacts on submerged aquatic vegetation will be negative. A few may be positive. The indirect effects are likely to be powerful, but are poorly understood. As a result, the transition of existing SAV populations to some future state is unlikely to be smooth or predictable, and our success in restoring SAV in the Chesapeake Bay will depend to a large degree on careful management, informed by continued research and monitoring.

Present-day efforts to improve the health and species diversity of the Chesapeake will be important in determining how the ecosystem responds to climate change. It is clear that the ability of ecological communities to resist and/or adapt to climate change is linked to their species and genetic diversity. In fact, community diversity, overall species richness, mixed assemblages of different plant species, genetic diversity within populations, and presence and diversity of grazer functional groups are all positively associated with resistance to climate stress (e.g., Ghedini et al. 2015). This seems to be true for SAV communities. For instance, genetic and species diversity improves SAV survival and the maintenance of ecosystem services in seagrass meadows (Duarte 2000; Ehlers et al. 2008; Hughes et al. 2010; Reynolds et al. 2012; Gustafsson and Bostrom 2013; Duffy et al. 2014) and freshwater SAV beds (Engelhardt and Ritchie 2001, 2002, Engelhardt et al. 2014). While monocultures or low diversity systems may expand most rapidly following a stress-induced population collapse (Stachowicz et al. 2013; Gustafsson and Bostrom 2013), diverse systems are clearly more resilient. Resilient seagrass communities are, in turn, easier to protect, manage, and restore (Unsworth et al. 2015). This highlights the importance of understanding SAV diversity, both natural and restored as transplants or through seeding, throughout the Chesapeake. Although climate change seems likely to continue and accelerate, we maintain some control over the present-day health, diversity, and size of SAV communities. Efforts to protect and restore SAV populations today, combined with serious efforts to limit anthropogenic climate change, are our best options for protecting the future of the Chesapeake Bay.

Acknowledgments

The authors acknowledge the assistance of Lee Karrh and Brooke Landry (MD DNR) and numerous members of the technical synthesis workgroup (2014-2017). Brooke Landry and Savanna Rain Riley assisted with editing and formatting. Financial support for this effort was provided by the U.S. Environmental Protection Agency and the Maryland Depart of Natural Resources.

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EVALUATION OF ECOSYSTEM SERVICES OF SAV IN THE CHESAPEAKE BAY

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ABSTRACT

Submerged aquatic vegetation (SAV) habitats in the Chesapeake Bay generate numerous ecosystem services that result in local, regional, and global benefits. This chapter accomplishes three objectives. First, the term "ecosystem services" is defined in relation to ecosystem function and structure, with particular emphasis on how ecosystem service measures vary in relation to socioeconomic and geographical characteristics. Methods for calculating ecosystem service metrics through the identification of cause-and-effect relationships are then reviewed. Finally, the existing literature that identifies, quantifies, and monetizes ecosystem services provided by Chesapeake Bay SAV habitats is synthesized and interpreted for quality and completeness. In general, SAV habitats are underrepresented in the broader scientific literature aimed at valuing ecosystem services, a trend that holds for the bay. However, numerous services have been quantified and monetized, including fishery enhancement and carbon sequestration, and this review suggests that the value of SAV habitats to humans is non-trivial. The published literature suggests that SAV likely produces substantial benefits as contributions to home values and fishing and hunting benefits. Further ecological and economic research is needed to generate benefit assessments of water quality improvements and erosion control.

EVALUATION OF ECOSYSTEM SERVICES OF SAV IN THE CHESAPEAKE BAY

As described throughout this volume, submerged aquatic vegetation (SAV, or seagrasses) generates many desirable ecological functions, from trapping sediment to supporting fish and waterfowl populations. As our understanding of the importance of healthy, self-sustaining ecosystems for human wellbeing has improved, efforts have been undertaken to quantify the tangible and intangible benefits humans receive from ecosystems, commonly known as *ecosystem services* (MEA 2005).

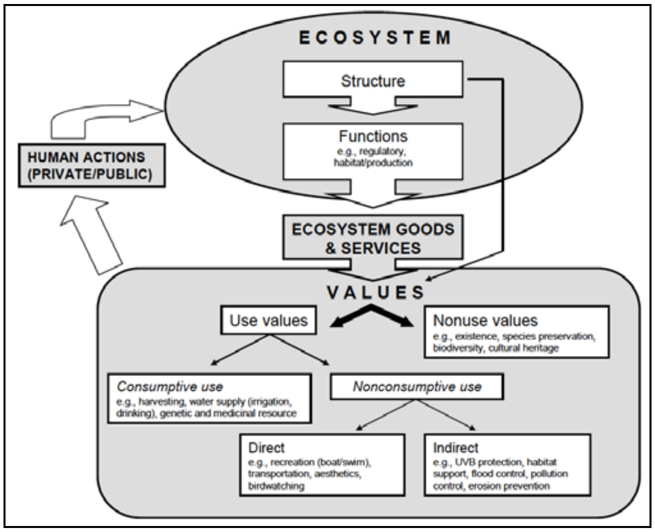


Figure 1. Connections between ecosystem structure/functions and services/values. Figure 7-1 from (NRC 2005).

The difference between ecosystem functions and services is effectively explained by figure 1. The "ecosystem" group includes the basic structures and functions that ultimately support ecosystem services, such as vegetation stem density or nutrient cycling. To quantify the benefits associated with changes in ecosystem structure and function, those changes must be linked to changes in the provision of ecosystem goods and services—potential benefits to human populations—such as change in availability of game fish or safe swimming opportunities. The *values* box shows that values can be broken down into two components: use and non-use values. Monetization of ecosystem services is the final step in the valuation process, and requires consideration of the setting in which ecosystem services are produced. For instance, fishery production in a coastal area near a large population center may be more valuable than a remote location simply because of the presence of more potential anglers.

