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Original Publication Citation

Arnold, T. M., Zimmerman, R. C., Engelhardt, K. A. M., & Stevenson, J. C. (2017). Twenty-first century climate change and submerged aquatic vegetation in a temperate estuary: The case of Chesapeake Bay. *Ecosystem Health & Sustainability, 3*(7), 1-20. doi:10.1080/20964129.2017.1353283

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ECOSYSTEM HEALTH AND SUSTAINABILITY, 2017
VOL. 3, 1353283
https://doi.org/10.1080/20964129.2017.1353283

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Twenty-first century climate change and submerged aquatic vegetation in a temperate estuary: the case of Chesapeake Bay

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ABSTRACT

Introduction: The Chesapeake Bay was once renowned for expansive meadows of submerged aquatic vegetation (SAV). However, only 10% of the original meadows survive. Future restoration efforts will be complicated by accelerating climate change, including physiological stressors such as a predicted mean temperature increase of 2–6°C and a 50–160% increase in CO_2 concentrations.

Outcomes: As the Chesapeake Bay begins to exhibit characteristics of a subtropical estuary, summer heat waves will become more frequent and severe. Warming alone would eventually eliminate eelgrass (*Zostera marina)* from the region. It will favor native heat-tolerant species such as widgeon grass (*Ruppia maritima*) while facilitating colonization by non-native seagrasses (e.g., *Halodule* spp.). Intensifying human activity will also fuel coastal zone acidification and the resulting high CO_2/low pH conditions may benefit SAV *via* a *"CO_2 fertilization effect."*

Discussion: Acidification is known to offset the effects of thermal stress and may have similar effects in estuaries, assuming water clarity is sufficient to support CO_2-stimulated photosynthesis and plants are not overgrown by epiphytes. However, coastal zone acidification is variable, driven mostly by local biological processes that may or may not always counterbalance the effects of regional warming. This precarious equipoise between two forces – thermal stress and acidification – will be critically important because it may ultimately determine the fate of cool-water plants such as *Zostera marina* in the Chesapeake Bay.

Conclusion: The combined impacts of warming, coastal zone acidification, water clarity, and overgrowth of competing algae will determine the fate of SAV communities in rapidly changing temperate estuaries.

ARTICLE HISTORY
Received 6 January 2017
Revised 29 June 2017
Accepted 4 July 2017

KEYWORDS
Submerged aquatic vegetation; climate; temperature; coastal acidification; Chesapeake Bay

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Estuaries in the twenty-first century will continue to be confronted with the chronic and unresolved challenges of the past (Kennish, Brush, and Moore 2014) and will be increasingly impacted by a changing climate (Silliman, Grosholz, and Bertness 2009; Lotze 2010), following a predictable sequence of anthropogenic events (see Jackson et al. 2001; Orth et al. 2017). Those working to protect and preserve estuarine ecosystems must now address these old challenges in the new context of accelerating global climate change. This is the case for the Chesapeake Bay, a North American temperate estuary fed by 150 tributary rivers and streams, which has been the focus of intensive conservation and management efforts for decades (Figure 1). Future climate forces will complicate these efforts because they will have profound impacts on submerged aquatic vegetation (SAV), which are foundational species (Carr et al. 2012).

The Chesapeake Bay was once renowned for expansive meadows of marine and freshwater SAV, including eelgrass (*Zostera marina*), widgeon grass (*Ruppia maritima)*, American wild celery (*Vallisneria americana*), coontail (*Ceratophyllum demersum*), common waterweed (*Elodea canadensis*), horned pondweed (*Zannichellia palustris*), water stargrass (*Heteranthera dubia*), and various pondweeds (*Stuckenia pectinata* and other *Potamogeton* spp.) (Figure 2). Historically, these species covered an estimated 250,000 ha, but today <10% of the original Chesapeake Bay SAV meadows survive (Moore, Wilcox, and Orth 2000; Orth et al. 2010b). 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 SAV loss in the Chesapeake Bay coincided with European colonization (Jackson et al. 2001; Yasuhara et al. 2012; Orth et al. 2017). In the 1930s, mass die-offs were triggered by the wasting disease pathogen, *Labyrinthula* spp., and a destructive hurricane (Orth and Moore 1983, 1984, 1986; Moore, Wilcox, and Orth 2000; Orth et al. 2006). Subsequent declines were associated with poor water quality and Hurricane Agnes in 1972 (Orth and Moore 1983; Kemp et al. 2005; Stevenson and Kearney 2005;

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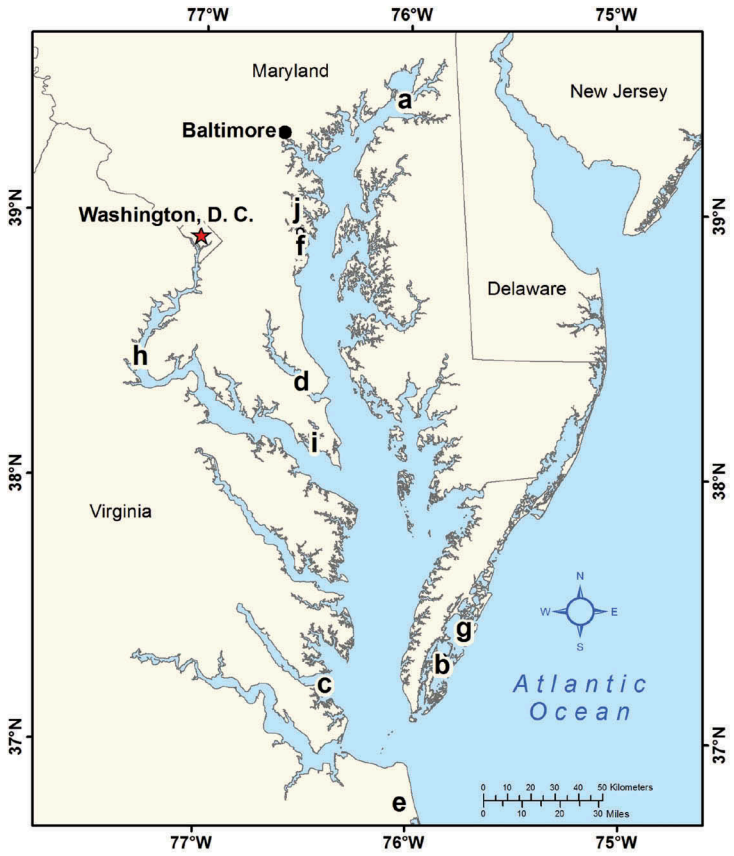

Figure 1. Map of the Chesapeake Bay and nearby coastal bays, relative to neighboring US states and urban centers. The locations of key study sites are indicated by letters here and in the article text.

