

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

Thomas M. Arnold¹, Richard C. Zimmerman², Katharina A. M. Engelhardt³, and J. Court Stevenson⁴

¹ Departments of Biology and Environmental Studies, Dickinson College, Carlisle, PA 17013

² Department of Ocean, Earth and Atmospheric Sciences, Old Dominion University Norfolk, VA 23529

³ Appalachian Laboratory, University of Maryland Center for Environmental Science, Frostburg, MD 21532

⁴ Horn Point Laboratory, University of Maryland Center for Environmental Science, Cambridge, MD 21613

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 losses 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 CO₂ 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 CO₂ / low pH conditions, shaped by diurnal, tidal, and seasonal cycles, may benefit SAV. The “CO₂ 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 (Silliman 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 spiralis*), 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, *Lyabyrinthula* 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, reseeded 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 km² 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 km² 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 CO₂ / 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 CO₂ 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 CO₂ 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 CO₂ 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 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 CO₂ emitted from human activities has been absorbed by the oceans, slowing the rate of global warming. However, the oceanic CO₂ 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 CO₂ 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 (CO₃²⁻) (Orr et al. 2005; Doney et al. 2009). Ocean acidification lowers the availability of CO₃²⁻, and therefore the seawater saturation states (Ω) with respect to several carbonate minerals, so that the formation and deposition of new CaCO₃ 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 CaCO₃ 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 CO₂) *via* biological processes, e.g., respiration and decomposition (i.e., heterotrophy), generating high CO₂ / 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 NO_x and SO_x combustion products. Combustion products can acidify estuarine waters directly and some (e.g., NO_x) 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 CO₂ (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 CO₂ 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 CO₂. Globally, estuaries are an important net source of CO₂ 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 CO₂ levels reduce the pH, CO₃²⁻ levels, and CaCO₃ mineral saturation states of coastal waters, just as in the open ocean. However, the precise relationships between excess CO₂ 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 CO₂ / acidity observed in estuarine waters results from *in situ* respiration of imported terrestrial and marine organic carbon, rather than the direct absorption of atmospheric CO₂. In general, estuarine waters are more susceptible to CO₂-induced acidification due to their reduced buffering 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 *p*CO₂ / pH conditions of estuaries are highly variable. Within the Chesapeake, its tributaries, and outer bays, *p*CO₂ 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 *p*CO₂ “hot spots” with *p*CO₂ levels >10,000 ppm (A.W. Miller, unpublished; Baumann et al. 2015). Plumes of high CO₂/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 *p*CO₂ 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 *p*CO₂ 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 CO₂ 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 CO₂ 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 pCO₂ 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 CO₂ 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 CO₂ / 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 CO₂ conditions may benefit SAV photosynthesis, which is often CO₂-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 $\leq 50\%$ 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. 2009; 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; Buapet 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 <100 ppm, 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 : $2074 \mu\text{mol kg}^{-1}$) and CO_2 enriched (pH: 6.2, total CO_2 : $3673 \mu\text{mol kg}^{-1}$) conditions and found a rapid 3x increase in photosynthetic rates, which allowed enriched plants to maintain a “positive whole-plant C balance” with only <3 h 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 $3610 \mu\text{M}$) 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 CO₂ 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 CO₂ 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 CO₂ 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 pCO₂ 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 CO₂/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 pCO₂ 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 CO₂ 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 “CO₂ 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 CO₂ 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 pCO₂ (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 CO₂ 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 “*CO₂ 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 CO₂ / 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 CO₂ / 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 CO₂ / 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 CO₂ / 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, *Labyrinthula* 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 CO₂ / low pH conditions generated by continuing coastal acidification can stimulate SAV photosynthesis *via* the “CO₂ 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 “CO₂ 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 sea 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 Department of Natural Resources.

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