Understanding and quantifying ecosystem services can aid in the communication of benefits to diverse stakeholders and help resource managers tasked with evaluating tradeoffs between alternative uses of coastal areas (e.g., preservation vs. coastal development). Subsequent valuation of ecosystem services allows for a common language (currency) to be used for project evaluation in a cost benefit analysis framework (Granek et al. 2010)**,** and provides information necessary to understanding how different beneficiaries gain or lose from an action. However, many Ecosystem services are difficult to value due to the fact that they are not traded on traditional markets, and thus have no prices attached to them. Even when ecosystems assist in the production of marketed goods (e.g., commercial fisheries), the contribution of an individual ecosystem in a specific time and place is difficult to discern. As a result, economists have developed a suite of methodological approaches to identifying the value of a variety of ecosystem services.

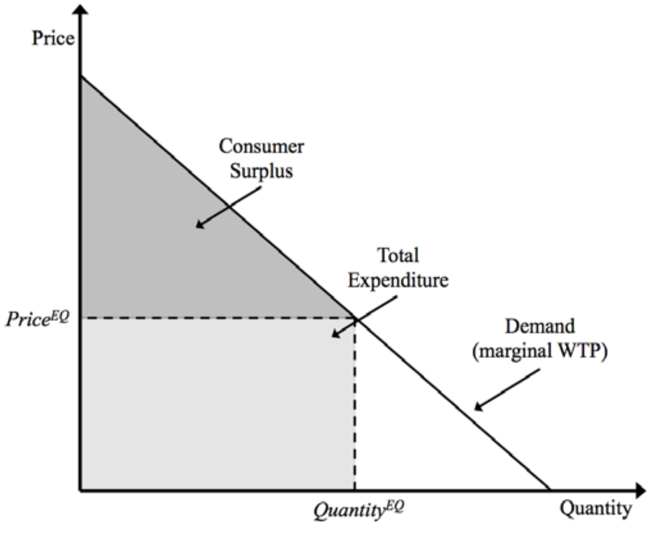
The remainder of this chapter proceeds as follows. First, we provide a brief overview of the conceptual basis for the valuation of ecosystem services and valuation methodologies that have been developed by economists. We then review the current research on the provision of ecosystem services by SAV habitats in the Chesapeake Bay and beyond.

Conceptual basis for economic value and empirical approaches to quantification and monetization

While there are alternative philosophical approaches to valuing ecosystem services, economists generally rely on a *utilitarian,* or anthropocentric, approach because it provides a practical way to assess tradeoffs. The utilitarian approach is rooted in economic theory that aims to efficiently allocate scarce goods and services by comparing whether society is made better off through alternative patterns of consumption or investments. This framework is distinct from philosophical approaches that assume ecosystems have intrinsic value (even in the absence of any human presence) or socio-cultural values beyond those generally considered in a utilitarian framework (MEA 2005).

Scarcity and marginal willingness to pay

At the heart of the utilitarian approach is the assumption that the value of something is best represented by measures of individual or group *willingness to pay* (WTP), given the quality of the good or service, the availability of substitutes, and other context variables that affect demand relative to supply. For goods traded on markets, the market equilibrium represents the point at which prices and WTP converge. This *marginal willingness to pay* (ie., observed price), can be interpreted as the value of providing one additional unit of the good or service. This is an important distinction; economic models designed to value ecosystem goods and services generally report marginal values (e.g., per unit area). While it is tempting to multiply marginal values by, for instance, habitat area in an effort to generate estimates of the total economic value of a particular habitat, this is, in general, not appropriate, even on a local scale (Barbier et al. 2008). *Total* WTP, a measure of the aggregate gross (before subtracting costs) benefits experienced by consumers in a market, is generally considered to be greater than total expenditure. Net benefits experienced by consumers in markets are then calculated as the sum of the difference between what people would have been willing to pay, and what they actually paid, and is commonly referred to as consumer surplus (see Figure 1).



For instance, consider the market for a commonly consumed, private good such as Bordeaux wine. During years of very low availability, the market price will be driven up by competition for the few bottles that are available. Those consumers that have a high willingness to pay will bid up the price on wine and the resulting *marginal* WTP (market price) will be high. During years of normal availability, the additional supply means that those high WTP consumers will not have to compete so vigorously, prices will drop, and a larger equilibrium quantity will be exchanged, at a lower average price. As a result, high WTP consumers will experience a greater "surplus" as compared to low-availability years.

While it would be ideal to map out the demand (WTP) schedule for every good or service, it is only possible to observe "marginal"—or incremental—WTP, because WTP is strongly dependent on *scarcity*. Generally speaking, the scarcer something is, the higher its marginal value, all else equal. Therefore, values that are based on a given level of abundance or consumption (i.e., what is actually observed) cannot, in general, be extrapolated to conditions where there is substantially less or more of that good or service supplied or demanded, or multiplied by the total consumption to generate an aggregate value.[1] The change in marginal value in response to scarcity is also dependent on the availability of substitute goods or services. This factor is often ignored in studies assessing the value of specific ecosystem services. For example, if both coastal marshes and SAV provide nutrient cycling benefits in a specific location, the benefit of restoring one or the other habitat will depend on the level of provision of the same service from the *other* habitat. Similarly, where affordable technical substitutes are available to provide a service (e.g., seawalls), an increase in the service resulting from habitat restoration may not generate the same value as compared to the case where technical substitutes are not feasible or prohibitively expensive.

