Submersed Aquatic Vegetation in Chesapeake Bay: Sentinel Species in a Changing World

ROBERT J. ORTH, WILLIAM C. DENNISON, JONATHAN S. LEFCHECK, CASSIE GURBISZ, MICHAEL HANNAM, JENNIFER KEISMAN, J. BROOKE LANDRY, KENNETH A. MOORE, REBECCA R. MURPHY, CHRISTOPHER J. PATRICK, JEREMY TESTA, DONALD E. WELLER, AND DAVID J. WILCOX

Chesapeake Bay has undergone profound changes since European settlement. Increases in human and livestock populations, associated changes in land use, increases in nutrient loadings, shoreline armoring, and depletion of fish stocks have altered the important habitats within the Bay. Submersed aquatic vegetation (SAV) is a critical foundational habitat and provides numerous benefits and services to society. In Chesapeake Bay, SAV species are also indicators of environmental change because of their sensitivity to water quality and shoreline development. As such, SAV has been deeply integrated into regional regulations and annual assessments of management outcomes, restoration efforts, the scientific literature, and popular media coverage. Even so, SAV in Chesapeake Bay faces many historical and emerging challenges. The future of Chesapeake Bay is indicated by and contingent on the success of SAV. Its persistence will require continued action, coupled with new practices, to promote a healthy and sustainable ecosystem.

Keywords: SAV, management, land use, climate change, water quality

Chesapeake Bay: 400 years of change

Chesapeake Bay is one of the largest and most important estuaries in the world. American history and much of the history of the Western world have been shaped by Chesapeake Bay. America's growth and development have likewise transformed the Bay dramatically. Modern Europeans first settled the shores of Chesapeake Bay in 1607 in what is now Jamestown, Virginia. At their arrival, they encountered a well-established and highly organized population of around 14,000 indigenous people, the Algonquin-speaking Powhatan Indians. Now, over 400 years since European settlement, a population of more than 18 million people dominates the Chesapeake Bay watershed (CBP 2016), so it is no surprise that the Bay of today is very different from the Bay of 1607.

The name Chesapeake comes from the Algonquin word *K'che-se-piak*, meaning "land along the big river." This big river had such a great wealth of natural resources that Captain John Smith, renowned early explorer, made special note of their abundance. Oysters, blue crabs, sturgeon, striped bass, and waterfowl were so plentiful that they supported much of the early population growth of this region.

Crucial to the abundance of these species were important foundational habitats that provided food, refuge, and nurseries, including submersed aquatic vegetation (SAV). Submersed aquatic vegetation was abundant in the shoals of the Bay and its rivers at the time of the first settlers (Brush and Hilgartner 2000, Lotze et al. 2006). These SAV meadows also protected shorelines from erosion, stabilized benthic sediments, captured suspended solids, and sequestered large amounts of carbon and nitrogen (Fourqurean et al. 2012, Lefcheck et al. 2017). These ecosystem services have increased in value as the human population has grown along the Bay's shorelines and throughout its watershed (Kemp et al. 2005) and in the face of global threats such as climate change (Najjar et al. 2010).

Humans have altered the landscape in myriad ways that have harmed the same resources that we increasingly value and rely on. Shorelines have been armored, the waters have been made eutrophic by nutrient pollution from humans and farm animals, and fisheries have been overharvested (Lotze et al. 2006, Beck et al. 2011, Gittman et al. 2016). All of these factors have contributed to a decline in SAV and the services they provide. With a steadily increasing population and new challenges continuing to arise, such as the introduction of nonnative species, aquaculture, and climate change (figure 1), the management of Chesapeake Bay SAV remains a prominent challenge in the twenty-first century.

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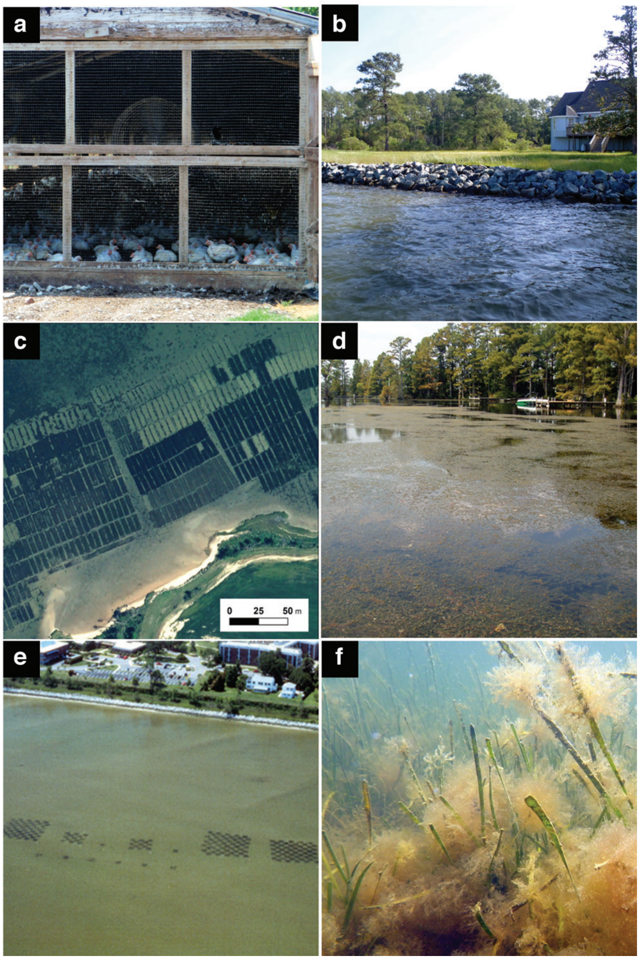

Figure 1. Issues and conflicts that directly or indirectly influence submersed aquatic vegetation (SAV) in the Bay. (a) The chicken population is rapidly increasing and produces large amounts of manure (Photograph: University of Maryland). (b) Hardened shoreline, which can negatively influence SAV habitat (Photograph: Brooke Landry). (c) Hard clam aquaculture plots in an area that once supported dense **Zostera marina** *(small amounts remain in the upper left of the image (Photograph: Robert Orth). (d) Dense beds of the nonnative* **Hydrilla** *now occur in low-salinity areas and have improved conditions in some meadows to allow native SAV to colonize (Photograph: Erin Shields). (e) An aerial image of a seagrass restoration area with individual plots of* **Z. marina** *arranged in a checkerboard pattern (Photograph: Robert Orth). (f) The abundance of macroalgae smothers* **Z. marina** *because of eutrophication (Photograph: Jon Lefcheck).*

A growing recognition of the consequences of the Bay's dramatic transformation and consequent impacts on human well-being resulted in substantial political attention paid to Chesapeake Bay in the 1970s. This led to the establishment of the Chesapeake Bay Program, a governance structure to oversee a multimillion dollar effort to restore the Bay (Orth et al. 2002). This effort included SAV studies to determine the causes and magnitude of its decline. The synthesis of this work and the recognition of the Bay's declining health led to the first Chesapeake Bay Agreement in 1983, which established long-term programs to monitor the Bay's water quality and natural resources (Orth et al. 2002). These monitoring data have been crucial for informing managers about the effectiveness of efforts to improve water quality and natural resources.

Submersed aquatic plants are indicators of the health of the Chesapeake Bay

Chesapeake Bay supports a diverse assemblage of more than a dozen species of SAV, whose distributions are generally influenced by their salinity tolerances (table 1; Moore et al. 2000, Orth et al. 2010a, Patrick and Weller 2015). Two species, *Zostera marina* (eelgrass) and *Ruppia maritima* (widgeongrass), inhabit the higher-salinity areas; the remaining species (including several nonnative ones) inhabit the lower-salinity and freshwater zones. Submersed aquatic vegetation species are rooted, so they are especially sensitive to and integrate across a variety of water-quality changes, such as nutrient enrichment and sedimentation. Therefore, changes in SAV populations can provide advanced warning for environmental degradation at specific locations throughout the Bay. Consequently, the abundance and diversity of SAV have been used by resource managers as a sentinel-species group to gauge the Bay's current condition, as well as the success of management efforts to improve local and Bay-wide water quality (Dennison et al. 1993).

A *sentinel* is something that watches, guards, and defends. In addition, the term *sentinel species* in conservation and ecology connotes an indicator of broader ecological function and/or an early warning of ecological impairment. Submersed aquatic vegetation is not only an indicator of water quality; it can also modify its environment to enhance its own abundance and therefore is a defender of water quality. It likewise acts as a defender of shorelines against erosion, as well as a defender of juvenile fishes and crabs by providing refuge or cover. Submersed aquatic vegetation is the epitome of a sentinel species because it is both an indicator and a defender, two roles that are further described below.

