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Recommended priorities for research on ecological impacts of ocean and coastal acidification in the U.S. Mid-Atlantic

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ABSTRACT

The estuaries and continental shelf system of the United States Mid-Atlantic are subject to ocean acidification driven by atmospheric CO_2, and coastal acidification caused by nearshore and land-sea interactions that include biological, chemical, and physical processes. These processes include freshwater and nutrient input from rivers and groundwater; tidally-driven outwelling of nutrients, inorganic carbon, alkalinity; high productivity and respiration; and hypoxia. Hence, these complex dynamic systems exhibit substantial daily, seasonal, and interannual variability that is not well captured by current acidification research on Mid-Atlantic organisms and ecosystems. We present recommendations for research priorities that target better understanding of the ecological impacts of acidification in the U. S. Mid-Atlantic region. Suggested priorities are: 1) Determining the impact of multiple stressors on our resource species as well as the magnitude of acidification; 2) Filling information gaps on major taxa and regionally important species in different life stages to improve understanding of their response to variable temporal scales and sources of acidification; 3) Improving experimental approaches to incorporate realistic environmental variability and gradients, include interactions with other environmental stressors, increase transferability to other systems or organisms, and evaluate community and ecosystem response; 4) Determining the capacity of important species to acclimate or adapt to changing ocean conditions; 5) Considering multi-disciplinary, ecosystem-level research that examines acidification impacts on biodiversity and biotic interactions; and 6) Connecting potential acidification-induced ecological impacts to ecosystem services and the economy. These recommendations, while developed for the Mid-Atlantic, can be applicable to other regions will help align research towards knowledge of potential larger-scale ecological and economic impacts.

1. Introduction

The Mid-Atlantic Coastal Acidification Network (MACAN), co-coordinated by the Mid-Atlantic Regional Council on the Ocean (MARCO) and the Mid-Atlantic Regional Association Coastal Ocean Observing System (MARACOOS), was established to address regional coastal and ocean acidification. MACAN[1] works to coordinate efforts and share information in order to develop a better understanding of the processes associated with ocean and coastal acidification, predict the consequences for marine resources, and devise local adaptation strategies that enable communities and industries in the Mid-Atlantic states to better prepare for changes expected due to ocean acidification. To achieve these overarching goals, the Mid-Atlantic requires a co-ordinated and comprehensive network of resource managers, academic and government researchers, and other stakeholders working together to answer important regional research questions. Additionally, to

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address specific MACAN themes, small working groups (10–15 people) have been established from MACAN membership. One such group includes all the authors here, with diverse affiliations and expertise, charged with prioritizing research on ecological impacts in the Mid-Atlantic region. The product of this working group is this review that synthesizes current acidification and multi-stressor ecological research, identifies the research gaps, and provides recommendations for future studies to improve understanding of ecological impact in the Mid-Atlantic. The synthesis of information presented here provides improved understanding of the ecological impacts of ocean and coastal acidification that is necessary to determine how individual organisms, communities, and ecosystems in the Mid-Atlantic respond to variability and long-term change. The aim of recommending the priorities described here is to inform the research community that can then respond effectively to advance our knowledge through efforts ranging from conducting additional studies involving important and vulnerable species to enhancing predictive ecosystem models and improving economic analyses and vulnerability assessments.

1.1. Background

The United States Mid-Atlantic coastal zone sits within the U.S. Northeast Shelf (NES), one of the most productive regions in the world (O'Reilly and Zetlin, 1998; Sherman et al., 2002). This region consists of a broad continental shelf marine system, several major river-dominated estuaries or bays with strong salinity gradients (e.g., Chesapeake Bay, Delaware Bay), and shallow coastal bays (e.g., Barnegat Bay, Chincoteague Bay). The area supports a diverse assemblage of commercially and recreationally important finfish (bony and cartilaginous) species (Gates, 2009; Sherman et al., 1996), as well as critical shellfish hatcheries, aquaculture, and oyster restoration areas.

Ocean acidification (OA), driven by the ocean's absorption of increasing atmospheric carbon dioxide (CO_2), is occurring globally and has increased average global seawater acidity since the beginning of the Industrial Revolution (Sabine et al., 2004). This rate of ocean acidification is unprecedented in at least the last 300 million years (Hönisch et al., 2012). In addition, the region's estuaries and coastal bays are prone to coastal acidification, high variability and extremes in high CO_2/low pH due to a combination of natural and anthropogenic (human-caused) biogeochemical and physical processes (Chen et al., 2012; Baumann and Smith, 2018). Thus, in some portions of the Mid-Atlantic region, pH changes may be dominated by ocean acidification, while changes in other portions may be strongly influenced by coastal acidification. The drivers of coastal acidification are diverse. Lower alkalinity from freshwater input in these estuarine systems decreases their buffering capacity to offset changes in dissolved CO_2, making coastal waters more susceptible to pH change (Salisbury et al., 2008; Johnson et al., 2013). However, depending on a watershed's geological formation, the amount of alkalinity input may vary. Likewise, outwelling from tidal wetlands can result in significant alkalinity and inorganic carbon input into coastal systems (Wang et al., 2016 and refs therein), both of which influence carbonate chemistry in ways that may affect coastal ecology. Additionally, these systems are shallow (some stratified, others unstratified), experience rapid temperature changes, receive substantial inputs of terrestrial organic matter and nutrients (Abril and Borges, 2004; Crosswell et al., 2012; Cai et al., 2017), and have high biological activity that strongly influences pCO_2 and pH (e.g., photosynthesis, benthic respiration, root respiration in tidal marshes). Together, these processes can cause substantial daily, seasonal, and interannual variability (Miller et al., 2009; Waldbusser et al., 2010; Cai et al., 2011; Hofmann et al., 2011; Duarte et al., 2013; Waldbusser and Salibury, 2014; Baumann and Smith, 2018) up to 2 pH units in a day (Miller et al., 2016). During primary production, photosynthesis increases pH due to uptake of CO_2; however, respiration and organic matter degradation lowers pH through the release of CO_2. The type of shallow system is also important to consider, as some coastal systems will seasonally stratify and can experience different environmental effects (e.g. hypoxia) compared to unstratified conditions (Hagy et al., 2004). Therefore, estuaries may switch between extremes of under- and over-saturated pCO_2, depending on the season, freshwater input, and phytoplankton biomass (Crosswell et al., 2012).

Increased nutrient input from wastewater treatment, changing land use, and application of fertilizers further enhances biological activity and respiration of organic matter (Kemp and Testa, 2011), leading to elevated CO_2, hypoxia (Hagy et al., 2004) and exacerbation of acidification in aphotic bottom waters (Borges and Gyoens, 2010; Cai et al., 2017). The Mid-Atlantic includes highly eutrophic ecosystems (e.g., Chesapeake Bay, Barnegat Bay) where increases in phytoplankton biomass and net primary productivity have been observed since the 1950s (Harding and Perry, 1997; Harding et al., 2002, 2014; Kennish et al., 2007). This phenomenon can cause elevated pH in surface waters, but decreased pH in underlying waters, especially in stratified coastal systems such as parts of the Chesapeake Bay.

Acidification may also frequently co-occur with other environmental stressors (e.g., warm temperatures, low dissolved oxygen), which may exacerbate organism responses (Harvey et al., 2013; Baumann, 2016; Gunderson et al., 2016) and the degree of acidification through complex biogeochemical processes (Cai et al. 2006, 2017). Any one stressor (such as temperature, hypoxia, or acidification) may not itself be an issue, due to the resiliency of many coastal species to fluctuating natural environmental conditions. However, when more than one stressor occurs simultaneously, an organism may become unable to fully withstand changes (Baumann, 2016). This is especially relevant for the U.S. NES, which is warming 2–3x faster than the global average (Wu et al., 2012; Forsyth et al., 2015; Zhang and Gawarkiewicz, 2015). Such accelerated warming is predicted to continue into the future (Saba et al., 2015). Specifically, bottom water temperature on the NES experienced an average increase of 0.2 °C per decade from 1982 to 2014 (Kavanaugh et al., 2017). Despite this body of research, ecological effects of ocean and coastal acidification in the Mid-Atlantic, and interactions of acidification with other stressors are not well understood.