More generally, many economic benefits associated with natural ecosystems are dependent on the presence of adjacent human populations, and therefore it is inappropriate to perform calculations without explicit consideration of socio-economic context in which they occur. Just as an ecologist would never assume that tropical and temperate fish populations are affected in a similar way by an identical reduction in coastal nutrient inputs, economists must value ecosystem changes within a context of beneficiary needs and desires (Wainger and Mazzotta 2011; Kennedy and Cheong 2013).

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[1] Scarcity is closely linked to *rivalry* and *excludability*, economic concepts describing, respectively, the degree to which one user's benefit from a service or good diminishes other users' subsequent ability to benefit, and the ease in which certain users are prevented from consuming benefits. For instance, a captured fish may only be consumed once, and thus is rival in appropriation; however, it is difficult to exclude users from coastal fisheries, hence the common condition of over-exploitation. Alternatively, the benefits of carbon sequestration are non-rival; the benefit coastal Marylanders experience from a reduced risk of climate change benefits associated with carbon sequestration services provided by SAV does not diminish the benefits experienced by Bangladeshis inhabiting the Ganges Delta region. Additionally, it is impossible to exclude individuals or groups from benefiting from climate benefits. In this latter case, climate regulation is considered a *global public good*. Non-excludability is a primary reason for ecosystem degradation. It is difficult for regulators or others to exclude certain uses, those that benefit from ecosystem goods or services will be reluctant to invest in their sustainable management, as others may simply free-ride.

In other words, the presence—or supply—of ecosystem *functions* (e.g., water filtration or disturbance regulation) is necessary, but not sufficient, for the assignment of value to ecosystem *services*. Changes in ecosystem functions (perhaps due to degradation or restoration) must first be defined in terms of the resulting impact on the provision of specific ecosystem services. For example, when nutrient cycling removes nutrients from the water column, it reduces the risk of illness from harmful algal blooms for tourists visiting a particular beach. This benefit can be valued by measuring willingness to pay for that change (Figure 1). This second step (valuation or monetization) is only valid when it considers how people use the ecosystem, the strength of their preferences, and their willingness to substitute other beaches.

For some ecosystem services, beneficiaries may include all humans (e.g., carbon capture and storage or biodiversity maintenance). In these cases, local considerations are less important However, services such as storm surge protection would only be considered valuable to humans if the supply of the service coincided spatially and temporally with the presence of human populations or capital assets, as well as storm activity.

Valuation of non-market goods and services

Whereas traditional exchange markets allow for the direct observation of prices (and thus marginal WTP), the goods and services provided by natural ecosystems are generally "consumed" outside of markets (i.e., they are "non-market" goods and services). As a result, prices and associated benefits are not directly observable. To address the challenge of missing markets, various methodologies have been developed to identify WTP for non-market goods and services. These methods include *revealed preference* and *stated preference* approaches. Revealed preference approaches rely on observing consumption or production decisions that are indirectly dependent on some environmental good or service. For example, homes adjacent to water with high clarity tend to be more valuable than those adjacent to water with low clarity, and observing housing markets may allow researchers to identify the added benefit, or the *implicit price*, of local water clarity (Freeman 1981). Similarly, the costs incurred by a family to visit the beach can be assumed to represent the minimum WTP for that recreational opportunity (Brown and Mendelsohn 1984). However, not all ecosystem services can be identified by these indirect methods, particularly non-use services. In these cases, stated preference approaches that rely on hypothetical surveys can be used instead. This report does not provide significant detail on individual valuation techniques but many publications are available to provide further information (Champ et al. 2003; NRC 2005; Freeman et al. 2014; Wainger 2014; Johnston et al. 2015)

Intrinsic and socio-cultural values can be incorporated in a utilitarian framework to the extent that they can be expressed as existence, altruistic, or bequest values. These *non-use* benefits refer to the satisfaction people derive from simply the knowledge that an ecosystem, species, or habitat is being preserved. It is well accepted that many people derive benefits from protecting species, ecosystems, or ecosystem attributes and maintaining them for others or future generations (NRC 2005; Turner et al. 2008). In contrast, *use* benefits are derived from direct on-site use or interaction with ecosystems (active use, e.g., raw material production and outdoor recreation) or from indirect off-site interaction (passive use, e.g., flood hazard mitigation). For example, recreational fishing is a use benefit of an ecosystem, while the ability to preserve recreational fishing for future generations is a *non-use* benefit.

Valuation of ecosystem service benefits is more reliable for use benefits than non-use benefits due to methodological issues. Benefits derived from improvements in such things as fishable or huntable species, human health, and property values can be deduced by observing human behavior. People reveal their preferences through their choices of how and where to recreate, how much to spend on health improvements, and how much extra they pay for homes with natural amenities. On the other hand, non-use values are less commonly monetized because they can only be valued using survey instruments in which people state their preferences. Stated preference approaches are considered less reliable than revealed preference approaches (Hausman 2012; Haab et al. 2013) but are necessary to provide a thorough accounting of benefits, particularly for remote, pristine habitats.[2] The value of general improvements to ecosystem condition and resilience can be evaluated using stated preference survey methods by asking people to consider paying for changes in a measurable characteristic that represents ecosystem condition. For example, a recent study of the value of water quality improvements in the Chesapeake Bay watershed found that, on average, people valued reductions in algae levels in lakes (Moore et al., in press), even if they were not lake users. This study reflects a common experience of economists that, if properly explained, many people are willing to pay for improvements in ecosystem integrity indicators for ecosystems that they do not necessarily use (e.g., Johnston et al. (2011).