Changes in Chesapeake Bay SAV abundance have been occurring since the European settlers cleared the first land (Brush and Hilgartner 2000), but recent and more dramatic changes began in the 1970s. Tropical Storm Agnes in 1972 was especially important because it caused unprecedented declines in many SAV populations (Orth and Moore 1983). Since then, we have witnessed profound alterations in the distribution and structure of SAV communities throughout the Chesapeake Bay and its tidal tributaries. The loss of these key plant communities launched an unparalleled examination into all aspects of SAV biology, ecology, management, conservation, and restoration. A seminal paper published in 1993 identified five key parameters—water clarity, suspended sediments, nitrogen, phosphorus, and chlorophyll *a*—that influence SAV abundance and distribution. Levels of these five parameters were identified as

Table 1. Species of the most common submersed aquatic vegetation found in the Chesapeake Bay and their common names.

Species	Common name
Ceratophyllum demersum	coontail
Elodea canadensis	common elodea
Heteranthera dubia	water stargrass
Hydrilla verticillata	hydrilla
Myriophyllum spicatum	Eurasian watermilfoil
Najas guadalupensis	southern naiad
Najas gracillima	slender waternymph
Najas minor	spiny naiad
Potamogeton crispus	curly pondweed
Potamogeton perfoliatus	redhead grass
Potamogeton pusillus	slender pondweed
Ruppia maritima	widgeongrass
Stuckenia pectinata	sago pondweed
Vallisneria americana	wild celery
Zannichelia palustris	horned pondweed
Zostera marina	eelgrass

habitat requirements for supporting SAV in the different salinity regions of the Chesapeake (Dennison et al. 1993). Those criteria gave resource managers very specific targets for water-quality improvements that would promote SAV recovery and by extension other valuable habitats and organisms, thereby establishing these important plants as sentinel species throughout the system.

In conjunction with water-quality restoration targets, resource managers have developed restoration goals for SAV area. The ultimate goal for SAV restoration in the Chesapeake Bay is 75,000 hectares Bay-wide, with interim goals of 36,500 hectares by 2017 and 52,700 hectares by 2025. The attainment of these and water-quality goals is now being assessed by an annual ecological report card, which provides performance-driven numeric grades that measure the ecosystem health of Chesapeake Bay (Williams et al. 2009). A variety of ecological indicators, in addition to SAV, determine the overall grade. These indicators are ranked against thresholds determined from ongoing monitoring programs, and all the indicators are combined into a Bay Health Index (figure 2). The annual Chesapeake Bay report card is an important tool for integrating diverse data types into simple scores that can be communicated to decision-makers and the general public (Williams et al. 2009). As a sentinel of Bay recovery, SAV resurgence can presage improvements in the overall Bay Health Index.

Submersed aquatic vegetation is a sentinel by being both an indicator and an ecosystem engineer

Dense aggregations of SAV can improve local water quality and buffer against inadequate growing conditions by engineering their own environment. For example, the physical structure of a plant bed decreases wave height and water velocity, which causes suspended particles to settle out of the water column and hinders resuspension (de Boer 2007). These effects increase light availability, which promotes photosynthesis and growth. Submersed aquatic vegetation beds can also reduce nutrient concentrations by assimilating dissolved nitrogen and phosphorus and by enhancing sediment denitrification (McGlathery et al. 2007). Consequently, phytoplankton and epiphytic algae growth becomes nutrient limited within the bed, further reducing shading and increasing light availability for SAV. These positive feedback systems continue to build as the bed expands and have been noted throughout the Chesapeake Bay (Ruhl and Rybicki 2010, Moore 2004, Patrick and Weller 2015) and the coastal lagoons of the Delmarva Peninsula (Orth et al. 2012).

When positive feedback processes operate, they can reduce the sensitivity of SAV to fine-scale changes in environmental conditions. This enhanced resistance dampens SAV's indicator role while increasing the importance of SAV as a defender of water quality. For example, large, dense SAV beds can buffer themselves against short-term disturbances such as hurricanes, as well as against gradual or moderate declines in water quality. Therefore, such beds could indicate better water-quality conditions than actually exist. However, the presence of SAV always indicates a minimum level of water quality, because even a large SAV bed will collapse if water quality declines enough. Therefore, positive feedback processes allow for the same external water-quality conditions to support alternate stable states: a large, dense SAV bed if conditions are already amenable, or bare sediment if poor conditions prevent vegetation from growing (figures 3a and 3b; Scheffer et al. 2001). Submersed aquatic vegetation species morphology, patch size, and bed density control the strength of self-stabilizing feedback loops and therefore the magnitude of decoupling between SAV response and external stressors (figures 3c and 3d; Luhar et al. 2008).

Promoting the use of submersed aquatic vegetation as sentinel species: Management, research, and public outreach

The Baywide decline of SAV in Chesapeake Bay, the focus on SAV by resource managers and politicians, and the inclusion of SAV in restoration targets in water-quality standards (figure 4a; supplemental table S1; Orth et al. 2010b) have increased attention from academics and ultimately from the public.

Between 1960 and 1980, only 29 Chesapeake Bay SAV-focused papers were published in the peer-reviewed literature (figure 4b). The number of publications has increased exponentially, and the scope of the research has also expanded to include the patterns of SAV distribution and abundance, reproductive ecology, the effects of environmental processes on SAV (and vice versa), modeling to predict future outcomes, the use of SAV as habitat by fauna,

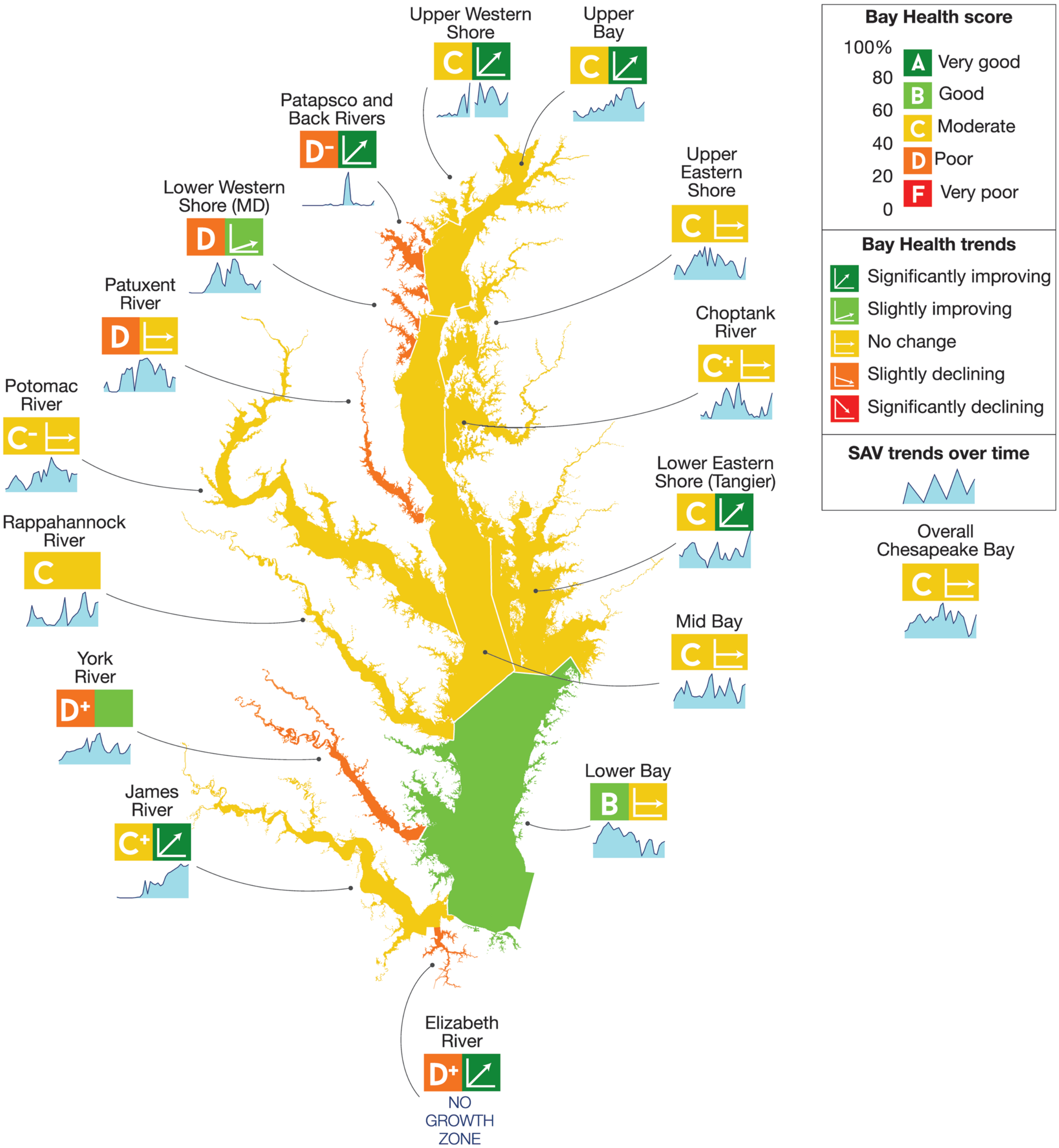

*Figure 2. The Chesapeake Bay report card compares seven indicators (dissolved oxygen, nitrogen, phosphorus, chlorophyll a, water clarity, aquatic grasses, and benthic community) to scientifically derived thresholds or goals. The indicators are also combined into an overall Bay Health Index, which is presented as a subregion percent score, yielding a letter grade like in a school report card. Many years' data are integrated to provide managers with information on trends that may be increasing, decreasing, or staying the same. Submersed aquatic vegetation time series are shown graphically for each subsection (*http://ecoreportcard.org*).*

and SAV restoration. A comprehensive bibliography of all peer-reviewed journal papers, conference proceedings, and book chapters focused on Chesapeake Bay SAV is available at *http://vims.edu/bio/sav/bibliography/Bibliography.html.*

Media coverage grew along with the research, bringing increasing public attention to SAV issues, especially with the annual report card of Chesapeake Bay health (figures 2 and 4c).