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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. 2010b). Modest gains were made in the 1990s but were offset by the failure of several eelgrass beds in the mid-bay from 2005 to 2010 (Orth et al. 2010b; Moore et al. 2012). Recently, encouraging recoveries of native aquatic vegetation in certain areas, for example, wild celery in the Susquehanna Flats (Figure 1(a)), have been documented. Also, reseeding efforts have been successful in establishing local populations of eelgrass in the Virginia coastal bays, areas characterized by good water quality (Figure 1(b)) (Orth et al. 2010a; Moore et al. 2012). However, eelgrass populations have not recovered in the larger polyhaline portion of Chesapeake Bay, where water quality remains poor. This history reflects global trends. Similarly, continued coastal development threatens seagrasses communities worldwide (Orth et al. 2005, 2006, 2012). Abundances have declined 29% globally since 1879 and for the last several decades seagrasses have been disappearing at a rate of 110 km^2 yr^{-1} (Lotze, Lenihan, and Bourque et al. 2006; Micheli et al. 2008; Waycott et al. 2009; Hughes et al. 2009). At current rates, 30–40% of world seagrasses and their associated ecosystem services could be lost in the next 100 years (Waycott et al. 2009; Hughes et al. 2009).

SAV are a critical component of many coastal ecosystems including the Chesapeake Bay, where they are bioindicators of ecosystem health. Their ecosystem services include: calming currents, filtering water, absorbing nutrients, and accelerating the settlement of marine larvae; serving as key primary producers with rates of productivity great than most terrestrial plant communities systems; and nourishing coastal food webs (e.g., Harrison and Mann 1975; Worm et al. 2006; Orth et al. 2006; Waycott et al. 2009). SAV also serve as habitat for fish, crustaceans, and shellfish, including species supporting commercial and recreational fisheries (Beck et al. 2001; Heck et al. 2003; Larkum, Orth, and Duarte 2006; Jones 2014). In the Chesapeake Bay, SAV are also grazed by migrating waterfowl (Stevenson 1988). Globally, the value of SAV can be quantified in terms of these ecosystem services, estimated at approximately $1.9 trillion per year. Waycott et al. (2009) estimated their value at as much as $28,916 ha^{-1} yr^{-1} (also see Costanza et al. 2014a, 2014b). By this measure, the value of Chesapeake Bay SAV beds would exceed $2.9 billion yr^{-1}. Dewsbury, Bhat, and Fourqurean (2016) recently

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Figure 2. Examples of Chesapeake Bay SAV communities impacted by changing climate conditions, including (a) Hacks Neck and Nandua Creek on the eastern shore of Virginia and (b) Round Bay in the Severn River near Annapolis, Maryland. Poly/meso-haline species include (c) marine eelgrass (*Zostera marina*) and (d) widgeon grass (*Ruppia maritima*) from the St. Mary's River (Maryland). Oligohaline and freshwater SAV include (e) *Vallisneria* spp and associated species from the Susquehanna Flats (Maryland) and (f) a bloom of invasive *Hydrilla verticillata* in the nearby Bush River. Photo credits: Tom Arnold, Brooke Landry, Todd Chadwell, Katia Engelhardt, and the University of Maryland Center for Environmental Science.

suggested that such indirect estimates may actually underestimate the true value of SAV communities. Others have emphasized that the "value" also reaches well beyond SAV communities themselves (Duarte 2000; Stevenson, Kearney, and Koch 2002; Jones 2014). More recently, an additional service of seagrass meadows has emerged with respect to the capture and long-term storage of "blue carbon" (Irving, Connell, and Russell 2011; Fourqurean et al. 2012; Greiner et al. 2013). Globally, underwater meadows can sequester approximately 10% of oceanic organic carbon, an estimated 27.4 Tg carbon yr^{-1} in the form of anaerobic, organic-rich loams (Duarte et al. 2010; Fourqurean et al. 2012). Carbon capture and storage has traditionally not been included in ecosystem service valuations of seagrasses; as a result, the true value of these communities remains underestimated.

SAV in the new Chesapeake

By the end of the century, the Chesapeake region will be subject to a mean temperature increase of 2–6°C and a 50–160% increase in CO_2 concentrations (Najjar et al. 2010). Here we consider how these two factors will affect the physiology of Chesapeake Bay SAV directly, as these are also widely applicable to other estuaries. Related factors, such as changes in rainfall and the frequency and intensity of storms, will have important indirect effects that will be more specific to each estuary (Day, Yanez-Arancibia, and Rybczyk 2011; Statham 2012; Porter et al. 2013; Kennish, Brush, and Moore 2014). The predicted 0.7–1.6 m of sea-level rise in the Chesapeake Bay region will also impact SAV (e.g., Patrick, Weller, and Ryder 2016). Rates of predicted sea-level rise differ for various estuaries, in other regions, and these have been discussed elsewhere (e.g., Najjar et al. 2010). Here we focus on the impacts of two components of climate change, warming and coastal acidification. These factors affect the physiology, growth, and survival of these estuarine plants. Their combined effects must be considered in future conservation efforts (Orth et al. 2017).

A warming estuary

Chesapeake Bay waters are predicted to warm by 2–6°C, on average, during the twenty-first century. This is similar to global forecasts for surface air temperatures and ocean surface temperatures, which are predicted to increase 1.1–6.4°C and 3–4°C, respectively (Levitus, Antonov, and Wang et al. 2001; Meehl et al. 2007; IPCC 2014). These increases in temperature would be in addition to the 0.8°C increase in mean global surface temperatures that has already occurred, as a result of atmospheric CO_2 exceeding 400 ppm. There are direct, first-order relationships between atmospheric carbon dioxide levels, air temperatures, and Chesapeake Bay water temperatures (Wood, Boesch, and Kennedy 2002). In some areas of the Bay, water temperatures are increasing faster than air temperatures (Ding and Elmore 2015). Following this trajectory, the Chesapeake Bay is likely to develop characteristics of a subtropical estuary by the next century. The most devastating temperature effects may result from an increased in the frequency, duration, and amplitude of periodic summer heat waves (IPCC 2014). 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 largest and most inconsistent warming will occur in shallow waters, where submerged vegetation grow, as well as in areas affected by urbanization (Ding and Elmore 2015). For many species of Chesapeake Bay SAV, even moderate warming can be problematic (Somero 2002; Hughes et al. 2003; also see Campbell, McKenzie, and Kerville 2006; Lee, Park, and Kim 2007).