For any type of valuation approach, measuring benefits requires establishing a series of cause and effect relationships that demonstrate effects of an action or natural disturbance. These *causal chains* are a series of linked models or functional relationships that 1) demonstrate the effects of a management action on ecological features and processes and 2) propagate those changes through the social and economic systems to reveal how they are valued (Wainger and Mazzotta 2011; Olander et al. 2015). For example, for the ecosystem service of recreational hunting, we would first estimate how management practices would change water quality and then SAV extent or condition. Next, we would evaluate how changes in SAV would be expected to increase waterfowl. Finally, we can use existing economic studies to estimate the value those additional birds would generate for hunters and bird-watchers.

Figure 2. Example causal chain for estimating the benefit of improved hunting opportunities associated with increased SAV extent or condition.

If any part of the causal chain cannot be estimated due to data or knowledge constraints, then robust monetary valuation may not be possible. However, non-monetary metrics can expand the set of ecosystem services analyzed by using indicators that reflect potential benefits, based on conditions that have been shown to be valued in prior studies or through market behavior (Wainger 2014). Beyond data gaps, some ecosystem service benefits are inherently difficult, or even inappropriate, to monetize because they represent intangible

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[2] For instance, economists relied primarily on stated preference approaches to assess damages following the Exxon-Valdez oil spill in Prince William Sound, Alaska.

benefits, such as the increased community interactions that can result from having an attractive natural setting in an urban environment (Peters et al. 2010) or spiritual and cultural conditions that are not amenable to monetization (Winthrop 2014).

Despite the evidence that SAV habitats are likely to provide significant non-use value, we cannot readily monetize these values without a substantial investment of new resources. What is tractable to monetize with existing data are the use benefits people derive from the presence of SAV offshore of their property, as well as abundance increases in species targeted for fishing, hunting, and wildlife watching. These values can be captured by applying information from past studies through economic benefit transfer. *Benefit transfer* is an empirical approach in which values measured for changes in previously studied sites are adjusted and applied to changes at a new site. However, the caveats above are important to consider when attempting to apply results from previous studies to new habitats (Johnston et al. 2015).

Further, from the environmental economics literature, we can deduce that ecological indicators that reflect aspects of ecosystem integrity and long-term viability can serve as benefit indicators. In many ways, SAV extent alone could be an indicator of the non-use values derived from system stewardship. For instance, SAV may only thrive when water quality is sufficiently supportive and is therefore an integrative indicator of ecosystem condition (Dennison et al. 1993).

Valuing future flows of ecosystem services

Since natural resources like SAV act much like capital assets, it makes sense to value them as such. Specifically, when calculating values, economists will often calculate the net present value of the current and future flows of goods and services habitats will provide. In the same way a private firm evaluates the benefit of moving forward with a new business opportunity or capital investment, natural resource economists rely on *discounting* to calculate the present value of an expected future stream of benefits, which puts future benefits and costs into present value terms (Arrow et al. 2013).

A *discount rate* is similar to the interest rates applied to financial transactions such as loans (Equation 1). Future benefits are worth less than benefits received today because of the *opportunity cost* of investment. Consider a simplified example of the decision to invest $100,000 today in a seagrass restoration project that is expected to yield one-time, inflation-adjusted benefits one year from now in the amount of $103,000. Without discounting, we can state this project yields $3,000 in net economic benefits, and should be pursued. However, if the inflation-adjusted interest rate on treasury bonds is 5%, we could have instead invested the $100,000 in bonds, yielding $105,000, or $5,000 in net benefits. In this circumstance, the restoration project would not pass the net present value test. In this hypothetical world, benefits from any restoration project must be discounted at 5% *per annum* to represent the opportunity cost associated with the delay between the time of investment and the time that benefits accrue. This example can be extended to the case of multiple periods of benefits and costs using Equation 1.

$$PV = \sum_{t} \frac{V_t}{(1 + r)^t}$$

Equation (1)

where V_t is the value of sequestration in any given year t and r is the discount rate. Net present value calculations can be highly sensitive to the discount rate, particularly when costs and benefits occur at different times (as is often the case with environmental restoration projects). For this reason and others, discounting is a controversial issue.[3]

The valuation framework presented above can, in theory, be used to evaluate the net economic impact of many decisions involving the preservation or conversion SAV and other valuable natural habitats. In practice, however, there are a number of obstacles, and the quantification and subsequent monetization of even *individual* Ecosystem services is challenging, much less the suite of services provided by complex coastal habitats. In the next section, we focus on specific ecosystem services provided by SAV habitats in the bay.

ECOSYSTEM SERVICES ASSOCIATED WITH SAV HABITATS IN THE CHESAPEAKE BAY

SAV—and in particular seagrass habitats—have been credited with providing a wide variety of ecosystem service benefits (Table 1). These benefits can be valued when causal chains can be established that trace how restoration actions propagate through ecological and socio-economic systems (e.g., Figure 2). While researchers have attributed monetary values to ecosystem services provided by a number of other coastal habitats (e.g., salt marshes and mangroves), SAV habitats have proven to be more difficult to assess for a number of reasons elaborated below. Further, the few studies that show statistically-significant, positive economic benefits rely on (a) a number of strong assumptions regarding the links between SAV spatial extent, density, etc., and the provision of services, and (b) a simplistic characterization of the socioeconomic context. A primary issue is that SAV often acts in concert with connected ecosystems to deliver services such as commercial and recreational fishery support. The co-dependencies can confound efforts to model cause and effect relationships between SAV and potentially valuable outcomes such as changes in fish abundance.