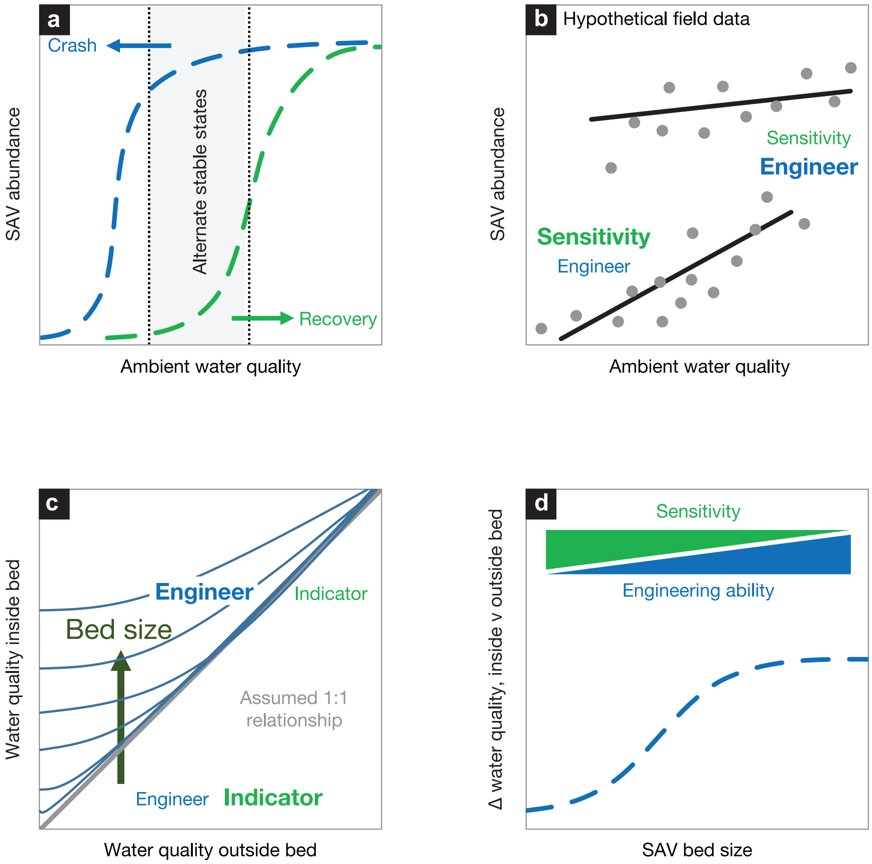

Figure 3. Submersed aquatic vegetation (SAV) species can improve water quality within SAV beds, making them ecosystem engineers and affecting their role as ecological indicators. Large SAV beds are less sensitive indicators of declining water quality because their self-buffering capacity decouples them from external conditions. Submersed aquatic vegetation is always a water-quality indicator, but the relationship between abundance and water quality is nonlinear and mutable. (a) The ambient water-quality threshold required for recovery may be higher than the threshold that can precipitate a population crash because feedback processes in established SAV beds buffer them against poor water quality. (b) Hypothetical data illustrating possible alternate stable states of SAV abundance and the responses of abundance to water-quality variation in each state. As bed size and SAV abundance increase, the capacity for ecosystem engineering increases, and the sensitivity to external forcing decreases. This panel also illustrates the challenge of fitting simple stressor–response relationships to data aggregated from both alternate states. (c) and (d) The relationship between water quality inside the SAV bed versus outside the SAV bed. The inside-versus-outside difference increases with bed size (stronger water-quality improvements within larger beds) and with declining water quality. When water quality is very good, there is little scope for further improvement within SAV beds.

Renewed interest in submersed aquatic vegetation has increased restoration efforts

The recent loss of SAV in much of its historical habitat and increasing attention among scientists, managers, and citizens has piqued interest in restoring SAV through transplanting adult plants and seeds to previously vegetated areas. Natural recovery or recolonization of SAV into formerly vegetated areas may fail because of continuing poor habitat conditions or insufficient source of seeds or colonizing plants. Since the first attempts were made in the late 1970s (Orth et al. 2010b), the number of restoration attempts has steadily risen (figures 1e and 4d). Unfortunately, there are few long-term successful projects (figure 4d).

Most restoration efforts have used *Z. marina*, a species that historically dominated much of the southern, higher-salinity portions of the Bay and that has undergone some of the greatest declines (Orth and Moore 1983, Lefcheck et al. 2017). Large-scale efforts (greater than 0.1 hectares) were made in the early 2000s, but few persisted for more than 5 years (Orth et al. 2010b). The majority of failures resulted from marginal to poor water quality and, more recently, from periods of high-temperature stress (Moore et al. 2014, Lefcheck et al. 2017). These failed restoration attempts suggest that the path to SAV recovery, whether natural or assisted, will require continued efforts to improve water-quality conditions to levels that support healthy SAV. However, the success of a large, seed-based restoration in Virginia's Coastal Bays (Orth et al. 2012) suggests that SAV restoration could enhance SAV populations throughout the Chesapeake after management efforts to improve water-quality conditions are successful.

Dynamic distribution and abundance of submersed aquatic vegetation: Broadscale insights

To better understand the recent dynamics of SAV populations throughout the Chesapeake Bay and its tributaries, an aerial SAV monitoring program was initiated in 1984 and repeated annually throughout the Chesapeake Bay. Approximately 170 flight lines are flown each year between May and October, yielding over 2000 photographs or digital images. Since the beginning of this program, SAV has proven to be incredibly dynamic, exhibiting long-term (decadal scale) increases and decreases in different regions of Chesapeake Bay, as well as large interannual variability within individual river systems and subestuaries (Li et al. 2007, Orth et al. 2010a, Patrick and Weller