Eelgrass *(Zostera marina)* is the dominate species in polyhaline regions of the Chesapeake Bay. It is a temperate species with an optimal water temperature of 10–20°C with 16–17°C best for seedling growth (Niu et al. 2012). At these colder temperatures growth is slowed (Nejrup and Pedersen 2008) but photosynthesis:respiration ratios are maximized (Marsh, Dennison, and Alberte 1986; Zimmerman, Smith, and Alberte 1989). Eelgrass growth rates increase linearly with a temperature increase from 5°C 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, Smith, and Alberte 1989; Niu et al. 2012) and dramatically increase mortality. Marsh, Dennison, and Alberte (1986) determined that above 30°C, *Zostera marina* has a negative net carbon balance and plants decline rapidly. Kaldy (2014) showed the temperature-induced increase in eelgrass respiration can be problematic even at temperatures between 10°C and 20°C when light is limiting photosynthesis. In theory, eelgrass could escape deleterious temperatures by retreating to deeper, cooler waters (Mckee et al. 2002; York et al. 2013); however, this 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 (Thayer, Kenworthy, and Fonseca 1984; Mckee et al. 2002; York et al. 2013). The poor tolerance of this species to elevated temperatures suggests a bleak future in the Chesapeake Bay.

Impacts of thermal stress on eelgrass have already been observed. Extended warm periods have been linked to population declines of eelgrass in the eastern Atlantic (Glemarec, Lefaou, and Cuq 1997). Acute warming from summertime heat waves has triggered shoot mortality and population declines. For example, in the Goodwin Islands and York River Chesapeake Bay National Estuarine Research Reserve in Virginia (Figure 1(c)), recent eelgrass diebacks were attributed to a greater frequency and duration of water temperatures above 30°C in 2005 (Moore and Jarvis 2008; Moore, Shields, and Parrish 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. Overall, 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, Moore, and Kenworthy 2012; Moore et al. 2012, 2014; Jarvis, Brush, and Moore 2014). These authors predicted that short-term exposures to summer temperatures 4–5°C above normal will cause regional die-offs and local extinctions of eelgrass (Moore, Shields, and Parrish 2014). They also forecasted that

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longer-term temperature increases of 1–4°C will significantly reduce or eliminate *Zostera marina* from the Chesapeake Bay (Moore et al. 2012, 2014). Further, more frequent summer heat waves where water temperatures reach 30°C are likely to trigger permanent phase change in shallow waters, which would prevent future recovery of eelgrass meadows (Carr et al. 2012). Similar losses will occur in the Bogue Sound-Back Sound in North Carolina (USA) (Micheli et al. 2008). Restored eelgrass meadows are also vulnerable (Tanner et al. 2010; Carr et al. 2012). The resiliency of natural versus restored eelgrass meadows is an unanswered question. However, it is clear that cooler temperatures and adequate water transparency often favor successful SAV restoration efforts (Orth et al. 2010a, 2012; Moore et al. 2012; Zimmerman et al. 2015).

Compared to eelgrass, widgeon grass *(Ruppia maritima)* has a more limited, patchy distribution. It tolerates a wider range of temperature and salinity conditions (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, Staver, and Staver 1993). Although biomass does not approach that of eelgrass in the lower polyhaline region of the Bay, it can be the dominant SAV in certain locations (Stevenson, Staver, and Staver 1993). Unlike eelgrass, *Ruppia* tolerates a wide range of water temperatures ranging from 7°C to 40°C. Ideal growth conditions range from 20°C to 25°C or even 18°C to 30°C (see Pulich 1985; Lazar and Dawes 1991; Moore, Shields, and Parrish 2014). Anderson (1969) sampled SAV from an industrial thermal plume on the Patuxent River (Maryland, USA; Figure 1(d)) and found that the lethal temperature was 45°C. However, temperatures beyond 23–25°C have a negative influence on photosynthesis. For instance, Evans, Webb, and Penhale (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 Vierssen, Van Kessel, and Van Der Zee 1984). If the Chesapeake becomes more subtropical, it may not be cold enough for *Ruppia* plants to reproduce by seed, reducing overall population resilience.

It has been suggested that *Ruppia's* wide temperature tolerance may make it a "winner" in a warmer climate, replacing eelgrass in much of the lower Chesapeake (Stevenson, Staver, and Staver 1993). This phenomenon has been observed in other regions. *Zostera*-to-*Ruppia* transitions occurred in San Diego Bay following the 1997–98 El Niño Southern Oscillation, leading Johnson et al. (2003) to predict that a warming of 1.5–2.5°C would facilitate a permanent transition from eelgrass to widgeon grass in this bay. However, it is unlikely that widgeon grass beds would ever replace those of eelgrass in terms of range, density, or the full suite of ecosystem services.

Freshwater plants are common in the lower salinity regions of the Chesapeake and these areas also have experienced significant warming (Seekell and Pace 2011; Ding and Elmore 2015; Rice and Jastram 2015). The physiological impacts are numerous. 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). However, the response of freshwater aquatic plants to climate warming is species-specific, and varies even for locally adapted "biotypes" (e.g., Barko and Smart 1981; Pip 1989; Svensson and Wigren-Svensson 1992; Santamaría and Van Vierssen 1997; Rooney and Kalff 2000; Sala et al. 2000; Amano, Iida, and Kosuge 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).

There is some information regarding the impacts of warming on native and non-native species of freshwater plants in the Chesapeake Bay. *Myriophyllum spicatum*, a non-native species, has a broad temperature range with optimal photosynthesis between 30°C and 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 23–30°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 27–35°C (Santamaría and van Vierssen 1997; Olesen and Madsen 2000; Beser 2007). However, 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°C 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 6-week period, whereas plants from Wisconsin (USA) could not. Warming also impacts the reproductive

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cycles of freshwater SAV. Germination for many species requires cold stratification. However, warmer conditions and an extended growing season 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, Probert, and Dawson 2008; Jarvis and Moore 2008; Yin et al. 2013; Bartleson, Hunt, and Doering 2014). Cao, Li, and Jeppesen (2014) observed that elevated temperature also increase growth of periphyton on aquatic macrophytes. This periphyton growth 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). A mixture of species provides 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 moderately increased temperatures may have neutral effects or even enhance species diversity within temperate freshwater aquatic plant communities (Grace and Tilly 1976; Haag 1983; Rooney and Kalff 2000; Lacoul and Freedman 2006). However, continued warming may eventually compromise and weaken diversity (e.g., Beser 2007). SAV diversity may decline 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 1974; Staver and Stevenson 1995).