An additional issue for valuation is the non-linearities or feedbacks that can occur in seagrass beds. Seagrasses modify the environment in ways that can promote seagrass growth (Chapter 3, this volume). As a result, a linear cause and effect relationship must be adapted to recognize that SAV both benefits from and creates water clarity. Finally, not all seagrass beds will provide the same functions. Some functions, such as wave attenuation, scale non-linearly with stem density and depend on distance to built infrastructure (Koch et al. 2009).

The complexity of SAV habitats (and estuarine ecology in general) suggest that valuation approaches will require sufficient resolution, in terms of bed characteristics and temporal and spatial detail, to both link SAV characteristics to service response variables and place SAV in proximity to beneficiaries (for those services for which proximity is relevant).

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[3] For a more complete explanation of this complex topic see ((Arrow et al. 2013; Cropper 2013)).

However, our review of published papers that sought to establish the SAV characteristics and conditions that impart value has found that the available literature is lacking in both the quantity of studies and the statistical and practical significance of conclusions. Thus, this section will explore, when appropriate and with context, examples of valuation efforts from beyond the Chesapeake Bay.

Recreational and commercial fishing

This particular ecosystem service has received the lion's share of attention from researchers, and thus we spend the majority of the subsection reviewing this literature. It is hypothesized that SAV may improve fishery outcomes in the bay through several mechanisms. First, SAV serves as a habitat or foraging ground for numerous commercially-important species, including blue crab (Orth et al. 1996), though specific impacts on other valuable species have been difficult to identify (Sobocinski et al. 2013). Additionally, SAV can improve water quality through nutrient cycling functions which may improve oxygen levels and benefit fisheries through mitigation of eutrophication.

Methodologies for quantifying and valuing the various ecosystem service benefits that result from fishery support ecosystem services differ depending on whether one is examining commercial or recreational fishing. The benefits of habitat or water quality improvements for commercial fisheries are commonly estimated by treating the stock or biomass density of the exploited species as an input to a production process, and then assuming that the environment affects stock level or growth in some manner.[4] Recreational fishing benefits are generally estimated using recreation demand models that estimate the welfare benefits that anglers receive based on conditions of where they fish (Newbold and Massey 2010). This approach utilizes *revealed preference* methods, relying on observing angler behavior and correlating decisions on where and when to fish with a number of variables, including trip cost, expected catch, regulations, and any number of environmental indicator variables. Benefits accrue through two pathways. First, habitat-driven improvements to the stock may lead to higher catch rates for legally sized fish, thereby increasing the benefits (welfare) experienced by anglers on any given trip. Second, improving catch rates will increase the likelihood that a given angler decides to spend a day fishing, thereby increasing overall participation. Survey methods are used to both parameterize the behavioral model governing angler decisions and estimate the net benefits generated by fishing.[5]

The first attempt to quantify the fishery support service of SAV in the bay was by Kahn and Kemp (1985). They developed a damage function model to put a lower bound on the potential economic losses associated with SAV degradation in the bay, showing that marginal

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[4] For instance, Barbier and Strand (1998) assume mangrove extent affects the carrying capacity of the shrimp fishery in Campeche, Mexico, estimating an equation of motion for the shrimp stock as $X_{t+1} - X_t = \overbrace{rX_t(K(M_t) - X_t)}^{Growth} - \overbrace{qE_tX_t}^{Harvest}$, where X_t is the stock of shrimp, and the carrying capacity $K(M_t)$ is a function of mangrove area.

[5] Economic value is predicated on establishing "willingness to pay," which in this case is estimated through consideration of real (permit, boat rental, etc.) and opportunity (time) costs associated with engaging in recreational fishing.

(incremental) damages to the commercial and recreational striped bass fisheries rise with more degradation, representing a scarcity effect. The coefficients on the statistical model, while qualitatively in line with expected relationships, were not statistically significant.

Anderson (1989) estimated, through a simulation based on an empirical model linking SAV extent to blue crab production, that benefits to the Virginia blue crab fishery would be on the order of $4.2 million per year (in 1987 dollars). Benefits would accrue to Virginia hard shell crab fishermen and consumers if restoration to 1960 SAV levels took place. Achieving that restoration would require an increase of 4,500 acres of SAV in Virginia waters compared to 1987.

This early start on understanding the economic importance of SAV did not continue, however, and only recently has another study attempted to place a value on the fishery support services associated with Chesapeake Bay seagrasses. Mykoniatis and Ready (2013) developed a model of the blue crab fishery in the bay. They first estimate a coupled bioeconomic model of the blue crab fishery, assuming seagrasses act as either *essential* or *facultative* habitat, then simulate the effect of a one-hectare change in seagrass extent They found the marginal effect of a loss of one hectare of seagrass is a loss in harvest and revenues of 6,749 pounds and $5,409, respectively. This result was statistically significant, but only when the model assumed seagrass to be an essential habitat. The implication of this assumption is that, in the absence of SAV, extinction would occur. However, when seagrass was assumed to be non-essential, facultative habitat, the statistical significance disappeared.

The lack of a significant body of research (or statistically-significant results) supporting the economic benefits to fisheries associated with SAV habitats should not be taken as evidence to the contrary. Identifying a statistically-significant relationship between SAV extent or density and fishery performance is difficult for a number of reasons, including the high correlation between SAV presence and water quality indicators and the sensitivity of seagrasses to transient environmental and physical disturbances (Orth et al. 2006). This suggests alternative approaches may be more effective in identifying habitat impacts. For instance, if SAV improves water quality and that causal link can be identified, it may be appropriate to borrow approaches from efforts to value changes in water quality, including eutrophication and drought (Massey et al. 2006; Huang and Smith 2011; Kennedy and Barbier 2016). Additional challenges include identifying the relationship between seagrass extent and density and subsequent habitat function, which, as is the case with many coastal habitats, may be non-monotonic (Barbier et al. 2008). Thresholds and non-linearities complicate the valuation process, which used techniques (as described above) that rely on *marginal* analysis.