2. Insights from current research

Projected increases in coastal and ocean acidification are expected to depress the aragonite saturation state (Ω_{arag}), a measure and proxy for calcifying conditions (e.g., Barton et al., 2015), and challenge the ability of calcifying organisms to deposit shell. Acidification has also been observed to affect hatching success, larval development, metabolic processes, immune response, organ development, acid-base regulation, and olfaction in both calcifying and non-calcifying organisms (reviewed in Fabry et al., 2008; Doney et al., 2009; Kroeker et al., 2010, 2013a; Waldbusser et al., 2014). However, this recent research has demonstrated highly variable responses of marine life to acidification and suggests the occurrence of species-specific differences, high phenotypic plasticity, and/or the potential for acclimation or adaptation that may lead to relative “winners” and “losers” in a future, more acidified ocean (Cooley et al., 2012). Neutral to negative impacts have been observed in several groups of organisms including crustaceans, mollusks, bony finfish, corals, echinoderms, and calcified algae (reviewed in Kroeker et al., 2010, 2013a, b) and elasmobranchs (Di Santo, 2015, 2016; Dixson et al., 2015). And, generally, compared to adults, younger life stages (e.g. larvae) of animals tend to be more sensitive to increases in pCO_2, decreases in pH, and changes in the saturation state of aragonite, in part due to effects on reduced calcification rates, increased dissolution rates, reduced growth, impaired development, acid-base disturbances, and/or changes in energy allocation (Crustaceans: Walther et al., 2010; Long et al., 2013; Mollusks: Miller et al., 2009; Kroeker et al., 2010, 2013a; Waldbusser and Salisbury, 2014; Waldbusser et al., 2014; Ramesh et al., 2017; Finfish: Esbaugh et al., 2012, 2016; Strobel et al., 2012; Green and Jutfelt, 2014). However, adult stages may be susceptible to changes in behavior or metabolism that could lead to increased predation and physiological stress (Tomanek et al., 2011; Dickenson et al., 2012). Also, because the larval stage of most meroplanktonic crustaceans and shellfish is pelagic while the adult stage is benthic, different acidification stressors and regimes may occur between life stages (Waldbusser and Salisbury, 2014). Conversely, some groups, including some phytoplankton and submerged aquatic vegetation (SAV), have responded positively to high CO_2 conditions in laboratory experiments reflected in increases in photosynthesis and/or growth (Phytoplankton: Crawfurd et al., 2011; King et al., 2015; Tatters et al., 2013; SAV: Lloyd et al., 1977; Zimmerman et al., 1997, 2015, 2017; Koch et al., 2013; Borum et al., 2016). But these benefits may come at a cost, for example in declines in the production of protective carbon-based secondary compounds in SAV (Arnold et al., 2012). Trade-offs may be the rule in a shifting environment; however, understanding and predicting such trade-offs require greater knowledge and more synthetic research.

Despite much uncertainty, some emerging trends in organism response to acidification appear to hold true for Mid-Atlantic species. These are summarized in the text below for major taxonomic groups and in Table 1 for economically important species, defined as commercial and/or recreational species managed by the National Oceanic and Atmospheric Administration (NOAA), individual states, the Mid-Atlantic Fishery Management Council (MAFMC), and/or the Atlantic States Marine Fisheries Commission (ASMFC). Also considered here as economically important are species prominent in the Mid-Atlantic region but managed by the New England Fishery Management Council (NEFMC) as well as SAV due to financial value from inputs to commercial fisheries and the ecological services and amenities they provide (Barbier et al., 2011; Guignet et al., 2017). We have made a thoughtful attempt to focus primarily on Mid-Atlantic species in the synthesis below, but species from other regions are included when discussing some cases where trends are consistent across major taxa. We limit this synthesis to crustaceans, mollusks, bony finfish, elasmobranchs, and primary producers because few to no acidification studies have focused on direct impacts to higher trophic groups such as marine mammals and sea turtles. However, given the closed physiological systems of mammals and turtles, any potential acidification impacts to these groups would likely be ‘bottom-up’, or indirect, through changes in biodiversity, changes in food source (predator-prey dynamics), and/or changes in sound amplification (Schmutter et al., 2017).

Crustaceans: Crustaceans include several important groups such as crabs, lobsters, shrimp, copepods, and krill. Crustaceans molt as they develop through several distinct life stages (e.g., nauplius, zoea, megalopa), creating a new calcium-containing cuticle exoskeleton at each molt. These molting processes could be affected by acidification-induced chemistry changes as was evident in American lobster (McLean et al., 2018) but negligible in blue crabs (Glandon and Miller, 2017). Elevated $p\mathrm{CO}_2$ has also been associated with reduced growth and slowed development in American lobster (Keppel et al., 2012; McLean, 2016; McLean et al., 2018) and larval northern shrimp (Bechmann et al., 2011) as well as reduced survival and growth of larval blue crabs (Giltz and Taylor, 2017; Tomasetti et al., 2018). Additionally, elevated $p\mathrm{CO}_2$ has shown negative impacts on behavior such as reduced feeding in shore (green) crabs (Appelhaus et al., 2012) and impaired chemoreception related to feeding in hermit crabs (Briffa et al., 2012; De la Haye et al., 2011; 2012) and blue crabs (Glaspie et al., 2017). Laboratory studies examining the interactive effects of elevated temperature and $p\mathrm{CO}_2$ on American lobster larvae (Waller et al., 2017), barnacle larvae (Pansch et al., 2012), juvenile blue crabs (Glandon and Miller, 2017, 2018), and larval northern shrimp (Arnberg et al., 2013) consistently demonstrated temperature had a greater adverse effect on survival, respiration, growth, development, and/or food consumption. However, changing $p\mathrm{CO}_2$ may have a complex effect on larval metabolism and behavior (Waller et al., 2017) and requires further attention.

Mollusks: Mollusks include bivalves (oysters, clams, scallops, mussels, etc.), gastropods (snails such as whelk and pteropods), and cephalopods (squid, octopus). Many commercially valuable bivalve species, such as the eastern oyster (*Crassostrea virginica*), northern quahog (locally known as hard clam; *Mercenaria mercenaria*), Atlantic sea scallop (*Placopecten magellanicus*), and bay scallop (*Argopecten irradians*) have been shown to be sensitive to ocean acidification directly through decreased larval survivorship (Green et al., 2009; Talmage and Gobler, 2009; White et al., 2013; Clark and Gobler, 2016), directly through impacts on calcification, reproduction, and/or growth (Desroisers et al., 1996; Berge et al., 2006; Gazeau et al., 2007; Beesley et al., 2008; Miller et al., 2009; Talmage and Gobler, 2009; Beniash et al., 2010; Waldbusser et al. 2010, 2011; Gobler and Talmage, 2013; Ivanina et al., 2013; White et al., 2013; Boulais et al., 2017) and indirectly through impacts on behavior (Amaral et al., 2012; Zakroff et al., 2018) and physiology including changes in metabolism, protein expression, and ingestion rates, among others (Beniash et al., 2010; Lannig et al., 2010; Chapman et al., 2011; Tomanek et al., 2011; Dickinson et al., 2012; O'Donnell et al., 2013; Ivanina et al., 2013; Vargas et al., 2013; Hawkins and Sokolova, 2017). Similarly, negative effects of acidification were determined for longfin squid (growth, hatching times, abnormal statolith: Kaplan et al., 2013; swimming behavior: Zakroff et al., 2018) and pteropods (calcification: Comeau et al., 2010; Bednarsek et al., 2012; behavior: Manno et al., 2012). Multi-stressor studies have illustrated that hypoxic conditions and the associated acidification had negative effects on bivalves (Gobler et al., 2014; Clark and Gobler, 2016) that were both additive and synergistic. Further, decreased salinity exacerbated the negative effects of lower pH on *C. virginica* juveniles (Waldbusser et al., 2011; Dickinson et al., 2012). Additionally, increased dissolution rates and/or decreased growth and calcification rates for bivalves were synergistically shown for combined decreasing seawater pH and increasing temperatures (Hiebenthal et al., 2013; Ries et al., 2016; Griffith and Gobler, 2017; Speights et al., 2017). Responses differed widely among mollusk groups (i.e., mussels, oysters: Gazeau et al., 2007; hard clams, bay scallops, oysters: Talmage and Gobler, 2009; and ocean quahogs: Stemmer et al., 2013) emphasizing that different mollusk groups could have different tolerances, sensitivities, and adaptive capacities under acidifying, and/or multi-stressor, conditions (Kroeker et al., 2010, 2013a). Some studies found positive effects of extreme acidification levels (pH level < 7.0), however, such as reduced susceptibility of polydorid parasitic infections in eastern oysters (Clements et al., 2017).