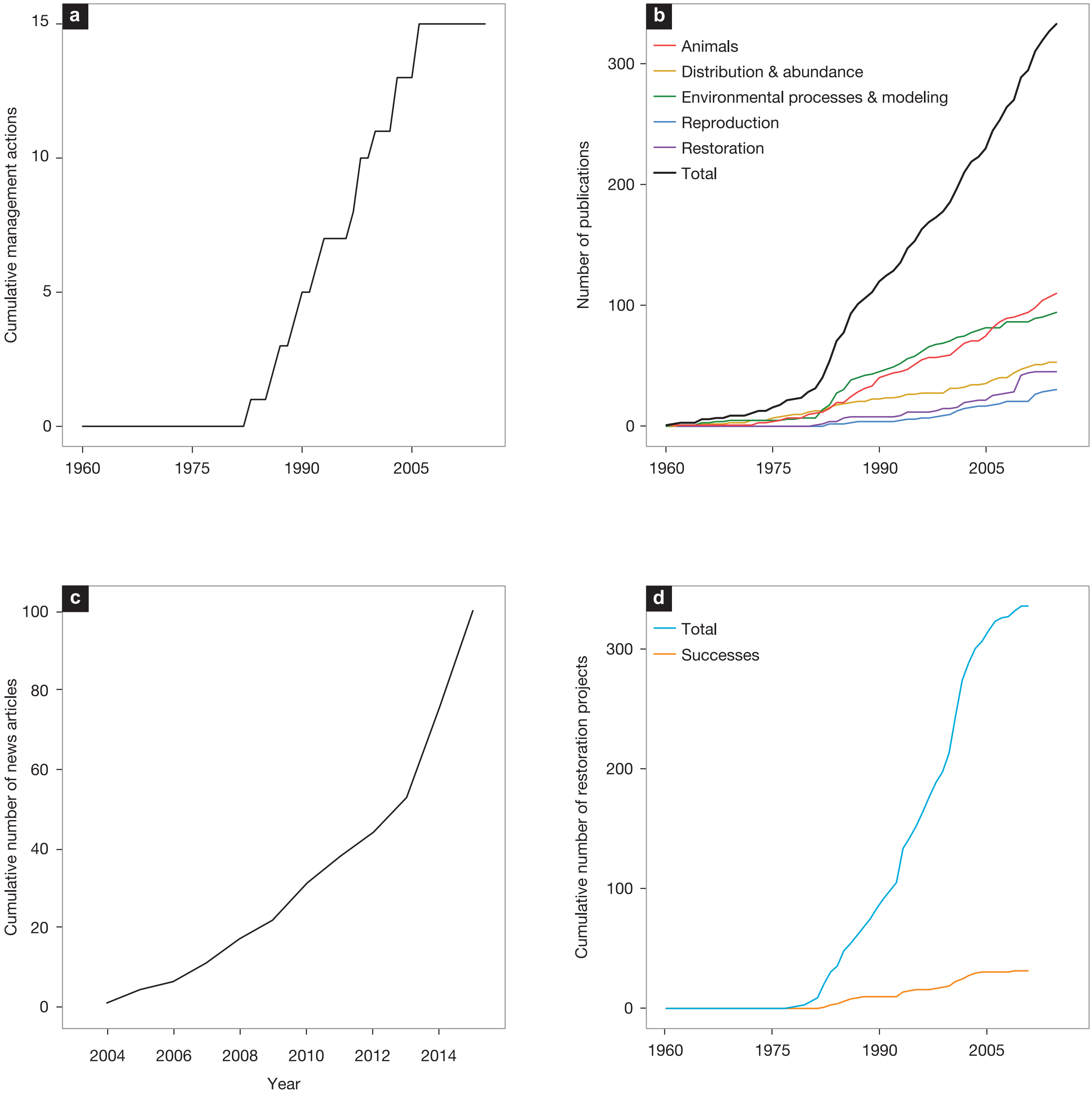

Figure 4. (a) Cumulative management actions (1980–2015) to protect, conserve, and restore SAV populations. (b) Cumulative peer-reviewed Chesapeake Bay SAV publications (1960– 2015) and five categories of publications. (c) Chesapeake Bay SAV media attention (cumulative since 2005). (d) Restoration efforts (cumulative 1975–2015, with the number of success projects surviving a minimum of 5 years).

2015, Lefcheck et al. 2017). Current SAV abundance remains well below established restoration targets for Chesapeake Bay (figure 5; Orth et al. 2010a). In 2015, total coverage was only 37,000 hectares, which was 38,000 hectares short of the ultimate restoration goal but which exceeded the interim restoration goal of 36,500 by 2017 (figure 5a).

Dynamic distribution and abundance of submersed aquatic vegetation: Local insights

Broadscale patterns in SAV coverage and density are important but may mask individual community responses at smaller scales. This point is crucial because species in different subestuaries of the Bay with different watershed and water-quality characteristics may be responding to different

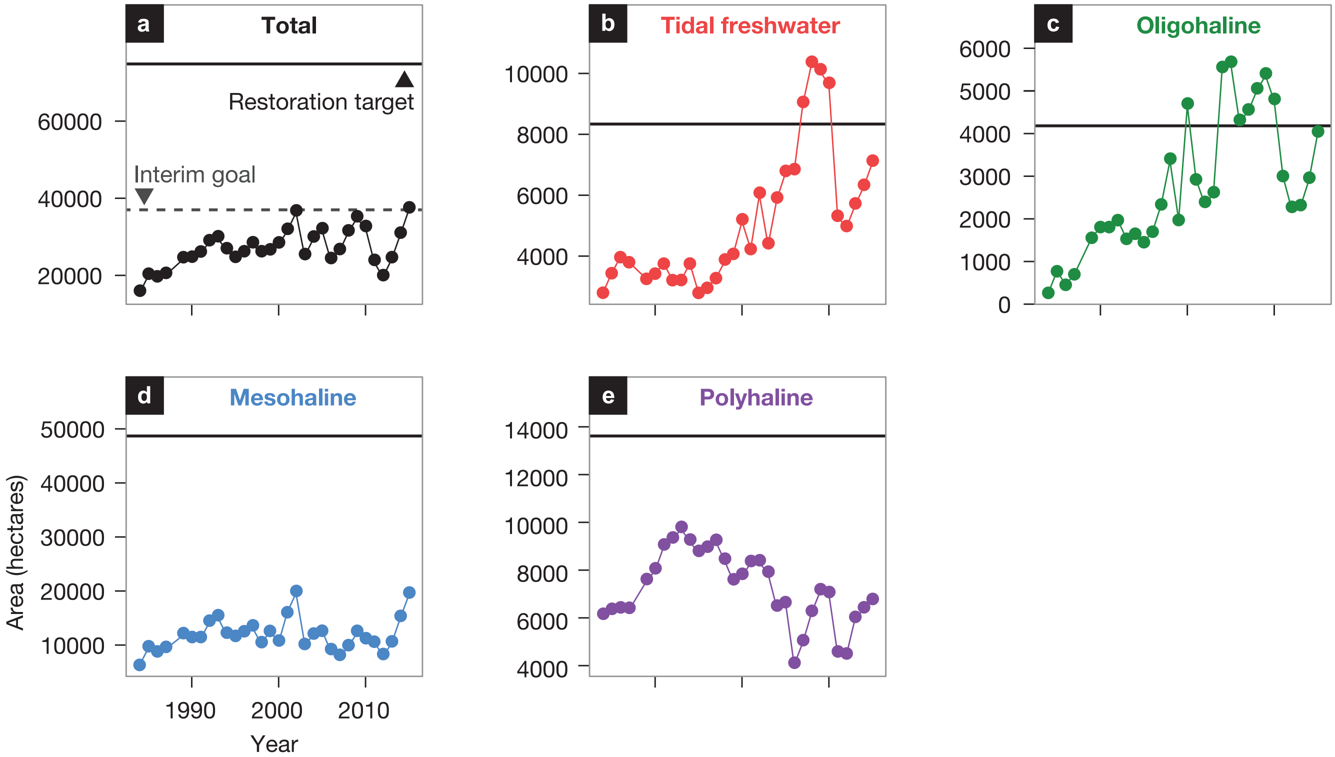

Figure 5. The abundance of SAV (circles) and the restoration targets (horizontal lines) developed for either the entire Chesapeake Bay or four different salinity regions: (a) baywide, (b) freshwater regions, (c) low-salinity regions, (d) medium-salinity regions, and (e) high-salinity regions. dashed horizontal line in (a) shows the 2017 attainment goal.

abiotic or biotic factors. The species driving recovery in subestuaries, where it does occur, may be different from the species that were previously lost, especially in the case of the arrival of invasive species. Here, we provide five case studies of differing SAV community responses that illustrate the diversity of patterns and factors influencing SAV dynamics across the Chesapeake Bay (figure 6).

Case 1: Reductions in nutrient loading promote submersed aquatic vegetation

Reductions in point-source nutrient loading have had clear positive benefits for SAV beds in oligohaline reaches of several Chesapeake Bay tributaries. Submersed aquatic vegetation was rare or absent in the upper Potomac and Patuxent rivers for well over a half century (figures 2 and 6a). Advances in wastewater treatment implemented in the early 1990s reduced algal production and improved water clarity. Submersed aquatic vegetation then re-established, spread rapidly through the systems, and continues to persist through today (Testa et al. 2008, Orth et al. 2010a, Ruhl and Rybicki 2010, Boynton et al. 2014). As nutrient loadings were further reduced, species diversity increased, and the proportion of native to nonnative species increased, strongly suggesting that environmental policies that reduce nutrients have improved habitat quality for both SAV and the species that depend on SAV (Rybicki and Landwehr 2007, Ruhl and Rybicki 2010).

Case 2: Massive resurgence in Susquehanna Flats

The most dramatic example of SAV recovery in the Bay is the large-scale resurgence in the tidal fresh region of upper Chesapeake Bay known as Susquehanna Flats. Positive feedback processes were likely central to the recovery and resilience of widespread SAV beds in the upper Bay (figures 2 and 6b). In the early twentieth century, the SAV community in Susquehanna Flats was a premier wintering waterfowl site on the mid-Atlantic coast. By the early 1970s, declines in water quality and the catastrophic flooding associated with Tropical Storm Agnes in June 1972 had essentially eliminated SAV from the Flats—and with it, the waterfowl (Bayley et al. 1978). In the early 2000s, a multispecies SAV meadow dominated by *Vallisneria americana* (wild celery) and *Heteranthera dubia* (water stargrass) began to expand to reach a maximum area of approximately 50 square kilometers (Orth et al. 2010a). Although modest reductions in nutrient loads from the Susquehanna watershed likely helped, a period of exceptional water quality during several consecutive dry years appears to have been the "final push" that triggered the resurgence (Orth et al. 2010a, Gurbisz and Kemp 2014).