Efforts to understand the links between SAV and fishery performance in other regions provide more evidence of the positive impacts. Most of these examples focus on tropical or sub-tropical climate regions, including the Mediterranean (Jackson et al. 2015), Australia (McArthur and Boland 2006; Watson et al. 2013; Blandon and zu Ermgassen 2014), and Indonesia (Unsworth et al. 2010). These studies estimate benefits by comparing fishery outcomes in areas with SAV to those in areas lacking SAV.

Jackson et al. (2015) built a seagrass residency index for commercial and recreational species in the Mediterranean Sea based on juvenile habitat requirements for various species. They estimate that 30-40% of commercial fishery revenue and 29% of recreational expenditures are associated with species that utilize seagrasses during at least one life stage. When adjusted for residence time, the authors estimate a direct annual contribution to commercial fisheries of €58–91 million, representing approximately 4% of total ex-vessel value, and to recreational expenditures of €112 million, or 6% of total recreation expenditure. These impacts are contrasted to the less than 2% of total area seagrasses occupy in the Mediterranean. Similarly, McArthur and Boland (2006) use a residency approach to calculate the reduction in revenue associated with a loss of 12,700 ha (16% of the total) of seagrass extent in the Northern Spencer Gulf off the coast of South Australia. The losses were deemed to be the result of storms and physical variables. They estimated the loss of seagrass resulted in a reduction of in ex-vessel value of AU$235,000 per year.

Blandon and zu Ermgassen (2014) use meta-analysis techniques to estimate the contribution of seagrasses to twelve commercially-exploited species in South Australia. Their empirical findings are used to inform a model to assess the benefits of seagrass restoration. They find that seagrasses enhance combined biomass at a rate of approximately 0.98 $\text{kg-m}^{-2}\ \text{yr}^{-1}$, which translates into an added stock value (not landings) of approximately AU$230,000 per hectare per year if all species are present. With an estimated restoration cost of AU$629,000 per hectare, they argue the fishery benefits of restoration outweigh the costs.

Watson et al. (1993) used a simulation model to estimate the annual contribution of 876 ha of seagrass habitat in Cairns Harbour (Queensland) to the local commercial prawn fishery. The simulation was employed—rather than simply examining commercial landings—to overcome the fact that prawns are able to utilize different habitats. Basing their simulation on scientific surveys of prawn abundance in seagrasses, the authors estimated the potential total annual yield from seagrasses for three commercial prawn species at 178 tonnes per year, with a landed value of AU$1.6 Million.

While some of the papers in this group are unable to account for other confounding variables, such as water quality and other ecological or socioeconomic factors that may influence both the presence of SAV and the performance of fisheries, overall the evidence is supportive of a positive role. Additionally, it is important to take into account the fact that SAV habitats in tropical areas are not directly comparable to those in temperate areas. The seasonal patterns affecting SAV extent and density in the Chesapeake Bay are likely different, if not absent, from these regions, and seagrass habitats in tropical areas are often part of a system of habitats, including mangroves, patch reefs, and sand flats, that all contribute to the successful recruitment of fish to reef habitats (Hylkema et al. 2015). It is, however, instructive to consider what has been found in these other studies.

Property protection

Coastal protection, sediment retention, and erosion control have been identified as Ecosystem services associated with SAV habitats (Koch et al. 2009; Barbier et al. 2011). There is evidence that SAV offers wave attenuation benefits, resulting in lower magnitude waves hitting shorelines and potentially mediating damages associated with storm events (Koch and Beer 1996; Prager and Halley 1999). Koch et al. (2006) found coastal protection to be highest when vegetation occupies the entire water column, implying service provision is dependent on having SAV present and at full height when storms occur. Similarly, SAV habitats in deeper waters are less likely to result in significant benefits since wave attenuation is lower. Stabilization of sediment by seagrass root structures may also result in reduced coastal erosion (Hemminga and Nieuwenhuize 1990).

Field studies have not, however, resulted in subsequent valuation efforts. Analysis is limited by an insufficient number of studies to resolve the complex relationship between disturbance intensity and frequency, sedimentation, turbidity, contributions of adjacent marsh, and SAV extent and density. Nonetheless, simulation models have been used to scale up field measurements and infer potential property damage protection from SAV (citations).

Property value enhancement

People can reveal their values for SAV and the ecosystem services that it provides through their market purchases. Hedonic analysis is a statistical method that uses property sales data to demonstrate the values for amenities—including natural amenities—that are capitalized in property value. The first application of the method suggested that homes in areas with good air quality had higher values than those in areas with poor air quality, all else equal (Smith and Huang 1993). Since those initial applications, hedonic analysis has been used to suggest the value of water quality, wetlands, beaches, open space, and other natural and human-made amenities (Leggett and Bockstael 2000; Geoghegan 2002; Landry and Hindsley 2010; Walsh et al. 2011; Boyle and Taylor 2015).

A recent comprehensive statistical analysis by Guignet et al. (2014) evaluated the relationship between SAV and home values in the Chesapeake Bay watershed. The analysis used property sales data for residential properties in eleven Maryland counties adjacent to the Chesapeake Bay from 1996 to 2008. The authors found that having SAV along the nearest shoreline was associated with a significant "price premium" for waterfront and near-waterfront homes. The price premium is the additional value that people are willing to pay for residential property that have adjacent SAV compared to a property without SAV, holding all else equal.