Bony finfish: Bony finfish refers to cold-blooded vertebrates with skeletons made of bone and includes fish such as herring, bass, and flounder. Variable responses in otolith formation (Checkley et al., 2009; Franke and Clemmesen, 2011; Munday et al., 2011; Frommel et al., 2012; Hurst et al., 2012; Bignami et al., 2013a, b), metabolic rates (Esbaugh et al. 2012, 2016; Ern and Esbaugh, 2016), and acid-base pathways (Esbaugh et al., 2012; Allmon and Esbaugh, 2017) illustrate species-specific differences in susceptibility to acidification. Increased tissue damage (Frommel et al., 2014: Atlantic herring; Chambers et al., 2014: summer flounder), negative impacts on metabolism (Franke and Clemmesen, 2011: Atlantic herring), and diminished growth and survival (Baumann et al., 2012; Miller et al., 2012; Murray et al., 2014; DePasquale et al., 2015; Stiasny et al., 2016) have been documented in laboratory acidification studies. In contrast, no effects on growth and survival (Sswat et al., 2018 a, b: Atlantic herring) or overall energy budget have been observed (Ern and Esbaugh, 2016: red drum). Juvenile scup (Perry et al., 2015) and red drum (Lonthair et al., 2017) were robust to high levels of ocean acidification in laboratory experiments and demonstrated overall physiological tolerance. However, a considerable number of studies, a majority with tropical bony fish species, found negative behavioral effects of OA on orientation and homing (Munday et al., 2009; Simpson et al., 2011; Devine et al., 2012), detection and avoidance of predators (Dixson et al., 2010; Ferrari et al., 2011, 2012a, b; 2013; Wang et al., 2017), and on prey detection and

Table 1
Review of acidification and multi-stressor studies conducted on economically important groups and species of the Mid-Atlantic. Blue = 5 or more studies conducted, Yellow = between 1 & 4 studies conducted. Responses may include one or more of these parameters: Survival, calcification rate, growth rate, development, fertilization success, hatching success, behavior, otolith formation, swimming ability, and swimming activity, and feeding. In some cases in individual studies, acidification may cause divergent responses in different parameters.

Group	Common name	Scientific name	# Acidification-only studies	# Multi-stressor studies (Acidification + other)	Response to acidification			References
					+	-	none	
Crustaceans	American lobster[b]	🟨 *Homarus americanus*	2	1		2		1, 2, 3
	Blue crab[d]	🟨 *Callinectes sapidus*	3	1		2	2	4, 5, 6, 7, 8
	Northern shrimp[b]	🟨 *Pandalus borealis*	2	1		2	2	9, 10, 11
Mollusks	Eastern oyster	🟦 *Crassostrea virginica*	9	5	2	11	1	12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24
	Northern quahog/Hard clam	🟦 *Mercenaria mercenaria*	4	7		9	1	13, 17, 19, 20, 21, 25, 26, 27, 28, 29
	Bay scallop[d]	🟦 *Argopecten irradians*	4	3		7		13, 19, 26, 27, 29, 30
	Ocean quahog[a]	🟨 *Arctica islandica*	1	1			2	31, 32
	Sea scallop[c]	🟨 *Placopecten magellanicus*	2	0		2		33, 34
	Longfin squid[a]	🟨 *Doryteuthis pealeii*	2	0		1	1	35, 36
Finfish	Atlantic herring[b]	🟦 *Clupea harengus*	3	2	1	4	4	37, 38, 39, 40, 41, 42
	Atlantic striped bass[b]	🟨 *Morone saxatilis*	0	1			1	43
	Cobia[b]	🟨 *Rachycentron canadum*	2	1		2	3	44, 45, 46
	Red drum[b]	🟦 *Sciaenops ocellatus*	4	1	1	1	3	47, 48, 49, 50, 51
	Scup[a,b]	🟨 *Stenotomus chrysops*	1	0			1	52
	Summer flounder[a]	🟨 *Paralichthys dentatus*	1	1		2		53, 54
	Weakfish[b]	🟨 *Cynoscion regalis*	0	1			1	55
Elasmobranchs	Coastal sharks[b]	🟨 Various	1	0		1		56
	Little skate[c]	🟨 *Leucoraja erinacea*		2		2		57, 58
SAV	Eelgrass	🟦 *Zostera marina*	>15	2	>15			59, 60, 61, 62, 63, 64, 65, 66
	Widgeongrass	🟨 *Ruppia spp.*	1		1			67
	Wild celery	🟨 *Vallisneria americana*	1		1			68
	Pomatogeton	🟨 *Potamogeton spp.*	1		1			69

a = species managed by the Mid-Atlantic Fishery Management Council (MAFMC).
b = species managed by the Atlantic States Marine Fisheries Commission (ASMFC).
c = species prominent in the Mid-Atlantic but managed by New England Fishery Management Council (NEFMC).
d = species managed by NOAA and/or individual states.

Table references: [1]Keppel et al., 2012; [2]McLean, 2016; [3]Waller et al., 2017; [4]Giltz and Taylor, 2017; [5]Glaspie et al., 2017; [6]Glandon and Miller, 2017; [7]Glandon et al., 2018; [8]Tomasetti et al., 2018; [9]Bechmann et al., 2011; [10]Arnberg et al., 2013; [11]Hammer and Pedersen, 2013; [12]Miller et al., 2009; [13]Talmage and Gobler, 2009; [14]Beniash et al., 2010; [15]Chapman et al., 2011; [16]Waldbusser et al., 2011; [17]Ivanina et al., 2013; [18]Gobler and Talmage, 2014; [19]Clark and Gobler, 2016; [20]Ries et al., 2016; [21]Hawkins and Sokolova, 2017; [22]Boulais et al., 2017; [23]Clements et al., 2017; [24]Speights et al., 2017; [25]Waldbusser et al., 2010; [26]Gobler and Talmage, 2013; [27]Gobler et al., 2014; [28]Miller and Waldbusser, 2016; [29]Griffith and Gobler, 2017; [30]White et al., 2013; [31]Hiebenthal et al., 2013; [32]Stemmer et al., 2013; [33]Desroisers et al., 1996; [34]Cooley et al., 2015; [35]Kaplan et al., 2013; [36]Zakroff et al., 2018; [37]Franke and Clemmesen, 2011; [38]Frommel et al., 2014; [39]Maneja et al., 2014; [40]Maneja et al. (2015); [41]Sswat et al., 2018a; [42]Sswat et al., 2018b; [43]Dixon et al., 2017; [44]Bignami et al., 2013a; [45]Bignami et al., 2013b; [46]Bignami et al., 2017; [47]Diaz-Gil et al., 2015; [48]Ern and Esbaugh, 2016; [49]Esbaugh et al., 2016; [50]Allmon and Esbaugh, 2017; [51]Lonthair et al., 2017; [52]Perry et al., 2015; [53]Chambers et al., 2014; [54]Davidson et al., 2016; [55]Lifavi et al., 2017; [56]Dixson et al., 2015; [57]Di Santo, 2015; [58]Di Santo, 2016; [59]Zimmerman et al., 1997; [60]Zimmerman et al., 2015; [61]Zimmerman et al., 2017; [62]Invers et al., 2001; [63]Palacios and Zimmerman, 2007; [64]Miller, 2016; [65]Miller et al., 2017; [66]Groner et al., 2018; [67]Borum et al., 2016; [68]Lloyd et al., 1977; [69]Arnold et al., 2012.

feeding (Cripps et al., 2011; Nowicki et al., 2012). Nilsson et al. (2012) found that these behavioral impairments were due to altered olfaction and an altered GABA-A neurotransmitter receptor. Because GABA-A is a ubiquitous major neurotransmitter receptor in the vertebrate brain and conserved in evolution, it has been proposed that similar behavioral effects will be seen in other fish (Nilsson et al., 2012). Yet Maneja et al. (2015) found no impact on swimming kinematics and foraging behavior of larval Atlantic herring and no significant proteome changes (Maneja et al., 2014). Recent multi-stressor studies in Mid-Atlantic estuaries and nearshore regions found that, typically, hypoxic conditions co-occur with reduced pH and are additive or synergistic in their impacts on fish (DePasquale et al., 2015; Davidson et al., 2016; Lifavi et al., 2017; Miller et al., 2016). However, in contrast to low DO exposure, high $p\mathrm{CO}_2$ did not have an effect on survival in any of the Mid-Atlantic juvenile species tested in Dixon et al. (2017; Atlantic silverside, striped killifish, mummichog, striped bass).