These direct physiological effects of thermal stress are familiar in regions beyond the Chesapeake. For instance, similar rates of warming have been reported in the Mediterranean, with comparable impacts on populations of *Posidonia oceanica* (between 1967 and 1992; Marbà and Duarte 1997; Jordà, Marbà, and Duarte 2012). Olsen et al. (2012) documented the impacts of warming from 25°C to 32°C on *Posidonia oceanica* and *Cymodocea nodosa* from the Mediterranean Sea, reporting reduced rates of growth, leaf formation, and leaf biomass per shoot. Climate-induced thermal stress is a concern for Australian seagrasses as well, where *Zostera muelleri* appears to be particularly vulnerable to warming (York et al. 2013). It is informative to compare the responses of *Zostera muelleri* from these sites with those of *Zostera marina* from the Chesapeake Bay. These species exhibit similar thermal tolerances, showing symptoms of stress at 30°C and mortality at 32°C (York et al. 2013). In Australia, a 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*. This transition state has persisted at one site for 33 years (York et al. 2013). Similarly, Thomson et al. (2015) reported a >90% die-back of the temperate seagrass, *Amphibolis antarctica*, in Shark Bay, Australia, following an extreme heat event in 2010–11. Further, in the Pacific Northwest (USA), Thom, Southard, and Borde (2014) demonstrated that elevated temperatures, among other factors, influence populations of *Zostera marina*; in their study, exposure to temperature extremes was associated with the lowest shoot densities. Clearly, continued warming may lead to the local extinction of seagrasses with low thermal tolerance in regions beyond the Chesapeake (Short and Neckles 1999).

There will also be indirect impacts of a warming climate on SAV. Climate warming will alter the diversity, composition, and functioning of SAV, grazers, fouling organisms, and pathogens (Blake and Duffy 2010, 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, and increases in harmful sediment sulfide levels (Goodman, Moore, and Dennison 1995; García et al. 2013). Whether warming will trigger outbreaks of the seagrass wasting disease, caused by the microbial pathogen *Labyrinthula* spp., remains to be seen (Kaldy 2014; Olsen and Duarte 2015; Olsen et al. 2015). These interacting forces are likely to trigger episodic events, pass ecological thresholds, trigger tipping points, and induce phase changes, making it difficult to accurately predict the future of SAV communities. Wood, Boesch, and Kennedy (2002) surmised that these complicating factors mean that transitions from temperate to subtropical communities will not be smooth.

It is possible to make basic predictions for Chesapeake Bay SAV based solely on temperature forecasts. An abundance of evidence suggests that the outlook would be very poor for eelgrass (*Z. marina*), a cool-water species. In contrast, warming will favor increased abundances of native thermotolerant species and facilitate the introduction of non-native subtropical species such as *Halodule wrightii*, which currently persists in Back Sound, North Carolina 150 km south of the Chesapeake Bay (Kenworthy 1981). It is important to note that it is highly unlikely that these species, or others, would replace the coverage or ecosystem services of eelgrass in the Chesapeake Bay. In addition, we envision that any transition would be marked by sudden and unpredictable changes in this ecosystem.

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Coastal zone acidification

Since the Industrial Revolution, atmospheric carbon dioxide levels have increased 40% from 280 to >400 ppm, the highest levels occurring on our planet in 800,000 years (Sabine et al. 2004; Feely et al. 2004; Doney et al. 2009). Approximately one-third of the CO_2 emitted from human activities has been absorbed by the oceans, slowing the rate of global warming (e.g., Caldeira and Wickett 2003; Doney et al. 2009). However, this drives the process of ocean acidification. In a sense, ocean acidification can be compared to the process of carbonation; in both, carbonic acid levels rise and pH drops as concentrations of dissolved CO_2 increase. More specifically, ocean acidification decreases pH and the availability of carbonate minerals in seawater. Acidification can have significant deleterious effects on organisms, especially on calcifying organisms that rely upon carbonate ions (CO_3^{2-}) for the construction of shells and skeletons (Doney et al. 2009). In the past 150 years as atmospheric CO_2 levels have increased, oceans have become net CO_2 sinks and average ocean pH has dropped from 8.21 to 8.10 (Royal Society 2005). By the end of the century, ocean pH is expected to fall another 0.3–0.4 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 CO_3^{2-} ions (Orr et al. 2005; Doney et al. 2009).

Within the Chesapeake Bay and other estuaries, the process is more complex and commonly called coastal zone acidification. Like ocean acidification, it generates high CO_2/low pH conditions. However, coastal zone acidification is primarily driven not by CO_2 absorption from the atmosphere but by biological processes such as respiration and decomposition; high CO_2 levels in estuaries are often the result of excess organic carbon. Coastal zone acidification is increasingly common in part because massive amounts of organic carbon pass through modern estuaries via the land–ocean continuum (Herrmann et al. 2015). This organic carbon is subsequently converted to dissolved inorganic carbon (DIC, includes CO_2) via biological processes, generating high CO_2/low pH conditions *in situ*. Other factors contribute to coastal zone acidification in the Chesapeake, including acid sulfate soils, larger-scale processes such as ocean mixing or coastal upwelling, and the atmospheric deposition of NOx and SOx combustion products. Combustion products can also acidify estuarine waters directly and some (e.g., NOx) also drive acidification by stimulating eutrophication. Indeed, eutrophication is a common cause of acidification in estuaries: nutrient enrichment stimulates the production of algal dissolved organic carbon (DOC), which fuels microbial respiration in anoxic bottom waters, generating high levels of CO_2 (Cai et al. 2011; Melzner et al. 2013; Wallace et al. 2014). Sunda and Cai (2012) surmised that eutrophication of the Chesapeake Bay will generate CO_2 release and acidification of 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). As a result, estuarine waters generate massive amounts of DIC. They release a fraction to the atmosphere as CO_2, they sequester and store some carbon, and they export the rest directly as organic carbon to the oceans (Jiang 2010).