They summarize their findings as, "On average, waterfront and near-waterfront homes within 200 meters of the shore sell at a 5% to 6% premium when SAV are present. Applying these estimates to the 185,000 acre SAV attainment goal yields total property value gains on the order of $300 to 400 million." Thus, the results suggest that if the SAV restoration goal was achieved, it would create a substantial value, as capitalized in current residential property values. This aggregated value could increase if waterfront or water-adjacent homes increased in the future.

The pathway of benefits from SAV to homeowners is not obvious and can only be clarified with further analysis. Although we can only speculate, SAV may add value to homes because people directly enjoy the SAV or because of its contributions to other services including more stable shorelines (less erosion), improved recreational fishing, improved waterfowl viewing or hunting, and better water quality. All of these factors have been shown to have significant value, using hedonic or other types of analyses, as discussed in other sections.

Recreation (other than fishing)

SAV likely supports recreational opportunities beyond those associated with fishing. Perry and Deller (1996) reviewed the factors affecting the distribution and abundance of waterfowl in the Chesapeake Bay. Observing a general decline in distribution and abundance, they implicated a loss of shallow water habitat, including SAV, as a driving force, along with reductions in water quality and increased human use of essential habitat areas. They noted a reduction in the amount of SAV consumed by waterfowl, and a general reduction in the diversity of food organisms in diets. However, they also observed that waterfowl indicators have generally benefited from the emergence of exotic SAV species. Erwin (1996) found both brackish marshes and shallow water habitats populated by SAV to provide important habitat for waterfowl in the Delaware Bay. Rybicki and Landwehr (2007) found waterfowl populations to be positively associated with SAV density (albeit an exotic species) in the upper-Potomac River estuary, adjacent to the Chesapeake Bay.

While there are no studies that attempt to value improvements to waterfowl hunting and viewing opportunities associated with SAV, there are several studies that examine the role of brackish marshes. For instance, Wainger et al. (2013) estimated the potential benefits of increasing the amount of wetlands available to ducks through the use of a "duck energy day" (DED) model, which assigns a DED metric—roughly analogous to capacity—to different land types. Their analysis suggests converting cropland and pasture to tidal wetlands yields duck hunting benefits of $7.56-8.49 and $3.78-4.21 per year in Maryland and Virginia, respectively. In the UK, Birol and Cox (2007) used a choice experiment and identified a positive willingness to pay for protection of an estuary that provided habitat for otters and birds (with positive values for each category of organism). More generally, Farber (1998) used a contingent valuation survey and found Louisiana residents were willing to pay $103-323 per household to preserve recreational hunting and fishing opportunities associated with a 650,000 acre wetland system (Terrebonne Parish wetlands), yielding a value of $170-535 per acre in year-2000 dollars. Finally, if anecdotally, there have been a number of news stories linking hunting and birding opportunities to SAV, and there appears to be widespread understanding, particularly in the hunting community, that SAV is a critical habitat for waterfowl, both in the bay and beyond.[6]

Avoided harms from climate change (carbon sequestration).

SAV beds can sequester substantial quantities of carbon (Chapter X), which can benefit people by reducing the magnitude of global climate change and associated risks. Additional sources of carbon sequestration are desirable to offset the buildup of carbon dioxide and other gases in the atmosphere that are contributing to the enhanced greenhouse effect. The pathways of potential harm from climate change are numerous and include increases in agricultural losses, property damage, land loss, morbidity and mortality, and economic disruptions (Tol 2008).

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[6] See articles in the Baltimore Sun http://www.baltimoresun.com/features/green/blog/bs-md-susquehanna-grasses-20140901-story.html, Game and Fish Magazine http://www.gameandfishmag.com/hunting/hunting_ducks-geese-hunting_at_aa120503a/, and the New Orleans Times-Picayune: http://www.nola.com/outdoors/index.ssf/2009/10/submerged_aquatic_vegetation_v.html.

The extent to which SAV protection and restoration in the Bay contribute to net carbon sequestration is considered a social benefit because it contributes to the total greenhouse gas reduction needed to reduce risks. However, the value of any incremental contribution cannot be precisely measured because benefits will depend on the total amount of greenhouse gases that are allowed to accumulate, the weather and climate changes that result, and the ability of people and organisms to adapt to those changes. To overcome modeling difficulties, an intergovernmental panel has developed a range of dollar value estimates of the incremental benefits per ton of carbon sequestered (under different assumptions), so that this benefit is not excluded from cost-benefit analyses for regulatory decisions (Greenstone et al. 2013).

The estimate of the benefits of greenhouse gas sequestration is referred to as the *social cost of carbon* and it represents the marginal damage caused by an additional ton of carbon dioxide emissions. The value was derived by using alternative policy scenarios to estimate a range of climatic responses. Using a suite of models and many assumptions about how climate change might affect economic activities, they projected likely economic harms. The most recent estimates for the global social cost of carbon vary depending on the discount rate used and time frame (Table 2). Using these values equates economic benefits of carbon sequestration to the damage costs avoided.