Elasmobranchs: This group is also referred to as finfish, but with cartilaginous skeletons, and consists of sharks, rays, and skates. Studies focused on ocean acidification impacts on elasmobranchs are much sparser compared to other taxonomic groups previously discussed. However, trends similar to those observed in other groups have emerged, including negative behavioral effects of OA on detection and avoidance of predators in smooth dogfish, *Mustelus canis* (Dixson et al., 2015). Furthermore, multi-stressor studies (temperature and $p\mathrm{CO}_2$) conducted on little skate (*Leucoraja erinacea*) embryos (Di Santo, 2015) and juveniles (Di Santo, 2016) revealed that increased acidification exacerbated temperature-induced reductions in body condition and aerobic scope, respectively, in Gulf of Maine populations.

Primary Producers: Primary producers, including phytoplankton and Submerged Aquatic Vegetation (SAV), are autotrophs and as such can alter the $p\mathrm{CO}_2$ via uptake during the process of photosynthesis. Phytoplankton are single-celled aquatic plants, also referred to as microalgae. Single-species laboratory studies world-wide have found either minor impacts of elevated $p\mathrm{CO_2}$ on photosynthesis (Beardall and Raven, 2004; Giordano et al., 2005), increases in growth rates of diatoms, dinoflagellates, and chlorophytes (Crawfurd et al., 2011; King et al., 2015; Tatters et al., 2013), decreases in growth and calcification rates of coccolithophores (Crawfurd et al., 2011; Lohbeck et al., 2012, 2013; Jin et al., 2013; Tatters et al., 2013; King et al., 2015), and increases in biomass and toxicity of harmful algal species *Alexandrium fundyense* (Hattenrath-Lehmann et al. 2015). Limited data also revealed variable acidification impacts on elemental composition (C:N:P) and nutritional quality (Bellerby et al., 2008; King et al., 2015; Bermúdez et al., 2016; Paul et al., 2016). Consistent with a meta-analysis of over 49 papers from single-species experiments (Dutkiewicz et al., 2015), two incubation studies with natural Mid-Atlantic phytoplankton communities under elevated $p\mathrm{CO_2}$ (Grear et al., 2017) and elevated $p\mathrm{CO_2}$/nutrient loadings (Young and Gobler, 2017) have demonstrated the potential for community shifts that could impact biogeochemical cycles and reverberate through the food web.

Rooted vascular plants that grow underwater in shallow, typically unstratified, coastal areas are termed collectively as SAV. The photosynthesis of most SAV species, including wild celery (*Valsineria americana*), widgeon grass (*Ruppia* spp.) and eelgrass (*Zostera marina*) is limited by present-day $p\mathrm{CO_2}$, yielding higher rates of photosynthesis under short-term elevated $p\mathrm{CO_2}$ conditions (Table 1; Lloyd et al., 1977; Koch et al., 2013; Borum et al., 2016; and references cited therein). Consequently, the negative effects of climate warming on heat-sensitive species such as eelgrass (Moore and Jarvis, 2008) may be at least partially offset in those species by increased photosynthetic rates resulting from elevated $p\mathrm{CO_2}$ in an acidified coastal environment, as demonstrated theoretically (Zimmerman et al., 2015) and experimentally (Zimmerman et al., 2017). Likewise, there is evidence that acidifying conditions may alter epiphyte communities more than nutrient enrichment in seagrasses, which could be an additional stress to SAV communities (Campbell and Fourqurean, 2014). However, photosynthesis does not necessarily translate to whole plant productivity, particularly when light or other factors may limit productivity (Ow et al., 2015, 2016). Additionally, elevated $p\mathrm{CO_2}$ may enhance SAV vulnerability to grazing, disease and decomposition through decreases in phenolic compounds (Arnold et al., 2012), so it is currently difficult to assess long-term impacts of elevated $p\mathrm{CO_2}$ on SAVs.

3. Research gaps and priorities

We describe here the urgent need for focused research to: 1) Determining the impact of multiple stressors on our resource species as well as the magnitude of acidification; 2) Filling information gaps on major taxa and regionally important species in different life stages to improve understanding of their response to variable temporal scales and sources of acidification; 3) Improving experimental approaches to incorporate realistic environmental variability and gradients, include interactions with other environmental stressors, increase transferability to other systems or organisms, and evaluate community and ecosystem response; 4) Determining the capacity of important species to acclimate or adapt to changing ocean conditions; 5) Considering multi-disciplinary, ecosystem-level research that examines acidification impacts on biodiversity and biotic interactions; and 6) Connecting potential acidification-induced ecological impacts to ecosystem services and the economy.

3.1. *Multiple Drivers of Acidification*

Understanding the processes driving the location, variability, and magnitude of acidification is essential for characterizing and projecting the conditions that local species experience. The major gaps in our understanding of how multiple external drivers impact the acidification of Mid-Atlantic estuaries can be summarized into four major categories. First, the relative sensitivity of estuarine carbonate chemistry to eutrophication versus fossil fuel acidification remains a challenge, primarily because the interaction is specific to each estuary's nutrient loading and the relative ocean versus freshwater influence. Secondly, future realizations of acidification in response to contemporaneous changes in temperature (but also physical mixing, stratification, and nutrient loading) are difficult to predict, thus demanding both empirical and modelling investigations into the relative role of these changes. Third, the characterization of riverine salinity, alkalinity, and pH appears to require much more attention, given that these properties have river-specific differences and will respond variably to future changes in land use and atmospheric deposition (Salisbury et al., 2008; Kaushal et al., 2013; Stets et al., 2014). Researchers must remain sensitive and vigilant to differences among coastal, estuarine, and open ocean ecosystems when measuring and quantifying the carbonate chemistry and avoid potential pitfalls (e.g., mistakes in $p\mathrm{CO_2}$ when making calculations from pH and total alkalinity [see Hunt et al., 2018; Abril et al., 2015]). Finally, we recommend research that investigates the mechanism, direction, and magnitude of acidification caused by other climate-induced changes such as sea level rise (SLR) that can impact biological communities and biogeochemical processes (e.g., photosynthesis/respiration, calcification/dissolution) that feedback into carbonate system dynamics in the Mid-Atlantic region. Developing models of coastal acidification that include the following controls on acidification is an important goal.

Nutrient loading leading to eutrophication has long been recognized to cause hypoxic events in Mid-Atlantic coastal regions (Hagy et al., 2004; Tyler et al., 2009). The microbial respiration that induces hypoxia also releases $\mathrm{CO_2}$, which adds to the burden of atmospheric $\mathrm{CO_2}$ in nearshore waters. Despite the long recognition of eutrophication as an issue of concern in the Mid-Atlantic region, the relative contribution of eutrophication to aquatic $p\mathrm{CO_2}$ levels is still not well understood (Breitburg et al., 2015) and emphasizes the need for studies aimed at quantifying this contribution. For example, eutrophication may decrease surface water $p\mathrm{CO_2}$ (and elevate pH) while increasing $p\mathrm{CO_2}$ (and lower pH) in deeper waters of stratified systems, but in very shallow unstratified systems, eutrophication may simply increase the magnitude of diel $p\mathrm{CO_2}$ (and pH, $\mathrm{O_2}$) variability. Understanding how the differences in the timescale of eutrophication-induced acidification in these two environments (months versus hours) is critical. Puget Sound researchers are beginning to distinguish $\mathrm{CO_2}$ contributions of different coastal processes to aquatic $p\mathrm{CO_2}$ levels (Feely et al., 2010), and their methods may be instructive for the Mid-Atlantic region.

Temperature is also steadily rising globally owing to rising levels of atmospheric $\mathrm{CO_2}$ and other radiatively active gases, and long-term increases in water temperature have been documented in Mid-Atlantic estuaries (e.g., Ding and Elmore, 2015; Testa et al., 2018). Higher temperatures not only affect chemical equilibria, but also directly affect marine organism physiology, raising metabolic and respiratory rates, sometimes beyond physiologically optimum conditions (Pörtner, 2010). Rising ocean temperatures drive some mobile oceanic species poleward in pursuit of ideal environmental conditions (Cheung et al., 2010; Sunday et al., 2012; Pinsky et al., 2013; Poloczanska et al., 2013; Kleisner et al., 2016; Morley et al., 2018), and changing distributions of many important fishery species are predicted to continue under projected climate change (Hare et al., 2016). While research on the interactive effects of temperature and acidification are growing, we recommend additional research in this area to increase our understanding of how this relationship will play out at individual-to-ecosystem scales.