The meadow now appears to be remarkably resilient, having survived an extreme flow event in 2011 (Tropical Storm Lee; figure 6b) because of the self-stabilizing effect of positive feedback processes (Gurbisz et al. 2016). The

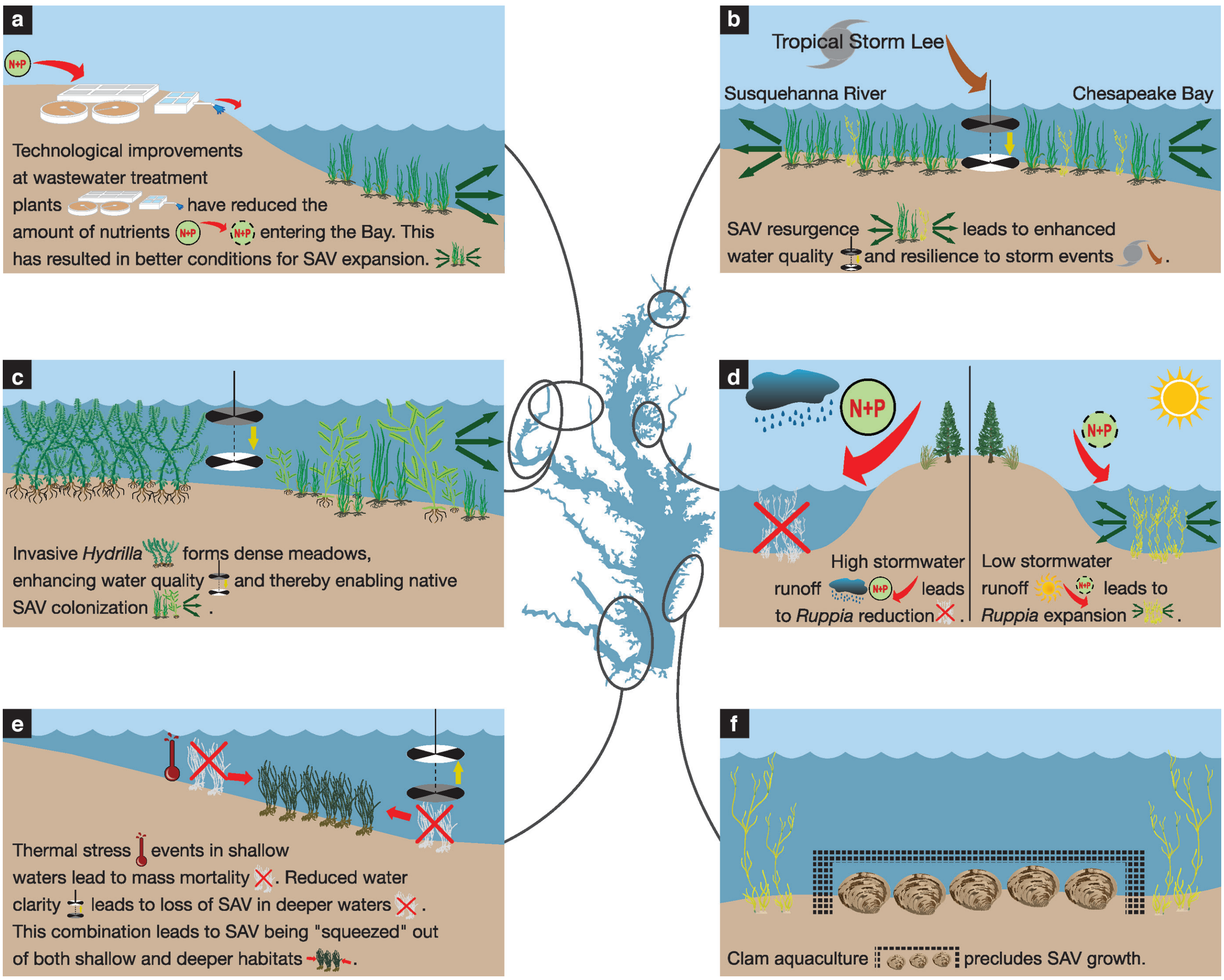

Figure 6. The processes and factors that influence SAV. (a) The removal of nutrients by advanced wastewater treatment improves water quality, allowing SAV to recolonize and expand into unvegetated areas. (b) The resurgence of SAV yields large expanses of SAV that become resilient to perturbations. (c) Invasive species have created conditions that now allow native species to recruit and survive. (d) Variation in runoff causes oscillations in turbidity and nutrient levels that drive boom or bust populations of **R. maritime.** ***(e) High temperature kills*** **Z. marina,** ***which is additionally stressed by high turbidity. (f) Netting is used in clam aquaculture to keep predators out but precludes SAV growth.***

Susquehanna Flats SAV beds now constitute 8% of all SAV in Chesapeake Bay and may be approaching historical levels of abundance and diversity. The Susquehanna Flats resurgence demonstrates that expansive, robust, and persistent restored SAV populations are achievable in Chesapeake Bay. More importantly, the Susquehanna Flats provides strong empirical support for the theory that positive feedback processes, whereby beds promote their own expansion through amelioration of local conditions, play an important role in SAV dynamics. This self-facilitation implies that efforts may simply need to "get the ball rolling" beyond a critical threshold in SAV bed size to yield sustained positive effects.

Case 3: The rise of invasive submersed aquatic vegetation species

Submersed aquatic vegetation species composition in Chesapeake Bay has changed dramatically over the last half century. Notably, a suite of nonnative SAV species have replaced or now compete with native species. For example, *Myriophyllum spicatum* (Eurasian watermilfoil) became a dominant species in the upper Bay in the early 1960s and declined precipitously two decades later (Bayley et al. 1978) but still occurs as a regular component of the freshwater SAV communities. In 1982, *Hydrilla verticillata* was discovered in the Potomac River near Washington, DC, and now dominates many of the tidal freshwater regions (figures 1d and 6c). The dense meadows formed by *H. verticillata* can enhance local water quality and so promote recolonization by native SAV species. Indeed, as water quality continues to improve, the proportion of native species has been increasing (Ruhl and Rybicki 2010), and in freshwater parts of the Bay, *H. verticillata* abundance is typically associated with higher species diversity. *H. verticillata* has also enhanced some ecosystem characteristics such as waterfowl habitat (Rybicki and Landwehr 2007). However, in many locations, *H. verticillata* still occurs in monospecific stands. Whether *H. verticillata* alone can provide other ecosystem services at levels similar to native species remains a question for future research.

Case 4: The peculiar case of *Ruppia maritima*

Mesohaline areas of Chesapeake Bay have seen both expansionss and retractions in the distribution of *R. maritima.* These patterns are well illustrated by the fluctuations in Choptank River SAV area (figure 6d). The boom-and-bust pattern appears largely responsive to total nitrogen and total phosphorus loads (Orth et al. 2010a), which are driven largely by stormwater runoff in the predominantly agricultural watershed. Wet years with high nutrient loads lead to reduced *R. maritima* area, and dry years with low nutrient loads lead to expanded *R. maritima* area. The volatility of *R. maritima* populations may have considerable influence on Bay-wide patterns, artificially inflating the values of recovery during dry years and vice versa in wet years.

Case 5: The dramatic collapse of *Zostera marina*

One of the more drastic stories of change in Chesapeake Bay SAV has been the loss of *Z. marina* in the high-salinity waters of the southern Bay. Following the passage of Tropical Strom Agnes in 1972, *Z. marina* disappeared from over 50% of its Bay-wide distribution and has never recovered (Orth and Moore 1983, Lefcheck et al. 2017). Since 1991, there has been a 30% decline in this species because of a combination of poor water quality and increasing temperatures (figure 6e; Lefcheck et al. 2017). The ecological and economic losses associated with this decline were calculated to be billions of US dollars, including the values of lost services such as carbon storage and fisheries production (Lefcheck et al. 2017). *Z. marina* is a cosmopolitan species distributed over the entire Northern Hemisphere, where it is likely to experience the same combination of stressors. Given that *Z. marina* in Chesapeake Bay is near its southern limit of distribution along the western North Atlantic, it may serve as an advance warning for populations elsewhere as global temperatures continue to rise.