The problem is compounded by the fact that estuarine waters are unusually sensitive to acidification. High CO_2 levels reduce the pH, carbonate (CO_3^{2-}) levels, and $CaCO_3$ mineral saturation states of coastal waters, just as in the open ocean. However, the degree of change is determined by the constantly changing chemical properties of coastal waters – their fluctuating salinities, temperatures, and nutrient compositions. In general, estuarine waters are more susceptible to CO_2-induced acidification due to their reduced buffing capacity from alkalinity, which is lower than in seawater (Miller et al. 2009; Hu and Cai 2013). Furthermore, not all estuaries or regions of estuaries are equally sensitive; some mid-salinity estuarine waters have particularly low buffering capacities and are especially vulnerable to acid stress (Hu and Cai 2013). In fact, the presence of a mid-salinity minimum buffer zone, areas especially prone to acidification, has been proposed for several of these estuaries, including the Chesapeake Bay (Hu and Cai 2013).

These changing biological, chemical, and physical factors make the partial pressure of carbon dioxide (pCO_2) and pH conditions of estuaries highly variable. Within the Chesapeake, its tributaries, and outer bays, pCO_2 concentrations commonly fluctuate from less than 100 to greater than 3000 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 instance, Zimmerman et al. (2015) reported daily fluctuations in pCO_2 concentrations in Owl Creek (Virginia, USA; see Figure 1(e)) ranging from 200 to 1000 ppm, with associated changes in pH. Similar daily fluctuations in the Rhode River (Maryland, USA; Figure 1(f)) typically range from 200 to 500 ppm, and are influenced by diurnal and tidal cycles and the presence of seasonal algal blooms (Whitman Miller, unpublished). These data also demonstrate that tidal wetlands generate high pCO_2 "hot spots" with pCO_2 levels >10,000 ppm (also see Baumann et al. 2015). For instance, surveys by Miller and Arnold in South Bay, Virginia (USA) (Figure 1(g)) reveal high plumes from marshes that sustain pCO_2 levels of 800–1000 ppm decreasing to 400–700 ppm in the center of this inland bay, 10 km away. Such plumes of high CO_2/low pH waters have been observed during

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ebbing tides in Chesapeake and elsewhere. This phenomenon seems to be common; however, the intensity of these "hot spots" may be impacted as wetlands themselves respond to climate change (e.g., Drake 2014). Conversely, high rates of estuarine primary production during the daytime can strip DIC from estuarine waters. For example, photosynthesis in spring algal blooms and healthy seagrass meadows can draw down pCO_2 levels to <100 ppm during the daytime, with an increase in pH of ~1–2 units. This is commonly observed in mesocosm experiments (e.g., Zimmerman et al. 2017) and eelgrass meadows. In South Bay, Virginia (USA), daytime photosynthesis reduces pCO_2 levels from ~600 ppm to 300 ppm or below (Figure 2). Where photosynthetic rates are high, diurnal fluctuations of two pH units are common, and such variation is nearly an order of magnitude greater than the projected global effects of acidification in the open oceans. In terms of pCO_2 concentrations, the natural fluctuations occurring in the Chesapeake Bay each day are approximately 50 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 United States and elsewhere (Raymond, Caraco, and Cole 1997; Cai and Wang 1998; Frankignoulle, Abril, and Borges et al. 1998; Borges, Delille, and Frankignoulle 2005; Akhand et al. 2012; Baumann et al. 2015).

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 sediment transport to the oceans (Schlesinger 1996). 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, climate change is likely to stimulate biological remineralization/decomposition of DOC to DIC and foster high CO_2 and low pH conditions. Warmer temperatures generally increase rates of respiration and decomposition, while decreasing the efficiency of photosynthesis. In the future, climate change is likely to push the noisy baseline of coastal acidification even higher.

In the Chesapeake Bay, coastal zone acidification has sometimes gone unnoticed, for two reasons: (1) no coordinated long-term effort had been implemented to monitor carbonate system parameters using reliable, modern methods and (2) the anthropogenic signal tends to be obscured by the typical variation in the estuarine carbonate system. Nonetheless, attempts have been made to reconstruct historical pCO_2 and/or pH values in the Chesapeake Bay. For example, Waldbusser et al. (2011) used water quality data from the Chesapeake Bay Program's Data Hub (http://www.chesapeakebay.net/dataandtools.aspx) from 1985 to 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, Santana-Casiano, and González-Dávila 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 toward the ocean may account for this observation. In their view, eutrophication triggered primary production (and a rise in pH associated with photosynthesis) at mesohaline sites. The resulting organic carbon subsequently drifted southward, triggering CO_2 production via heterotrophy in the polyhaline (with a corresponding decrease in pH). This view highlights some of the challenges involved in studying acidification in estuaries, where significant lateral transport of organic carbon (both DOC and particulate organic matter (POM)) is to be expected.

There is an increasing understanding of the impacts of acidification on marine and aquatic plants. It is important to recognize from the start that SAV have a unique place at the center of the estuarine carbonate system; submerged aquatic plants are directly impacted by high CO_2/low pH conditions but, 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).

In general, high CO_2 conditions may benefit SAV photosynthesis. For many species of SAV, photosynthesis is often limited by inadequate CO_2 availability because they lack effective carbon-concentrating mechanisms for photosynthetic exploitation of bicarbonate (HCO_3^-), an alternative form of carbon. In this regard, seagrasses are unlike many algae which often have the ability to utilize HCO_3^- as an additional source of inorganic carbon when CO_2 is limiting. For example, most marine algae derive 90% or more of their photosynthetic carbon requirements from HCO_3^-, but marine seagrasses manage to satisfy only ≤50% of their carbon requirements in this way (Zimmerman et al. 1995, 1996; Beer and Koch 1996; Beer and Rehnberg 1997; Zimmerman et al. 1997; Invers et al. 2001; Björk et al. 1997; Jiang, Huang, and Zhang 2010). In addition, some freshwater SAV species are almost completely reliant on dissolved aqueous CO_2, and light-saturated photosynthesis is typically CO_2-limited in low alkalinity water (Lloyd, Canvin, and Bristow 1977). As a result, a high CO_2/low pH environment may release SAV from CO_2 limitation, making them

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more productive (e.g., Björk et al. 1997; Ow, Uthicke, and Collier 2016; Zimmerman et al. 2015; Takahashi et al. 2016). This phenomenon has been termed the "*CO_2 fertilization effect*." Such conditions also benefit SAV by reducing photorespiration, a process which essentially competes with photosynthesis (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).