Table 2. Social Cost of CO_2, 2010-2050 (2007$ per metric ton of CO_2) from (Interagency Working Group on Social Cost of Carbon 2013)

Discount Rate	**5.0%**	**3.0%**	**2.5%**	**3.0%**
Year	**Avg**	**Avg**	**Avg**	**95th percentile**
2010	11	33	52	90
2015	12	38	58	109
2020	12	43	65	129
2025	14	48	70	144
2030	16	52	76	159
2035	19	57	81	176
2040	21	62	87	192
2045	24	66	92	206
2050	27	71	98	221

Note: Both the average value of damages and the 95th percentile of damages are shown for the 3% discount rate. The fourth column, "which represents the 95th percentile SCC estimate across all three models at a 3 percent discount rate, is included to represent higher-than-expected impacts from temperature change further out in the tails of the SCC distribution." (**SCC 2013**)

Using the Social Cost of Carbon to project value of restored SAV beds

Existing SAV beds maintain large quantities of carbon in aboveground biomass, belowground biomass, and sediments rich in organic material (i.e., submerged soil). The majority of long-term storage is in the submerged soils, which store, on average, double the amount of carbon as terrestrial soils (Fourqurean et al. 2012). The exact amount of carbon sequestered depends on the given SAV bed's soil depth and carbon density.

SAV restoration projects offer opportunities to sequester significant amounts of carbon, since restored SAV rapidly accumulates organic carbon in their soils (Duarte et al. 2013). A field study conducted in the Virginia portion of the Bay showed that 10 years after restoration of SAV, annual accumulation was approximately 36.68 g C m^{-2}, or 1.35 metric tons of CO_2 ha^{-1} (Greiner et al. 2013). Whether SAV is a net carbon sink or source depends on its metabolism, specifically whether its gross primary production rates are greater than its respiration rates (Duarte et al. 2010)**.**

Using a present value equation (Eqn 1-Intro), we can estimate the future stream of benefits per hectare of restored SAV over the period 2015 - 2025. First, we multiply the Greiner et al. (2013) estimate of 1.35 metric tons of CO_2 ha^{-1} sequestered per year with an intermediate value for the social cost of carbon for 2015 of $43.44 (2015 dollars). Next we apply a 3% discount rate[7] to estimate a present value of about **$610 per hectare** for the 10 years of restored mature SAV beds. This number ranges from $540 for the 5% discount rate to $630 for the 2.5% discount rate. If we used the 95th percentile values and the 3% discount rate, the present value would rise to $1,800 per hectare for the 10-year period.

The $600 per hectare estimate for the 11 year period analyzed could change dramatically under different assumptions. Some authors have suggested that social costs of carbon estimates are too low (Ackerman and Stanton 2012) and may be closer to $900/tCO2 (in 2010 dollars), if more extreme climate scenarios were considered. Workers also disagree on the appropriate discount rate (Arrow et al. 2013; Cropper et al. 2014) and the calculations of the present values of a future stream of benefits are quite sensitive to this assumption, with higher discount rates resulting in substantially smaller values. In general, this approach to estimating values for SAV embeds many strong assumptions that affect the estimates of economic benefits of carbon sequestration and thus, value estimates should be used cautiously.

Table 1. Ecosystem services, processes and functions, important controlling components, examples of values, and human drivers of service loss for seagrasses (adapted with modifications from Barbier et al. (2011)).

Ecosystem services	Ecosystem processes and functions	Important controlling components	Ecosystem service value examples
Coastal protection/ erosion control	Attenuates and/or dissipates waves; provides sediment stabilization and soil retention in vegetation root	Wave height and length, water depth above canopy, seagrass bed size and distance from shore, wind climate,	Estimates unavailable

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[7] The 3% value is the middle value used in the analysis. See introduction for definition of discount rate.

	structure	bathymetry, seagrass species and density, reproductive stage	
Erosion control	Provides sediment stabilization and soil retention in vegetation root structure	Sea level rise, subsidence, tidal stage, wave climate, coastal geomorphology, seagrass species and density	Estimates unavailable
Water quality improvement	Provides nutrient and pollution uptake, as well as retention, particle deposition	Seagrass species and density, nutrient load, water residence time, hydrodynamic conditions, light availability	Estimates unavailable
Fishery enhancement	Provides suitable reproductive habitat and nursery grounds, sheltered living space	Seagrass species and density, habitat quality, food sources, hydrodynamic conditions	Restoration of 4,500 acres of SAV in the bay would increase blue crab fishery value by $4.7 million per year in 1987-dollars, with improvements accruing to both consumers and producers (Anderson 1989).
Carbon sequestration	Generates biogeochemical activity, sedimentation, biological productivity	Seagrass species and density, water depth, light availability, burial rates, biomass export	$113 Million if all 185,000 acres are restored (PV of carbon sequestration 2015-2025)
Tourism, recreation, education, and research	Supports SCUBA and snorkel operations for observation of associated fauna	Biological productivity, storm events, habitat quality, education and research funding, diversity	Estimates unavailable

CONCLUSIONS

The few research efforts that have attempted to quantify the value of ecosystem services associated with SAV in the bay have been primarily focused on fishery support services and, more recently, water quality benefits accruing to adjacent homeowners. This should not be taken as an indication of low or non-existent value of other services (wave attenuation and erosion control, other water quality benefits, non-fishing recreation, etc.), but rather a call for new research efforts to understand the benefits associated with these complex habitats. In particular, understanding the relationship between water quality and SAV is a significant challenge for valuation because of this problem of identifying causation. Given the importance of water quality for recreation, commercial fishing, home values, and overall ecosystem integrity, understanding these links is an important future step. If SAV presence does indeed lead to improvements in water quality, that broad function may result in significant benefits across a spectrum of ecosystem services. On the other hand, if the relationship is primarily in the other direction (water quality driving SAV extent), it is important to parse out the relative impacts of water quality improvements on home values and fishery performance, so that the contribution of SAV can be independently identified.

With additional research commitments, it can be expected that the body of evidence supporting the positive economic contributions of SAV habitats to the Chesapeake Bay region and beyond will grow, increasing public awareness and, hopefully, providing a basis for increased support of conservation and restoration activities

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