Chesapeake Bay watershed and its influence on submersed aquatic vegetation: More people, more animals, more fertilizer

Like estuaries and coastal waters throughout the world, the Chesapeake Bay faces environmental threats from human activities in its watershed and along its shoreline, and many of those threats affect SAV throughout the Bay. Nutrient pollution (nitrogen and phosphorus) from agriculture, developed lands, sewage, and fossil-fuel combustion cause coastal eutrophication by stimulating plant growth, including phytoplankton, nuisance algae, harmful algal blooms, epiphytes, and invasive plants (Nixon 1995, Paerl et al. 2014). Agriculture, forest loss, and construction also generate sediment that can cloud water or cover plants (Kemp et al. 2005). Sediments, phytoplankton, and epiphytes on leaves together reduce available light, leading to widespread SAV declines (Waycott et al. 2009). Armoring shorelines to protect property from erosion, storms, and rising sea level adds stress by increasing turbidity and deepening the nearshore zone (Nordstrom 2014, Dethier et al. 2016), which can further reduce SAV abundance (Findlay et al. 2014, Patrick et al. 2014, Patrick and Weller 2015).

Human population in the Bay watershed has changed dramatically in the twentieth century, increasing from 8.4 million in 1950 to 18.1 million in 2015 (figure 7a; CBP 2016). The population is now projected to reach 21.4 million by 2040 (CBP 2016). Driven by the population surge, developed land area has increased from 9.8% of the watershed area to 17.2% between 1974 and 2012 (figure 8; data extracted and synthesized from Falcone 2015). About one-fourth of the new development was converted from farmland, but the remainder replaced forest, wetlands, and other natural areas (data extracted and synthesized from Falcone 2015). The area planted in crops declined 40% from 1950 to 2012 (Lamotte 2015), as did the application of inorganic phosphorus fertilizer (figure 7b; Sekellick 2017). In contrast, the application of nitrogen fertilizer increased more than fivefold between 1950 and 2000 (figure 7b), reflecting global increases driven by the availability of inexpensive nitrogen fertilizer (e.g., Galloway and Cowling 2002).

Animal agriculture in the Chesapeake watershed has also expanded greatly by exploiting feed imported from the Midwest (Beegle 2013). For example, there was a sixfold increase in the production of broiler chickens throughout the watershed between 1954 and 2012 (figures 1a and 7c; Lamotte 2015). Feed imports from outside the watershed bring additional nitrogen and phosphorus into the watershed, creating an excess that drives water pollution when the nutrients in manure ultimately drain into the Bay (Jordan and Weller 1996, Beegle 2013).

High nitrogen, phosphorus, and sediment loads have been identified as central culprits in the poor health of Chesapeake Bay (Boesch et al. 2001, Kemp et al. 2005), leading to a federal mandate to reduce those loads (the total maximum daily load, or “pollution diet”) and a multistate effort to meet that mandate coordinated by the Chesapeake Bay Program (Linker et al. 2013). Those efforts are now generating a detectable reduction in nutrient inputs. Nitrogen fertilizer applications have declined

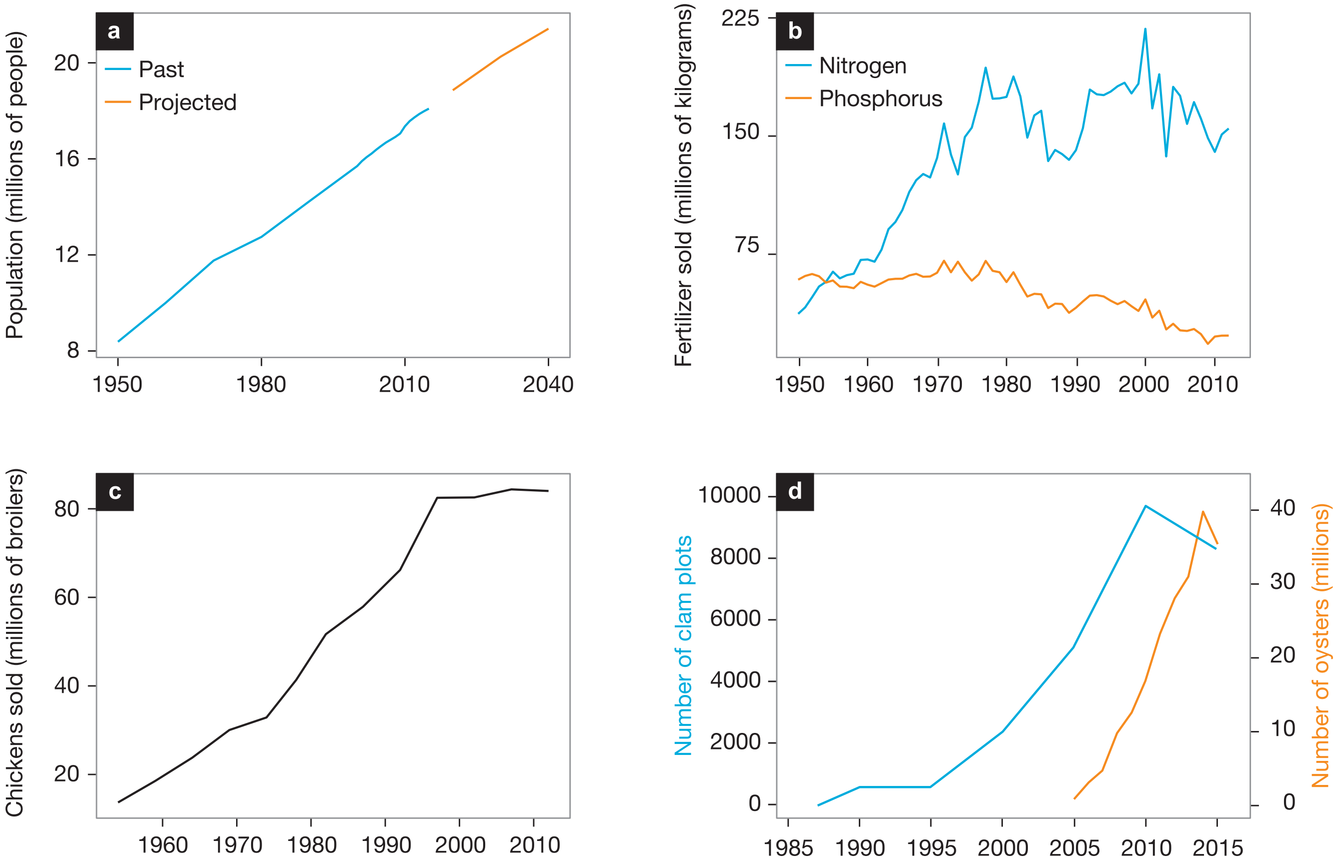

Figure 7. (a) Population trends from 1950 to the present and future predictions through 2050. The gap occurs because recent years of actual data are not included (data from* www.chesapeakebay.net/indicators/indicator/chesapeake_bay_watershed_population*). (b) Amounts of nitrogen and phosphorus in fertilizer sales (1950–2012; data from Sekellick 2017). (c) Broiler chicken production (from LaMotte 2015). (d) The number of plots planted with hard clams (1987–2015) and the number, in millions, of aquacultured market oysters sold by Virginia growers (2005–2015; oyster data from Hudson and Murray 2016).

since peaking in approximately 2000 (figure 7b; Sekellick 2017). Reductions in nitrogen emissions mandated by the Clean Air Act have sharply reduced nitrate nitrogen levels in streams draining forested watersheds by a median of 41% from 1986 to 2012 (Eshleman and Sabo 2016). Despite the increasing population, major advances in wastewater treatment between 1985 and 2014 have roughly halved the total discharge of nitrogen from sewage treatment plants and eliminated almost three-fourths of the phosphorus discharge (*www.chesapeakebay.net/data/downloads/bay_program_nutrient_point_source_database*). Monitored nitrogen loads entering the Bay from four major rivers (the Potomac, James, Rappahannock, and Patuxent rivers) declined 3%–13% between 2006 and 2015, and phosphorus and suspended-sediment loads also declined in two of the rivers (Moyer 2016). However, nitrogen, phosphorus, and suspended-sediment loads from five other major rivers showed no trend or even increases in the past 10 years (Moyer 2016), indicating the ongoing challenge of reducing diffuse pollutant loading to the Bay.

Submersed aquatic vegetation in a changing world: Local and global change will affect the future of Chesapeake Bay

In addition to anthropogenic pressures from an increasing human population in the watershed, stress from climate change and fishing practices may further challenge SAV conservation and restoration efforts. The Intergovernmental Panel on Climate Change (IPCC 2014) has predicted increasing temperatures, more variable weather patterns, rising sea levels, and coastal acidification. Changes in fishing and aquaculture practices may also alter aquatic food webs that control SAV abundance. Research suggests that these interacting stressors will affect SAV growth and survival although future SAV trajectories, like the changes in stressors, remain uncertain and open to human mitigation.

Chesapeake Bay waters have already warmed in recent decades (figure 9a; Kaushal et al. 2010, Lefcheck et al. 2017) and are expected to warm by an additional 2°C–6°C by 2100 (Najjar et al. 2010). These increases will be accompanied by more frequent and prolonged heat waves (IPCC 2014).