At the same time, SAV may counteract acidification by removing CO_2 from the water via daytime photosynthesis. 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 (Semesi, Bjork, and Beer 2009; Buapet et al. 2013; 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 <300 ppm, as coastal waters enter eelgrass meadows during the daytime (Figure 3). 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 the response of specific SAV to acidification, alone or in concert with other environmental factors such as warming and light availability.

For *Zostera*, high CO_2/low pH conditions are often beneficial. Under such conditions, photosynthetic carbon assimilation is increased and photorespiration, which can reduce photosynthetic capacity of eelgrass by 40%, is decreased (e.g., Thom 1995; Zimmerman et al. 1997; Palacios and Zimmerman 2007; Alexandre et al. 2012; Buapet et al. 2013). The most convincing evidence has been provided by Zimmerman and coworkers who have simulated coastal acidification in manipulative experiments with eelgrass for nearly two decades. First, they compared the performance of *Z. marina* under ambient (pH: 8.2, total CO_2: 2074 µmol kg^{-1}) and CO_2 enriched (pH: 6.2, total CO_2: 3673 µmol kg^{-1}) conditions and found a rapid 3× 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: 8.1–6.4, total CO_2 range: 2225–3610 µM) over a period of 1 year. Here, the combination of CO_2 enrichment and high light yielded a significantly higher reproductive output and an increase in belowground biomass (which exhibited higher levels of carbohydrate reserves) and the proliferation of new shoots.

Zimmerman et al. (2017) recently conducted a long-term (18 months) experiment with eelgrass from Virginia growing in outdoor aquaria exposed to the natural seasonal cycles in irradiance and water temperature. They demonstrated that tolerance of high summer water temperatures increased linearly with CO_2 availability, resulting in increased rates of plant survival and vegetative growth, plant size, accumulation of internal carbon reserves (sugar), and flowering shoot production the following spring (Figure 4). Formulations resulting from these

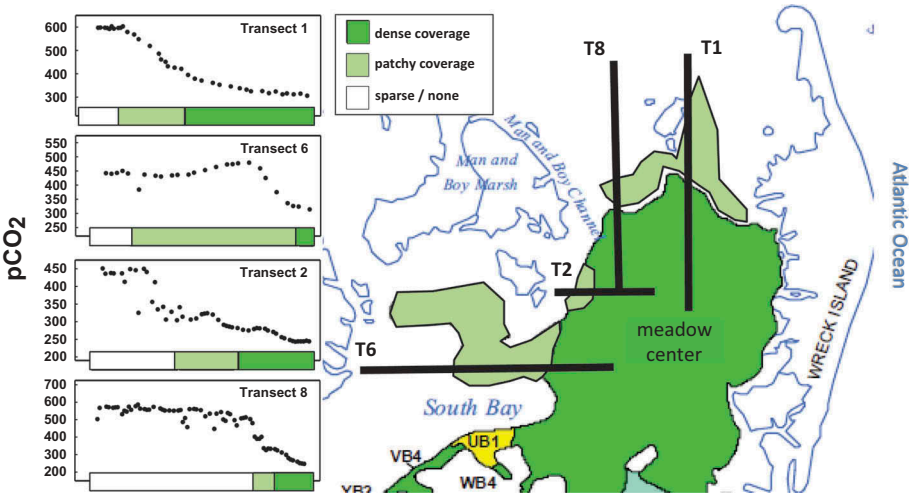

Figure 3. Reduced pCO_2 values within a *Zostera marina* meadow in South Bay, Virginia. Readings taken at canopy height using a pCO_2Scout underway pCO_2 instrument (designed by A.W. Miller; described in Arnold et al. 2014) along transects from 10:00 am to 2:00 pm 4 June 2014. Nearby pCO_2 values ranged from 450 ppm to nearly 800 ppm where marsh efflux was high. These values were reduced by eelgrass photosynthesis by ~300 ppm. At the meadows center pCO_2 levels were occasionally as low as 100 ppm. Dataset from A.W. Miller, A. Reynolds, and T. Arnold; Eelgrass density maps from the Virginia Institute of Marine Studies (Orth et al. 2005, 2006).

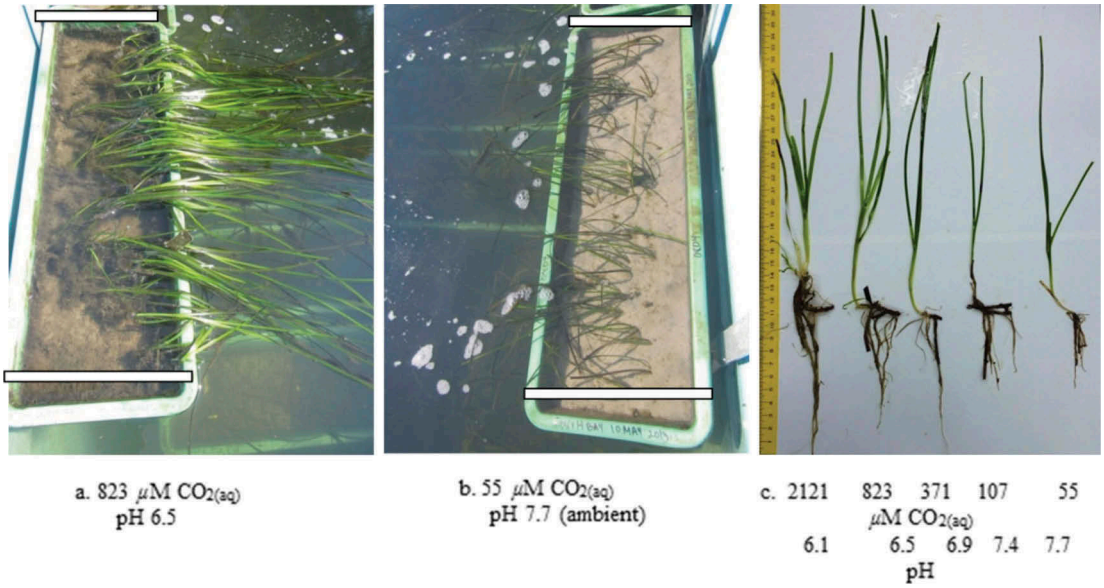

Figure 4. Photographs from the impacts of CO_2 enrichment experiments showing dramatic growth of eelgrass growing at (a) 823 μM $CO_{2(aq)}$, pH 6.5 compared to those growing under ambient conditions (b) 55 μM $CO_{2(aq)}$, pH 7.7 at the end of Summer 2013. White bars at the top and bottom of the pictures are 20 cm long. (c) Photograph illustrating the differences in eelgrass shoot sizes for plants grown across a CO_2 gradient in October 2014. Zimmerman et al. (2017) *Mar. Ecol. Progr. Ser.* Vol. 566: 1–15, reprinted with permission.