Episodic pulses of freshwater runoff from storms and the increased occurrence of significant rainfall events in the region (Melillo et al., 2014) contribute to the dynamism of Mid-Atlantic estuarine and marine environments, and also have the capacity to significantly impact nearshore carbonate chemistry including saturation state (e.g., Salisbury et al., 2008; Johnson et al., 2013). Storm runoff is primarily derived from rainfall, which has low pH from equilibrating with atmospheric CO_2 concentrations, zero salinity, and low/zero alkalinity. In the absence of storms, river discharge into the Mid-Atlantic has relatively steady alkalinity and calcium ion concentrations, but the alkalinity-discharge relationship is nonlinear at high flow rates (Sarah Cooley, unpublished, based on USGS datasets). This floods watersheds with fresher water that includes terrestrial-derived organic and inorganic carbon (Bauer et al., 2013) and exhibits highly variable alkalinity, pH, and calcium ion concentrations over the course of seasons and even days to weeks. Terrestrial organic carbon, as well as resuspension of buried organic matter in ocean sediments, can trigger microbial activity increasing the biologically sourced CO_2 burden in coastal waters (Bauer et al., 2013; Cai et al., 2011, 2017). Changes in land use, weathering, and atmosphere-land interactions are also associated with changing river alkalinity across the U.S. (Kaushal et al., 2013; Stets et al., 2014), and in some cases can act to buffer acidification (i.e., bicarbonate production as a result of recent accelerated silicate and carbonate weathering in large rivers; Kaushal et al., 2013). Nearshore carbonate chemistry in the Mid-Atlantic will likely continue to change at the same time as atmospheric CO_2-driven ocean acidification progresses. The extent of this change, and the relative contribution of the different processes that control the amount of freshwater inflow and its alkalinity, should be a focus of future research.

Another confounding factor may be sea level rise (SLR), which is not only a driver of change itself by simply inundating coastal ecosystems, but also a driver of change by altering the interaction of physical and biological ecosystem elements. SLR will affect the extent and location of estuarine/coastal mixing of fresh and salt water (Miller et al., 2009), but there are many unknowns with respect to its impact on carbonate chemistry dynamics. SLR could drive mismatches between bottom topography/substrate and water chemistry and changes in light penetration due to changes in water depth, clarity, and stratification that can in turn impact rates of primary productivity and phytoplankton biomass. Tidal (nuisance) flooding will increase the frequency and amount of organic and/or acid species washing into coastal waters (including sewage; Flood and Cahoon, 2011), depressing pH directly or through microbial respiration and possibly having toxic effects on marine life. There may be other consequent impacts of these changes on sediment biogeochemical processes (e.g., Cai et al., 2017), such as altered carbon deposition rates or availability of alternate electron acceptors (e.g., sulfate), whose ultimate impacts on acidification still need to be determined. How coastal habitats respond to rising sea level (e.g., whether tidal wetlands will keep pace or become submerged; Raposa et al., 2016) will affect the influence of tidal outwelling of dissolved inorganic carbon (DIC) and alkalinity requires further attention.

3.2. Gaps for major taxa

An initial effort needs to be put forth to conduct a quantitative meta-analysis synthesizing existing ecological impacts research to determine sensitivities among and within regionally important Mid-Atlantic species and individual biological processes. This should include considerations for different life stages (i.e. larvae, juvenile, adult, etc.). Future acidification research should also direct focus on specific species or groups that are regionally important. The “importance” of a species or group can be defined in several ways, including abundance or rarity, ecosystem role, economic, or cultural importance. Some species are important because they provide critical habitat e.g., biogenic habitat structures such as coral and oyster reefs, or seagrass habitats (National Research Council, 2010). Cold-water coral reefs such as those in the Mid-Atlantic provide habitat for juvenile finfish and may be at particular risk from ocean acidification (Guinotte et al., 2006; IPCC, 2014; Perez et al., 2018). In contrast, oyster reefs (Waldbusser et al., 2013) and seagrasses (Hendriks et al., 2014; Garrard et al., 2014) may in fact provide some local buffering effect from ocean acidification. SAV and many mollusks are termed ecosystem “engineers” due to their important ecological function including nutrient removal, habitat creation, and food source (Jones et al., 1994; Gazeau et al., 2007; Gurbisz et al., 2017). Oysters have ecological, economic, cultural, and historical importance in the Mid-Atlantic region (Wilson et al., 2005), and oyster restoration areas in the region are becoming more prominent. Economically important species in the Mid-Atlantic, as defined above, include SAV and several bivalves, crustaceans, bony finfish, and elasmobranchs (Tables 1 and 2). Atlantic sea scallops (*Placopecten magellanicus*) are one of the most economically important and highly productive single-species commercial fisheries in the United States (Hart and Chute, 2004). Clams (Atlantic surfclam, *Spisula solidissima*; and Ocean quahog, *Arctica islandica*) make up a substantial volume of the commercial catch in the Mid-Atlantic region. Blue crabs (*Callinectes sapidus*) and hard clams (*Mercenaria mercenaria*) have great historical relevance in the region, and while sea scallops (*P. magellanicus*) are relatively more economically valuable, bay scallops (*Argopecten irradians*) have been targeted for restoration efforts in Virginia. Some migratory species are also considered important, particularly diadromous fish species that migrate between the ocean and estuaries as part of their life histories and encounter large ranges of environmental conditions. Additionally, research should be directed towards species that not only are considered vulnerable based on recent research findings (above and Table 1) but also have not yet been investigated for acidification and/or multi-stressor impacts, specifically those economically important species listed in Table 2. Of the 35 species managed by the Mid-Atlantic Fisheries Management Council (MAFMC) and the Atlantic States Marine Fisheries Commission (ASMFC), 69% (24 species) have not yet been investigated for acidification impacts (Table 2) and only 2 out of the remaining 11 species (Atlantic herring, *Clupea harengus*; Red drum, *Sciaenops ocellatus*) have been the focus of multiple (five or more) studies testing the impacts of acidification (Table 1). Compared to other groups such as shellfish and bony finfishes, acidification-focused research on elasmobranchs is sorely lacking and future research should address these gaps as they often times serve as top predators in pelagic marine ecosystems. Similarly, predators on commercially important shellfish species in benthic systems, including whelks (*Busycon* spp. and *Busycotypus* spp.), muricids (*Urosalpinx* sp.), and naticids (*Natica* sp.), should be considered in acidification-focused research.

The severe lack of these first-level acidification studies greatly reduces the research community's ability to assess potential impacts to food webs and the regional economy and society. Furthermore, there is demonstrated substantial variation in response to acidification across species, life stages and environments that can attributed to not only plasticity in acclimation capacity but also the experimental methodologies used (timescale of exposure, $p\mathrm{CO_2}$/pH magnitude and variability applied, etc.). Future research on regionally important species also needs to broaden and investigate multiple life stages and incorporate natural variability and multi-disciplinary research needs (e.g., multiple stressors, trophic interactions) through improved experimental design.

3.3. Recommendations for Experimental Design Improvements

Over the past few decades, there has been a growing effort to understand the effects of increasing $p\mathrm{CO_2}$ on marine ecosystems. Although these efforts have improved understanding of organismal responses to acidification, Wahl et al. (2015) highlighted several unknowns that could not be fully explained by most previous research efforts. We expand here to describe both the limitations of previous experimental approaches and offer guidance for improvements in order to address the complexity of the coastal environment.

Multiple species assemblages and multi-stressor studies are still rare (Boyd et al., 2018). The majority of studies conducted world-wide that investigate organismal response to environmental stressors (e.g., high $p\mathrm{CO2}$/low pH, warm temperatures, low DO) are conducted on single species in the laboratory and usually test only one stressor. These studies are relatively inexpensive and are ideal for controlling variables and optimizing replication, but they do not represent realistic

Table 2
List of economically important species of the Mid-Atlantic for which no acidification or multi-stressor (acidification + other) studies have been published.