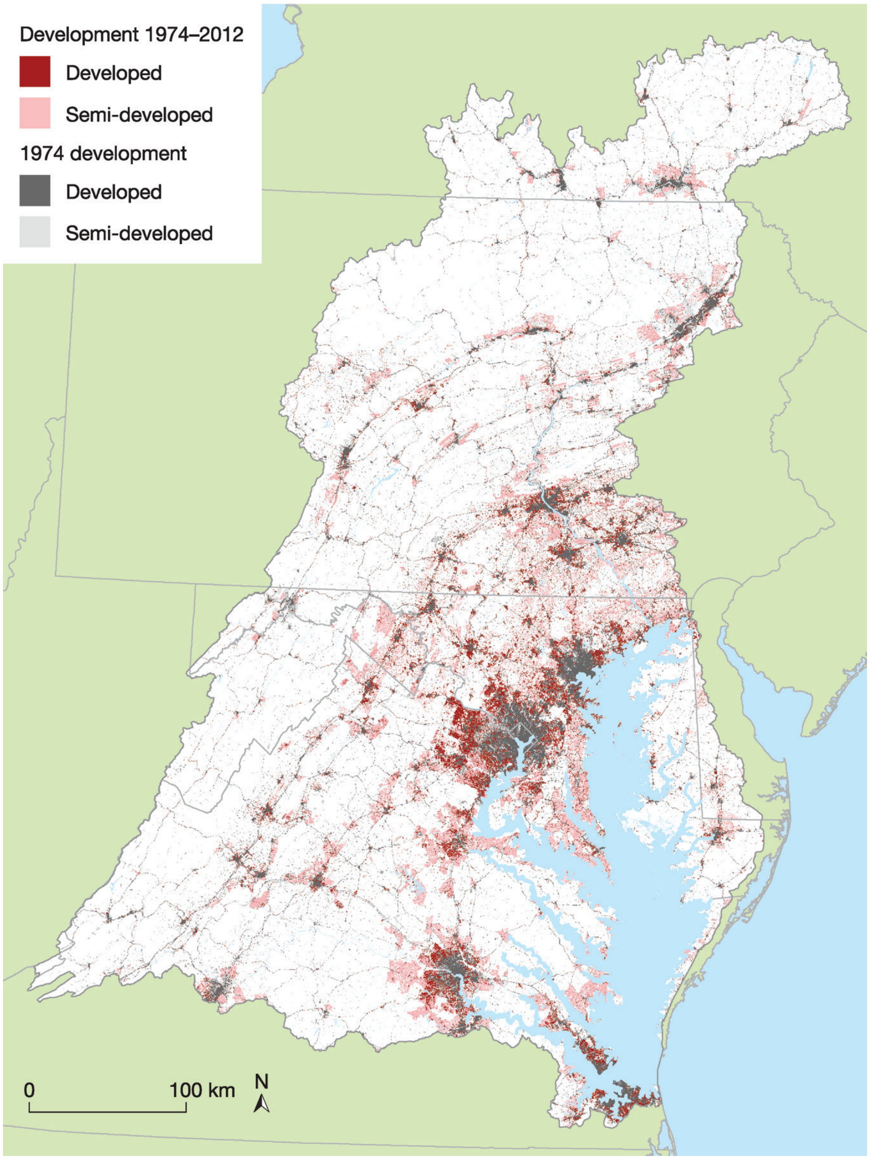

Figure 8. The expansion of developed land in the Chesapeake Bay watershed from 1974 to 2012. The shades of gray show land already developed in 1974, and the shades of red show land developed between 1974 and 2012 by conversion of agricultural land, forests, and wetlands. The developed and semideveloped categories are from aggregating seven developed land subclasses and three semideveloped subclasses (data extracted and synthesized from Falcone 2015). Abbreviaion: km, kilometers.

Optimal temperature ranges vary among species of SAV, so some species may benefit, whereas others will suffer from elevated temperatures (e.g., Moore et al. 2014), resulting in changing and perhaps less stable SAV communities. This is already observable in one species, *Z. marina*, whose distribution has been negatively influenced by increasing water temperatures only in the past decade (Lefcheck et al. 2017).

The future climate will also be more variable, and wetter winters and springs are predicted for the Chesapeake region (Najjar et al. 2010). Wetter winters and springs, combined with earlier snowmelt, will likely promote earlier spring plankton blooms (Najjar et al. 2010). Lower spring water clarity can be especially detrimental to young (and short) SAV plants (Rybicki and Carter 2002, Patrick and Weller 2015). Precipitation events may also be more intense and episodic, separated by longer dry periods (Najjar et al. 2010), and such changes can alter watershed inputs and salinity. More intense storms could interact with the high flows from urbanized watersheds to deliver more severe episodic nutrient and turbidity pulses that could reduce the light available for SAV. Past tropical storms have had negative (Patrick and Weller 2015) or even catastrophic (Orth and Moore 1983) effects on SAV, so any changes in the intensity, frequency, and timing of tropical storms are important for SAV persistence.

Sea level has been steadily rising since the early twentieth century (figure 9b; Holgate et al. 2013, PSMSL 2016) and will likely continue to rise by 70–160 centimeters in the Chesapeake Bay by 2100 (Hilton 2008, Najjar et al. 2010). Because SAV is limited to shallow waters, rising seas will reduce available habitat in locations where SAV is unable to migrate inland or facilitate sediment accretion to keep pace with sea-level rise. On many shorelines, anthropogenic shoreline hardening will prevent inland migration and may reduce the potential for accretional responses to sea-level rise. Sea-level rise, combined with greater variability in precipitation and runoff, will likely increase salinity intrusion and salinity variability (Najjar et al. 2010). Chesapeake Bay bottom waters are already becoming more saline because sea-level rise increases tidal influx from the ocean (Hilton et al. 2008). Changes in salinity will affect the distribution of SAV because salinity largely determines which SAV species can potentially inhabit a site (Moore et al. 2000, Orth et al. 2010a, Patrick and Weller 2015).

Rising sea levels and stronger storms will encourage even more shoreline armoring to defend property against flooding and erosion, and shoreline armoring can reduce SAV abundance (Patrick et al. 2014, 2016). Defined migration corridors for SAV would ensure shoreward migration can occur, so conservation efforts that prioritize preserving of low-lying land adjacent to SAV habitat should help protect SAV. Salt marshes are being inundated rapidly in Chesapeake Bay (Kirwan et al. 2016) and need to trap and

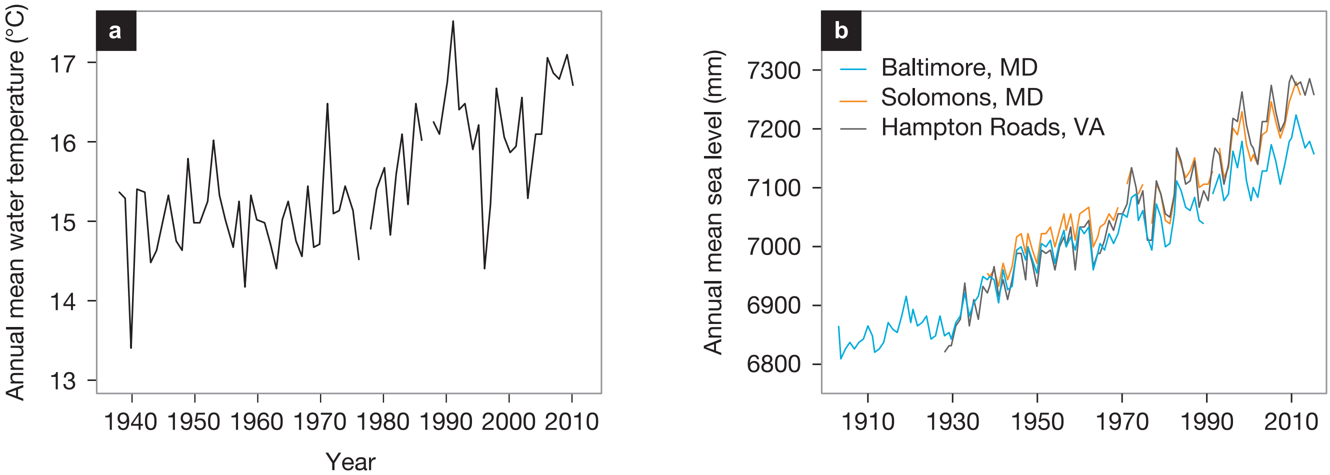

Figure 9. (a) The average annual water temperature at the University of Maryland's Solomons Laboratory (1937–2010; data from Kaushal et al. 2010). (b) The sea-level rise at three Chesapeake Bay locations (1910–2015; from Holgate et al.2013, PSMSL 2016). Abbreviations: °C, degrees Celsius; mm, millimeters.

bind sediments to grow vertically to avoid drowning. SAV beds could also trap sediment to track rising sea level, but any benefit from that could be outweighed by the negative effects of increased sediment loads on water clarity and SAV photosynthesis. Land subsidence due to groundwater pumping and isostatic adjustment of the Earth's crust after the Ice Age glaciers melted from Canada and the northern United States exacerbates global sea-level rise and gives the southern Chesapeake Bay region the highest rate of relative sea-level rise on the US Atlantic coast (Eggleston and Pope 2010). Responses in the Chesapeake Bay will then provide a preview of likely outcomes of sea-level rise for the rest of the Atlantic coast.