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experiments enabled Zimmerman et al. (2015) to model the combined impacts of acidification, warming, and irradiance on eelgrass. As with the experimental results, model calculations revealed that high CO_2 conditions projected for the end of the twenty-first century can alleviate the deleterious impacts of warming on eelgrass (Figure 5). For example, they observed that eelgrass required 5 h of light-saturated photosynthesis to balance its "respiratory load" in cool waters (10°C) compared to 9 h in warm waters (30°C), demonstrating the peril of climate warming for eelgrass in the Chesapeake Bay. However, they also showed that under acidified conditions, corresponding to CO_2 concentrations predicted for the end of century, eelgrass was able to balance its respiratory load in only 4.8 h, even at 30°C. From these datasets the authors developed the *GrassLight* model, which predicted that for *Zostera* pCO_2 levels of 600 ppm 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, allowing for the survival of eelgrass at temperatures that would otherwise trigger mortality.

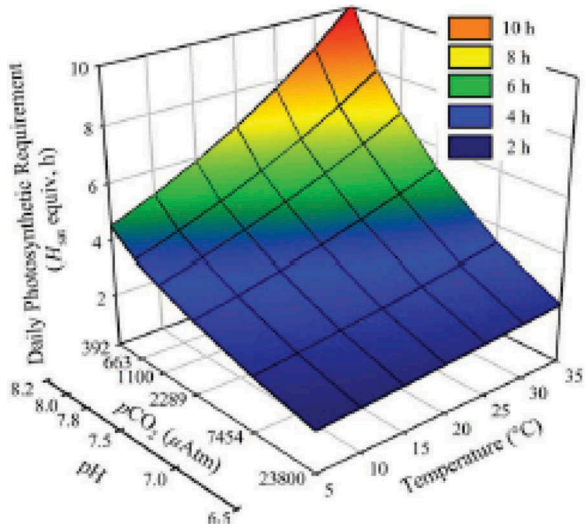

Figure 5. Interactive effects of temperature and CO_2 enrichment on the daily photosynthetic requirement to maintain positive whole-plant carbon balance in *Zostera marina*. With sufficient light availability, the "CO_2 fertilization effect" associated with coastal acidification can offset the deleterious effects of elevated temperatures. Reprinted with permission from Zimmerman et al. (2015), *Limnology Oceanograhy* 60: 1781–1804.

High CO_2/low pH conditions may also 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). These conditions, combined with the superior temperature tolerance of *Ruppia*, may favor for this species in a future Chesapeake Bay. Additional supporting evidence for this phenomenon comes from studies of 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. Björk 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*

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uninervis, and T. hemprichii exposed to pCO_2 levels ranging from 442 to 1204 ppm for 2 weeks in the lab (Ow, Uthicke, and Collier 2016). Higher seagrass productivity has also been observed for natural populations near high CO_2 vents, where these conditions are the natural result of underwater volcanic activity (Hall-Spencer et al. 2008; Fabricius et al. 2011; Takahashi et al. 2016).

Fewer studies of high CO_2/low pH conditions 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, for example, in the upper Potomac River (Figure 1(h)) and at the head of the Chesapeake (Carter et al. 1988; Staver and Stevenson 1995). 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 and Bowes 1980), assuming bicarbonate is available. For example, Olesen and Madsen (2000) found that the growth of the freshwater macrophytes *Elodea canadensis* and *Callitriche cophocarpa* from Denmark increased in response to both increasing temperatures and inorganic carbon availability, indicating the presence of some CO_2 fertilization effect in these species. However, they also found that given time and appropriate temperatures these plants acclimated to better capture inorganic carbon when levels were lower.

In short, the CO_2 fertilization effect seems to be most beneficial for seagrasses, but may also increase the growth of freshwater SAV as well. It is important to note, however, that even among the seagrasses some species benefit more than others from elevated CO_2 and, as a result, continued acidification may contribute to shifts in benthic species composition (e.g., Ow, Uthicke, and Collier 2016).

The great challenge of predicting the effects of acidification on SAV communities stems from the fact that indirect effects can be at least as important as the direct effects on individual plants, but are much more difficult to predict (Kroeker et al. 2013a, 2013b). 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, Price, and Smith 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. In a 6-week mesocosm experiment, Martínez-Crego, Olivé, and Santos (2014) observed rapid epiphyte overgrowth, which suppressed the expected benefits of elevated pCO_2 (800 ppm), on *Zostera noltii* under both low- and high-nutrient conditions. Acidification is also likely to benefit macroalgae, especially those without effective carbon-concentrating mechanisms. Acidification often increases rates of photosynthesis, nutrient assimilation, growth, and reproduction of fleshy seaweed species (Koch et al. 2013; Baggini et al. 2014; Burnell et al. 2014; Johnson, Price, and Smith 2014; Duarte et al. 2016; Kübler and Dudgeon 2013). Kroeker et al. (2013b) noted that in acidified conditions, fleshy seaweeds can rapidly overgrow other species, dominate ecosystems, and cause phase changes in plant communities. It is important to note that the dramatic overgrowth of fouling organisms observed in some studies and attributed to CO_2 might be due to the difficulty of maintaining realistic levels of micrograzing in mesocosm experiments. However, macroalgal overgrowth has been observed in open *in situ* CO_2 enrichment experiments. Regardless, when considering the future of Chesapeake Bay, we need to consider the possibility that the CO_2 fertilization effect may benefit fleshy macroalgae more than submerged vascular plants, allowing them to overwhelm the slower-growing plants under future climate conditions (e.g., Martínez-Crego, Olivé, and Santos 2014). In addition, acidification may also allow non-native fleshy seaweeds to invade new areas, especially when combined with higher temperatures (Kübler and Dudgeon 2015).