Group	Common name	Scientific name
Molluscs	Atlantic surfclam[a]	*Spisula solidissima*
	Illex squid[a]	*Illex illecebrosus*
Crustaceans	Atlantic deep-sea red crab[c]	*Chaceon quinquedens*
	Horseshoe crab[b]	*Limulus polyphemus*
	Jonah crab[b]	*Cancer borealis*
Finfishes	American eel[b]	*Anguilla rostrata*
	Atlantic croaker[b]	*Micropogonias undulatus*
	Atlantic mackerel[a]	*Scomber scombrus*
	Atlantic menhaden[b]	*Brevoortia tyrannus*
	Atlantic Sturgeon[b]	*Acipenser oxyrinchus*
	Black drum[b]	*Pogonias cromis*
	Black sea bass[a,b]	*Centropristis striata*
	Bluefish[a,b]	*Pomatomus saltatrix*
	Butterfish[a]	*Peprilus triacanthus*
	Monkfish[a]	*Lophius americanus*
	Offshore hake[c]	*Merluccius albidus*
	Red hake[c]	*Urophycis chuss*
	River herring[b]	*Alosa pseudoharengus, Alosa aestivalis*
	Shad[b]	*Alosa sapidissima*
	Silver hake[c]	*Merluccius bilinearis*
	Spanish mackerel[b]	*Scomberomorus maculatus*
	Spot[b]	*Leiostomus xanthurus*
	Spotted seatrout[b]	*Cynoscion nebulosus*
	Tautog[b]	*Tautoga onitis*
	Golden tilefish[a]	*Lopholatilus chamaelonticeps*
	Blueline tilefish[a]	*Caulolatilus microps*
	Winter flounder[b]	*Pseudopleuronectes americanus*
Elasmobranchs	Spiny dogfish[a,b]	*Squalus acanthias*
	Winter skate[c]	*Leucoraja ocellata*

[a] Species managed by the Mid-Atlantic Fishery Management Council (MAFMC).

[b] Species managed by the Atlantic States Marine Fisheries Commission (ASMFC).

[c] Species prominent in the Mid-Atlantic but managed by New England Fishery Management Council (NEFMC).

conditions nor incorporate additive, antagonistic (less than additive), or synergistic (more than additive) effects from other abiotic and biotic factors and thus are unable to inform on population and community responses, or on indirect effects such as predator-prey interactions (Andersson et al., 2015). Additionally, in most of these studies, organisms are exposed to constant conditions, not the variable conditions organisms would see naturally on daily, seasonal, and/or episodic timescales. Likewise, organisms in the natural environment would experience multiple, non-static stressors including temperature, DO, and salinity.

Experiments using stable conditions are insufficient for species that spend all or part of their life cycle in coastal and/or estuarine environments because these areas experience greater swings than the open ocean in $p\mathrm{CO}_2$/pH over daily, monthly, and seasonal timescales (Hoffmann et al., 2011; Duarte et al., 2013). In fact, some coastal areas can experience $p\mathrm{CO}_2$/pH shifts over a 24-h period that far exceed the changes expected for the open ocean over the next decade and century (Hofmann et al., 2011; Waldbusser and Salisbury, 2014; Wallace et al., 2014; Baumann et al., 2015). Many natural and human-induced episodic phenomena or seasonal processes, including upwelling, eutrophication, low-oxygen zones, and freshwater inputs can spatiotemporally affect water chemistry and lower the pH (Gobler et al., 2014; Waldbusser and Salisbury, 2014). Yet the effects of episodic or seasonal $p\mathrm{CO}_2$ increases on coastal organisms have not been adequately addressed by most laboratory experiments, which base $p\mathrm{CO}_2$ treatment levels on projections for the open ocean. The few studies that conducted experiments to test the effect of fluctuating $p\mathrm{CO}_2$ on Mid-Atlantic species have shown mixed results, producing no effect, positive effects and negative effects when compared to static controls (Clark and Gobler, 2016; Keppel et al., 2016; Gobler et al., 2014; Mangan et al., 2017). Natural fluctuations of a stressor likely represent alternating stress and release from stress, but these fluctuations may be detrimental (high metabolic costs of repeated recovery) to physiological performance over time in some organisms. Likewise, because these processes driving organismal response occur at different timescales, exposure time to experimental treatment conditions needs to be relevant. It is largely unknown how naturally variable carbonate chemistry affects many Mid-Atlantic species due to lack of targeted experiments and/or field investigations that include simultaneous acidification and biological monitoring, but we recommend this be a focus of ongoing research. However, in order to move this area of research forward, we also need a solid understanding of what the natural variability is in Mid-Atlantic waters and this will require a comprehensive monitoring strategy (Goldsmith et al., 2019).

Experimentally differentiating the causative effect of acidification on an individual organism, a population, or community is becoming increasingly important. An increase in seawater $p\mathrm{CO}_2$ leads to concurrent changes in pH, bicarbonate ion concentration ($[\mathrm{HCO}_3{}^-]$), and carbonate saturation state. All of these changes can produce negative (or positive) effects by themselves. Increases in $[\mathrm{HCO}_3{}^-]$ may support increased calcification rates up to a point while at the same time decreases in saturation state produces increased dissolution (Cyronak et al., 2016). In addition to aragonite saturation state of water (Ω_{arag}), calcification may also be governed in many species by the substrate to inhibitor ratio (SIR = ratio of bicarbonate ions to hydrogen ions, Fassbender et al., 2016), suggesting that researchers will do best to control and measure appropriate chemical parameters, which will be dependent on the organisms studied. In order to gain a greater understanding of the mechanisms that produce negative effects, experiments need to be designed in a way that will allow the researcher to differentiate which stressor causes which effect. Few experimental studies have varied the carbonate parameters independently of one another to determine their individual impacts (Jury et al., 2010; Waldbusser et al., 2013, 2014; Gazeau et al., 2014; Thomsen et al., 2015), and studies of this nature need to be conducted on locally important species. Such an approach could advance the overall science as well as fulfill regional research needs. Methods to manipulate stressors independent of one another are provided in Gattuso et al. (2010), as well as in the previously listed citations.

Essential to advancing the understanding of organismal responses to acidification are more studies that: 1) include real-world variability and gradients, to be applied to the larger system; 2) increase replication within and between experiments to increase robustness in estimates of $p\mathrm{CO}_2$ sensitivity and improve results of modelling efforts; 3) increase transferability of results to other systems or organisms, for example, experiments designed to understand mechanisms underpinning biological responses; and 4) evaluate community and ecosystem response. Laboratory experiments will need to incorporate larger ranges of $p\mathrm{CO}_2$ treatments, higher $p\mathrm{CO}_2$ levels, longer-term (chronic) exposures, and a greater number of treatment levels to produce adequate response curves and better indicate tipping points. Future laboratory studies should also address the effects of multiple stressors in addition to $p\mathrm{CO}_2$/pH in order to gain a more mechanistic understanding of how $p\mathrm{CO}_2$ affects organisms in stressful, fluctuating temperature, DO and other conditions, as well as organism acclimation or adaptation potential, including intraspecific variation and transgenerational adaptation described in the following section. More complex laboratory experiments, however, will require sophisticated facilities such as those at the US National Oceanic and Atmospheric Administration's (NOAA's) James J. Howard laboratory in Sandy Hook, NJ, where a method for conducting large-scale multivariable OA experiments was developed (described in Chambers et al., 2014). Briefly, the treatments are produced by a gas-exchange column that has numerous outflow taps spread evenly from the column inflow to its outflow, and the flow rate to the column of both seawater and CO_2 gas are adjusted to produce consistent readings over time at each outflow tap. This system is ideal for replicating a large number of treatment levels (up to 24) while also constraining costs. Further advances in our understanding of ecosystem responses to acidification would also benefit greatly from multi-year experiments conducted *in situ* using free ocean pCO_2 enrichment (FOCE) systems (Arnold et al., 2012; Andersson et al., 2015) that can incorporate natural populations with natural cycles of variability in light, temperature, salinity and pH/pCO_2.

3.4. Acclimation/Adaptation Capacity of Organisms

The key questions regarding acclimation and local adaptation for a broad range of species, populations, and communities are: 1) What is the potential for epigenetic change (short time scales; phenotypic) and evolution (long time scales; genetic adaptation) in marine species during exposures to multiple environmental stressors, including acidification? 2) Do carry-over effects improve acclimatization to environmental stressors? and 3) What are the physiological (energetic) costs of acclimation and can those costs be compensated with food availability now and in the future? Understanding the rates of acclimatization and/or adaptation are also important, as these may occur too slowly to outpace the current rate of acidification.