Coastal acidification is a complex environmental challenge driven by terrestrial carbon inputs, respiration, and photosynthesis, as well as increasing atmospheric carbon dioxide (CO_2). Although the current diel and spatial variability in pH far exceeds the magnitude of the expected change in average pH by 2100, Chesapeake Bay is expected to become more acidic (Zimmerman et al. 2015). Because SAV photosynthesis can be carbon limited, acidification can provide a CO_2 fertilization effect that reduces photorespiration, improves photosynthetic efficiency, and increases plant growth (Zimmerman et al. 1997, 2017, Palacios and Zimmerman 2007, Najjar et al. 2010, Buapet et al. 2013, Koch et al. 2013). However, higher CO_2 can also reduce the production of plant phenolics and so increase the susceptibility of SAV to grazing (Arnold et al. 2012). Recent studies suggest that the benefits of CO_2 fertilization could be large enough to offset the negative effects of high temperature on *Z. marina* in the mid-Atlantic area of the United States, but increasing temperatures may eliminate *Z. marina* before the positive benefits of CO_2 fertilization can take effect (Moore et al. 2014).

Submersed aquatic vegetation can also be influenced by perturbations to the local food web. For example, grazing by small, epifaunal invertebrates prevents the overgrowth of fouling algae and is essential to the persistence of temperate *Z. marina* communities (Orth and van Montfrans 1984). Those invertebrates are also food for smaller predators, which in turn are eaten by larger predators that move offshore, thereby cycling and exporting primary productivity out of the Chesapeake Bay. Coastal pressures that interrupt this food chain can have cascading effects on *Z. marina*. Overfishing removes large predators, releasing smaller predators to consume more invertebrates, indirectly facilitating the overgrowth of eelgrass by epiphytic algae (figure 1f; Duffy 2006). Recent experiments showed that simulated effects of overfishing and loss of grazing invertebrates had much stronger consequences for *Z. marina* than did fertilization by nutrients (Duffy et al. 2015), so animals appear crucial to the persistence of at least one species of SAV in the Bay. Management may benefit from adopting a broader view of the controls on SAV abundance to include the effects of higher trophic levels.

The influence of animals on SAV is not limited to larger mobile species. Shellfish aquaculture is an expanding enterprise throughout Chesapeake Bay, particularly along the Eastern Shore of the southern Bay. Shallow water clam (*Mercenaria mercenaria*) plots (figure 1c) can preclude SAV growth by competing for area on the bottom (figure 6f). The total area of clam plots is still small relative to total SAV area, but the number of individual clam plots has been increasing dramatically in the last two decades (figure 7d). Recent efforts have also advocated aquaculture to supplement or even replace natural harvest of oysters (*Crassostrea virginica*) in the mid-Atlantic area of the United States (Hudson and Murray 2016). Expanding oyster aquaculture could compete with SAV for limited bottom in shallow areas or, in the case of floating bag operations, shade the bottom, as was noted in the increase in the sale of market oysters produced by the aquaculture industry (figure 7d). Moving forward, conserving SAV and its benefits and the increased economic value of aquaculture could be an emerging management challenge.

Conclusions

Many factors have affected Chesapeake Bay SAV over the past 400 years. Submersed aquatic vegetation is both a sentinel of this change and a valuable resource affected by it. Most of the stressors on SAV are human in origin, especially the nutrient and sediment inputs that have reduced light availability and altered the abundance, composition, and distribution of SAV. Federal and state actions have had some success in reducing watershed impacts on the Bay, but emerging stresses—including a changing climate, rising sea level, expanding urbanization, and expanding fisheries—will require new approaches. The Bay of the future might look very different from the Bay of today, just as the Bay of today looks very different from the one first encountered by the European colonists.

What, then, can be done to ensure a healthy, productive, and enduring SAV community in the Bay in the years ahead? We offer several suggestions.

First, limiting human impacts can benefit SAV by improving water quality. Submersed aquatic vegetation will never thrive as long as light levels are low in the Bay; this is a basic, unavoidable biological constraint. Alleviating light stress by improving water clarity may allow SAV to cope with increasing temperatures, sediment pulses associated with storms, and sea-level rise. Great strides have been made in watershed management over the last two decades, and these efforts need to be continued throughout the Bay's large watershed, such as successfully implementing the total maximum daily load (the pollution diet; Linker et al. 2013). In addition, recent studies of Chesapeake Bay subestuaries demonstrate that nearby land use strongly affects water quality and SAV abundance (Patrick et al. 2014, 2016), suggesting that changes in local land management are especially important to restoring water quality and SAV. Mitigating anthropogenic pressures that degrade water clarity, such as nutrient and sediment loading from the watershed, can help SAV absorb additional disturbances and therefore increase SAV resilience to climate-related stressors (Yakuub et al. 2014).

Second, we must address the emerging issues of population increases, climate change, and fisheries and aquaculture expansion (described above) in setting environmental goals. Some solutions are more straightforward, including replacing bulkheads and riprap with natural shorelines, such as marshes, which protect shorelines and have additional ecological benefits (Gittman et al. 2016). Some stressors, such as climate change, are under global and not local control, but adjusting water-quality targets to offset losses from global climate change may provide one solution.

Third, we must change our perspective about what is normal for the Bay ecosystem. The rise of the exotic species *Hydrilla verticillata* has irrevocably changed the freshwater regions of the Bay. Future strategies may need to accept this fact and manage around (or even for) *H. verticillata* and other successful nonnative species. Those strategies will require a critical evaluation of the ecosystem services provided by invasive species versus native ones, insight that is lacking in the Chesapeake Bay and in many other places. The evaluation of organismal functional traits may provide one way to quantify the contributions of different species. Traits reflect species' tolerances to disturbance (Mouillot et al. 2013), as well as their effects on primary productivity and other ecosystem functions (Cardinale et al. 2012). Inferences based on traits can be more easily generalized than inferences based just on species identities.

Fourth, we should continue to collect SAV monitoring data and analyze the resulting data to better understand the factors that influence SAV distribution and abundance. Submersed aquatic vegetation monitoring data have already been analyzed to assess Bay-wide status and trends of SAV, and the monitoring data have also enabled investigations of SAV responses to human activities and environmental conditions at much finer scales (e.g., Orth et al. 2010a, Patrick et al. 2014, Patrick and Weller 2015, Patrick et al. 2016, Lefcheck et al. 2017). The manifold values of these data result directly from the comprehensive spatial coverage and the temporal continuity provided by long-term annual sampling over many decades.

The Chesapeake Bay has long provided a leading example of how multiple governments and stakeholders can cooperate to set environmental goals and implement management actions aimed at restoring a large and complex system. The continued challenges in meeting environmental goals provide an opportunity to lead the way forward with continued cooperation. This will require acknowledging and understanding the controllable and noncontrollable stressors, integrating an adaptive perspective into management decisions based on available science, and continuing to champion the water-quality controls that are already working. Chesapeake Bay SAV and the critical habitat it provides for many species will be very visible and tangible measures of Bay restoration progress that resonate with the public in ways that less tangible metrics of progress may not. The future of Chesapeake Bay is indicated by and contingent on the success of SAV.

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Supplemental material

Supplementary data are available at *BIOSCI* online.

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Robert Orth (jjorth@vims.edu) is a professor, Kenneth Moore is a professor, Jonathan Lefcheck is a postdoctoral associate, and David Wilcox is a GIS project manager at the Virginia Institute of Marine Science at the College of William and Mary, in Gloucester Point, Virginia. William Dennison is vice president for science applications and a professor, Jeremy Testa is an assistant professor, and Rebecca Murphy is a research scientist at the University of Maryland Center for Environmental Science, in Cambridge, Solomons, and Annapolis, Maryland, respectively. Cassie Gurbisz is a postdoctoral associate at the National Socio-Environmental Synthesis Center, in Annapolis, Maryland. Jennifer Keisman is a biologist at the US Geological Survey, in Baltimore, Maryland. Brooke Landry is a natural resource biologist at the Maryland Department of Natural Resources, in Annapolis, Maryland. Christopher Patrick is an assistant professor in the Department of Life Sciences at Texas A&M University, in Corpus Christi, Texas. Donald Weller is a senior scientist and Michael Hannam is a postdoctoral fellow at the Smithsonian Environmental Research Center, in Edgewater, Maryland.