High CO_2/low pH conditions may also threaten seagrasses by increasing grazing rates (Tomas et al. 2015). Arnold et al. (2014) observed that rates of fish grazing on *Zostera noltii* increased dramatically from high CO_2/low pH waters near an acid spring in Australia, 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. Conversely, Martínez-Crego, Olivé, and Santos (2014) found no impact of CO_2 enrichment on grazing rates on *Zostera noltii* grown in mesocosms, despite some impacts of acidification and fertilization on plant nutrient levels. However, these

and other authors did find that grazers can have an important positive impact by protecting seagrass communities when they preferentially consume epiphytes and fleshy seaweeds, which threaten to overgrow slower growing seagrass under high CO_2 conditions (Reynolds, Paul, and Emmett 2014; Martínez-Crego, Olivé, and Santos 2014; Baggini et al. 2015; Ghedini, Russell, and Connell 2015).

Finally, future acidification, alone or in concert with other factors, may increase the susceptibility of seagrasses to disease outbreaks. High CO_2/low pH conditions cause the loss of antimicrobial phenolics in many seagrass species (Arnold et al. 2012; Arnold et al. 2014; but see Martínez-Crego et al. 2014; Figure 1 sites (i), (j)). Phenolic acids known to inhibit the growth of the seagrass wasting disease pathogen, *Layrinthula* spp., were reduced by as much as ~95% under "acidified" conditions. Such decreases in protective phenolic compounds have been linked to wasting disease outbreaks and seagrass mortality (e.g., Vergeer and Develi 1997; Buchsbaum, Short, and Cheney 1990; Vergeer, Aarts, and De Groot 1995). Interestingly, acidification also reduces the concentration of bioactive polyphenols in brown algae (e.g., Korbee et al. 2014; Yildiz and Dere 2015).

What then can we predict for SAV in a high CO_2 Chesapeake Bay? It is clear that high CO_2/low pH conditions often stimulate SAV photosynthesis and growth via the CO_2 fertilization effect. This powerful effect can, in certain circumstances, offset the deleterious effects of climate warming, improving the prognosis for eelgrass in the Chesapeake. However, this precarious balancing act deserves additional study as local acidification may not keep pace with warming and because high CO_2 conditions are also known to benefit fouling organisms and grazers, and to compromise disease resistance by inhibiting phenolic acid accumulations. This balance between the potentially positive effects of high CO_2, a parameter that is highly variable even at local scales, and the overwhelmingly negative effects of regional warming is likely to determine the future of key species of SAV in the Chesapeake Bay.

It is worth considering one additional factor in this impending balancing act. The *"CO_2 fertilization effect"* depends heavily on adequate water transparency to drive photosynthesis (Batiuk, Orth, and Moore et al. 1992; Dennison et al. 1993). Without adequate sunlight, high CO_2/low pH conditions are not beneficial. Light levels can also directly impact the ability of SAV to withstand elevated temperatures; insufficient light levels weaken plants by altering the photosynthesis:respiration balance and depriving plants of photosynthate for growth (e.g., Moore et al. 2012). In addition, poor water transparency can prevent SAV from retreating to deeper, cooler waters (Thayer, Kenworthy, and Fonseca 1984; Mckee et al. 2002; York et al. 2013). This highlights the critical need to meet water quality targets, by managing nutrient and sediment loadings, in order to protect and restore SAV resources in the future.

Outlook for the twenty-first century

Regional warming alone threatens to eliminate *Zostera marina* from the Chesapeake Bay. Other, heat-tolerant species may benefit, but these species are unlikely to match *Z. marina* in terms of their range or ecosystem services. On the other hand, the potential benefits of carbon dioxide fertilization has the potential to rescue some species of SAV; however, this will depend upon the rate of future acidification, continued improvements in water clarity to support photosynthesis, and the ability of SAV to "outgrow" fouling organisms that might also benefit from high CO_2/low pH conditions. It is critical that we improve our understanding of how deleterious regional warming and the potential carbon dioxide fertilization effect of local coastal acidification may or may not counterbalance one another in the near future. Also, indirect effects of climate on consumers, competitors, and disease agents are poorly understood but likely to be powerful forces shaping future communities. Currently we know enough to expect that the transition of existing SAV populations to some future state is unlikely to be smooth, predictable, or easily reversible. The degree of success in restoring, protecting, and managing SAV in the Chesapeake Bay and elsewhere will depend our ability to manage the traditional challenges of the twentieth century along with the emerging challenges of accelerating climate change.

It is important to note that present day efforts to improve the health and species diversity of estuaries will be important in the future. The ability of ecological communities to resist and/or adapt to future 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., Reusch et al. 2005; Ghedini, Russell, and Connell 2015). For SAV communities, genetic and species diversity improves SAV survival and the maintenance of ecosystem services in seagrass meadows (Duarte 2000; Ehlers, Worm, and Reusch 2008; Hughes, Best, and Stachowicz 2010; Reynolds, McGlathery, and Waycott 2012; Gustafsson, Boström, and Unsworth 2013; Duffy et al. 2015) and freshwater SAV beds (Engelhardt and Ritchie 2001, 2002; Engelhardt, Lloyd, and Neel 2014). While monocultures or low-diversity systems may expand most rapidly following a stress-induced population collapse, diverse systems are more resilient (Stachowicz et al. 2013; Gustafsson, Boström, and Unsworth 2013). Resilient seagrass communities are,

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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. Although climate change seems likely to continue and accelerate, we maintain some control over the present day health, diversity, and size of SAV communities in estuaries. Efforts to protect and restore populations today, combined with serious efforts to limit anthropogenic climate change, are our best options for protecting the future of SAV in the Chesapeake Bay.

Acknowledgments

This review was adapted from the author's contributions to the *Chesapeake Bay Submerged Aquatic Vegetation (SAV) Habitat Requirements and Restoration Targets: A Third Technical Synthesis* funded by the U.S. Environmental Protection Agency through a Chesapeake Bay Implementation Grant authorized by section 117 of the Clean Water Act. The authors acknowledge the assistance of Brooke Laundry (MD DNR) and numerous members of the technical synthesis workgroup (2014–2017). Brooke Laundry and Savanna Rain Riley assisted with editing and formatting. This project has been funded wholly or in part by the United States Environmental Protection Agency under assistance agreement CB96314201 to the Maryland Department of Natural Resources. The contents of this document do not necessarily reflect the views and policies of the Environmental Protection Agency, nor does the EPA endorse trade names or recommend the use of commercial products mentioned in this document.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This project has been funded wholly or in part by the United States Environmental Protection Agency under assistance agreement CB96314201 to the Maryland Department of Natural Resources.

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