While studies reporting acidification impacts on organisms worldwide are growing rapidly, few focus on potential acclimation and adaptation capacities and strategies (Kelly and Hofmann, 2013; Riebesell and Gattuso, 2015) and to our knowledge only two such studies have focused on local Mid-Atlantic species (Murray et al., 2014; Griffith and Gobler, 2017). Therefore, our knowledge of the evolutionary potential of organisms and populations in response to acidification is extremely limited. As a result, here we summarize information gained from mostly non-local acidification-related acclimation/adaptation studies in order to serve as an example to move research forward in the Mid-Atlantic. Potential acclimation and adaptation strategies range from migrations that alter geographic distributions, such as those demonstrated by marine fishes in response to warming seawater temperatures (Sunday et al., 2012; Pinsky et al., 2013; Poloczanska et al., 2013; Kleisner et al., 2016; Morley et al., 2018), and acclimation through intraspecific diversity or physiological phenotypic plasticity and genetic adaptation (Collins and Bell, 2004, 2006; Pistevos et al., 2011; Sunday et al., 2011; Lohbeck et al., 2012, 2013; Foo et al., 2012; Malvezzi et al., 2015). Changes in geographic distribution of marine fishes have been correlated with increasing temperatures, but no studies have linked similar large-scale shifts of populations directly to acidification. Instead, extinctions may occur at localized "hotspots" of acidification (Kelly and Hofmann, 2013; e.g., upwelling areas, estuarine areas with recurring high productivity and hypoxia), illustrating the need for biological, chemical, and physical monitoring in these areas.

An increasing number of studies have demonstrated high phenotypic and/or genotypic variance and genetic adaptive capabilities within individuals of the same species in response to elevated pCO_2. Clones of a single bryozoan species (Pistevos et al., 2011), strains of a coccolithophore species (Langer et al., 2009), and selectively-bred lines of a species of rock oyster (Parker et al., 2011) all exhibited different sensitivities to acidification. The ability for one individual to perform better than another within the same species suggests the potential for adaptive capability. Studies that have experimentally tested for genetic adaptation are limited to species or taxa that have short lifespans (e.g., phytoplankton) to reduce logistical complexity associated with maintaining organisms in a controlled laboratory setting (Kelly and Hofmann, 2013). Interestingly, a wide range of genetic adaptive capabilities was evident in just a few of these such studies on the coccolithophore alga *Emiliania huxleyi* (Lohbeck et al., 2012, 2013) and the green alga *Chlamydomonas* (Collins and Bell, 2004). Differential adaptive capacities such as these may drive changes in community composition with repercussions throughout the food web and in global biogeochemical cycles. The reasons for high phenotypic plasticity or genetic variance between species and the ability for acclimation or adaptation in some organisms has been the subject of recent discussion. For instance, there is evidence that organisms regularly experiencing large natural fluctuations in chemistry (e.g., species in Mid-Atlantic bays and estuaries) may be more tolerant of acidification compared to organisms in more stable environments (e.g., non-estuarine species) (Evans et al., 2013; Pespeni et al., 2013; Hofmann et al., 2013; Lonthair et al., 2017) and thus may be more prepared to acclimate and adapt to more extreme future conditions. However, organisms living in these habitats could also be the first to reach their pH and saturation state tolerances. If those organisms are already close to their acclimatization or adaptation capacities, they may not be able to handle further changes in pCO_2, pH, or both. Conversely, species living in offshore environments may be better adapted to more stable conditions, and there is much uncertainty as to if and how these species will acclimate or adapt to projected slow, progressive increases in pCO_2 and reductions in pH and saturation state. Therefore, future research on organism acclimation and adaptation, in combination with continuous monitoring, will be important to understand the potential resilience of both near-shore coastal and offshore Mid-Atlantic communities to increased acidity.

Transgenerational exposures are also believed to contribute to the ability to adapt to ocean acidification, whereby adults exposed to elevated pCO_2 can pass on non-genetic inheritances to their offspring, termed a carry-over effect, that may enhance their survival and success (Parker et al., 2012, 2015; Murray et al., 2014; Goncalves et al., 2016; Ross et al., 2016). Larval Sydney rock oysters, *Saccostrea glomerata*, bred from adults exposed to elevated pCO_2, were more resilient to acidification than wild larvae and were larger than larvae spawned from adults in ambient conditions (Parker et al., 2012, 2015). However, these positive carry-over effects were not sustained when exposed to other stressors such as increased temperature or reduced food (Parker et al., 2017). In a recent transgenerational exposure study where the parental generation of two North Atlantic bivalves, hard clam *Mercenaria mercenaria* and bay scallop *Argopecten irradians*, was exposed to high pCO_2, their offspring were more negatively impacted by low pH and other stressors compared to control conditions (Griffith and Gobler, 2017). Several other studies have demonstrated negative carry-over effects through decreased egg production and fecundity in adults and decreased hatching success, larval development, and survival in many marine species (reviewed in Kroeker et al., 2010; Kurihara et al., 2008; Parker et al., 2010; Kawaguchi et al., 2011, 2013; Borges et al., 2018). Therefore, future research needs to evaluate the prominence of positive or negative carry-over effects in Mid-Atlantic species and whether these are relevant in the local ecosystems where multi-stressors occur. Multigenerational studies would also provide knowledge on whether these carry-over effects are heritable and can impact organism fitness.

Finally, mechanisms that organisms use to cope with acidification, including changes in metabolism, acid-base regulation, and calcification, are predicted to be energetically costly, but few studies have attempted to quantify these associated costs (i.e., Parker et al., 2012; Heuer and Grosell, 2016). Increased energetic costs resulting from acclimation processes could potentially decrease the energy available for defenses, growth, and reproduction. Therefore, food supply may play an important role in compensating for these additional energetic costs, and ultimately in the ability for organisms to acclimate or adapt, survive, and succeed when experiencing acidification and other stressors (Saba et al., 2012; Seibel et al., 2012; Ramajo et al., 2016; Hurst et al., 2017). Some marine calcifiers demonstrate resilience in their calcification and growth rate responses to acidification if supplied with sufficient food (Ramajo et al., 2016). High food availability also outweighed adverse effects of high pCO_2 exposure in juvenile *Mytilus edulis* (Thomsen et al., 2013). Future experiments, field studies, ecosystem-based assessments and model projections should therefore not only determine the energetic costs required for acclimation but also consider available food supply and food quality.

3.5. Ecosystem-level Research Considerations

It is difficult to summarize the ecosystem-level effects of acidification because the range of ecological effects is very broad, the organizational levels (i.e. individual, population, community, ecosystem) are deep, interactions are complex, and the biogeography and habitats from open ocean to estuary vary significantly. Despite being an important goal, we are just beginning to understand ecosystem-level impacts of coastal acidification including biodiversity and biotic interactions (predator-prey, trophic transfer, suspension feeding, benthic-pelagic coupling). Here we have incorporated ideas only based on the ecological effects on living organisms, and we did not include consideration of non-living environments or habitats.

Biodiversity: Biodiversity increases the stability of an ecosystem, known as the general diversity-stability theory (McCann, 2000). One variation under this overarching theory termed the insurance effect theory (McCann, 2000) describes that under low biodiversity conditions, if a key species is lost, there is potential for severe impacts to the food web. This would result in significant changes to an ecosystem (e.g., regime shifts) and ecosystem services (National Research Council, 2010). There is concern that acidification, and interactions with multiple stressors, could reduce biodiversity of the ocean via direct impacts to a species, or indirectly through competitive interactions and linkages in the food web, or decreased habitat once created by key functional species (National Research Council, 2010; Cooley et al., 2012). One experimental study conducted in Plymouth, United Kingdom on a marine invertebrate community of mollusks, arthropods, and nematodes showed decreased biodiversity with increased pH after 60 days (Hale et al., 2011). Furthermore, the changes in community composition anticipated with acidification may pave the way for invasive estuarine or marine species that replace native species (Schmutter et al., 2017). Determining potential climate-change related trends in biodiversity requires long-term ($>$ 20 years) community-scale experiments and long-term carbonate chemistry monitoring, neither of which have been a strong focus of Mid-Atlantic acidification research.

Determining thresholds or critical tipping points for if and when species may be lost, which threatens biodiversity, remain unknown (National Research Council, 2010). Techniques for identifying tipping points before they occur and monitoring for symptoms that may indicate a regime shift are new and young areas of research (National Research Council, 2010) and require attention in the Mid-Atlantic. Attributing changes in biodiversity directly from acidification through ecosystem monitoring remains a challenge due to the presence of mobile organisms and the inability to distinguish between multiple drivers. Additionally, the extent to which individual organisms, populations, communities, and ecosystems are able to acclimate or adapt to current and projected rates of environmental change as described above will be a factor in driving trends in biodiversity over time in the region. Therefore, a combination of long-term ecosystem monitoring and experimental studies will be necessary to overcome methodological challenges and incorporate natural processes and acclimation strategies in order to determine potential trends in biodiversity.

Biotic Interactions: Altered biotic interactions (predator-prey, trophic transfer, suspension feeding, benthic-pelagic coupling) promulgate through populations and communities through compromised food web integrity and energy flow, and these changes in ecosystem structure and function are expressed as regime shifts, decreases in population sizes, and/or changes in water clarity and carbon sequestration (National Research Council, 2010; Cooley et al., 2012). How acidification will affect biotic interactions and how those will play out over time on ecosystem scales is largely unknown. Food web interactions and community dynamics will become more difficult to predict under acidified conditions and thus more difficult to manage (Watson et al., 2017). Experiments seeking to understand the changes to biotic interactions caused by acidification have grown in recent years and have illustrated a variety of potential ways that acidification may impact these relationships. These include: 1) Temporal and spatial shifts in interactions (e.g., shifts in the timing of development relative to food availability) (Lord et al., 2017); 2) Physiological (metabolism, acid-base balance, calcification) changes that influence feeding rates or increase susceptibility to predation (Queirós et al., 2015; Lord et al., 2017; Sadler et al., 2018); 3) Neurological and behavioral impairments in key functional groups that reduce effectiveness of prey detection and capture ability (Dixson et al., 2015; Queirós et al., 2015; Glaspie et al., 2017; Yu et al., 2017); and 4) Limitations of food resources required to fulfill high energetic demands required to cope with acidification (Saba et al., 2012; Seibel et al., 2012; Ramajo et al., 2016; Hurst et al., 2017).

Despite several recent studies, the degree to which biotic interactions will be impacted in general is largely unknown (Glaspie et al., 2017; Kroeker et al., 2017). Determining how changes in these interactions will propagate through the food web and affect other ecosystem services remains a challenge for projecting impacts to upper trophic levels (e.g., marine mammals, sea turtle, sharks). Ecosystem models will be key to address potential acidification impacts of this scale, especially due to limitations in spatiotemporal ocean acidification data and *in situ* systematic ecosystem dynamics. The use of ecosystem models will also aid in the generation of testable hypotheses, which could inform the design and implementation of observations or experimental studies we have not yet identified as a need. We recommend this approach in future studies of populations dynamics and community structure. We also need to understand the degree to which there are or will be alternative prey species available and readily consumable in an ecosystem that could increase resilience to acidification (Cooley and Doney, 2009).

3.6. Connecting Potential Impacts to ecosystem services and the economy

Mid-Atlantic coastal and ocean ecosystems support tourism, recreation, and commerce (including seafood harvests and ancillary industries from marinas to boat repair to accounting); protect coastlines from storms, coastal flooding, and erosion; and recycle nutrients (National Research Council, 2010; Cooley et al., 2009). Potential shifts in composition, structure, and functions of ecosystems impacted by acidification, specifically, changes in abundance, distribution, or size-at-age of target species modifying fishery yields and harvest sustainability calculations, may affect the goods and services those ecosystems provide (National Research Council, 2010). Consequently, potential impacts would influence, and be influenced by, numerous ecological and socioeconomic factors (Ekstrom et al., 2015).

Economic scenario analyses (e.g., Cooley and Doney, 2009; Punt et al., 2014; Cooley et al., 2015) and vulnerability assessments (e.g., Ekstrom et al., 2015; Mathis et al., 2015; Hare et al., 2016) can shed light on the social-economic impacts of potential management decisions that respond to acidification and other drivers. Planning for and developing management strategies that anticipate the changes from acidification can partially mitigate negative socioeconomic impacts, and perhaps take advantage of new opportunities (Schmutter et al., 2017). However, these economic scenario analyses use simple assumptions due the limited data available, leaving a large degree of uncertainty about the projected acidification impacts on a population and harvest levels. Additionally, a unique challenge is that ocean acidification has a long timescale, in which impacts are likely to grow into the foreseeable future (Cooley and Doney, 2009), rather than have short-term impacts that are wholly responsive to year-to-year management adjustments (Cooley et al., 2015). Slower, progressive changes such as those examined for fish responses to warming (Pinsky and Fogarty, 2012) can result in a gradual evolution of ecosystem services. But this can be challenging to plan for (Cooley et al., 2015) and even more challenging to incorporate in management (e.g., Link et al., 2015). Because acidification overlaps with multiple drivers, including nutrient loading, warming temperatures, sea level rise, etc. (Schmutter et al., 2017), marine ecosystem services will be shaped by a combination of forces. Thus, future research looking into potential economic impacts from acidification on the Mid-Atlantic region should consider a wider array of impacts including both direct and indirect ecosystem impacts, multiple stressors, and potential for acclimation or adaptation (Cooley and Doney, 2009). Incorporating additional ecosystem variables and empirical studies into economic models will create more robust predictions through improved model parameterization.

4. Summary of recommended research priorities

The breadth of research conducted thus far has not only been valuable in understanding ecological impacts on Mid-Atlantic species in response to acidification (as summarized here in Table 1), but also in highlighting significant knowledge gaps in our understanding of how acidification impacts the dynamic coastal Mid-Atlantic ecosystem currently and in the future. However, the present combination of highly variable observed responses, small-scale laboratory experiments, and limited species-specific and ecosystem-scale acidification studies hampers researchers' ability to assess the level of impact to be expected from acidification in this region and what that will mean for our coastal communities. Here, we recommend research priorities to fill these gaps:

- *Multiple Drivers of Acidification*:
    - ○ Develop models to quantify the relative controls on coastal acidification: anthropogenic CO_2, eutrophication, temperature, freshwater runoff, SLR
    - ○ Investigate how acidification and climate-induced changes to biological communities will feedback into biogeochemical processes that drive carbonate system dynamics
- *Gaps for Major Taxa*:
    - ○ Conduct a meta-analysis synthesizing existing research on Mid-Atlantic species to quantify biological responses and sensitivities to acidification and multi-stressors
    - ○ Focus studies on regionally important species/life stages that have not yet been investigated for acidification and/or multi-stressor impacts
    - ○ Expand research on target species and life stages considered vulnerable to acidification based on research findings
- *Recommendations for Experimental Design Improvements*:
    - ○ Inclusion of multiple species assemblages
    - ○ Testing responses from multiple stressors
        - Elevated $p\mathrm{CO}_2$, low dissolved oxygen, elevated temperature, etc.
    - ○ Incorporation of natural variability (daily, monthly, seasonal, episodic) of single and multiple stressors
    - ○ Conduct studies to differentiate the causative effect of acidification (changes in $p\mathrm{CO}_2$, pH, and/or saturation state) on an individual organism
- *Acclimation/Adaptation Capacity of Organisms*:
    - ○ Determination of the mechanisms and rates of acclimatization and/or adaptation in regionally important nearshore coastal and offshore species under constant and fluctuating conditions
    - ○ Conduct transgenerational studies on regionally important species
    - ○ Evaluate the role food quantity/quality plays in acclimation potential
- *Ecosystem-level Research Considerations*:
    - ○ Determine thresholds or tipping points for if and when a species may be lost due to ongoing acidification
    - ○ Develop ecosystem models to determine how altered acidification-induced changes in biotic interactions will impact the food web, populations dynamics, and community structure
- *Connecting Potential Impacts to Ecosystem Services and the Economy*:
    - ○ Incorporate additional ecosystem variables into economic models to improve predictions of economic scenario analyses and vulnerability assessments

This document emphasizes research priorities on ecological impacts in the Mid-Atlantic for both practitioners and funding agencies that, if considered, will enable the community to better understand how acidification may impact important habitats and species in the region and be better prepared to manage for an acidifying environment.

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