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JSR SPECIAL SECTION OA PRIMER AND INTRODUCTION

Having watched the flood and ebb of research on shellfish responses to ocean acidification over the past 13 y now, I am struck by the many advances we have made as a community on this topic, as well as the many still outstanding questions we cannot yet conclude.

It has been a privilege serving as a guest editor for this compilation of articles. I first need to thank the seven excellent lead authors for their contributions and patience with the process. These articles help bring attention to advances in ocean acidification research among shellfish biologists and ecologists as well as the many important industry partners who support research and the society that produces this journal. Second, the Ocean Acidification Program of the National Oceanic and Atmospheric Administration helped financially support the publication of these articles. Finally, the shellfish industry partners who have been adapting to our changing ocean and engaging policy makers in Washington DC about the threat and responses to ocean acidification. Their work has helped ensure this topic remains as a high priority in legislative and management realms.

Despite these research and policy efforts, the collective community is still trying to determine how significant this section may in fact be for both commercially and ecologically important shellfish. Ocean acidification came to the forefront of the U.S. West Coast's oyster industry concerns in the late 2000s (Mabardy et al. 2015) when it became clear that despite decades of successful production of Pacific oyster seed in the region's hatcheries, the ocean's chemistry had begun to change in ways previously not experienced (Barton et al. 2015). Although it is well known that the U.S. Pacific Northwest coast experiences seasonal upwelling, bringing with it nutrient- and CO_2-rich waters to the nearshore and estuaries, these hatcheries were only able to continue producing oyster seed by chemically buffering the incoming ocean water (Barton et al. 2015). The addition of anthropogenic carbon to those metabolically active waters pushes the conditions more rapidly across what appear to be proximate thresholds for Pacific oyster larvae both in hatcheries (Barton et al. 2015), and in coastal bays and estuaries of the region (Hales et al. 2017, Pacella et al. 2018). Feely et al. (2016) estimated the increase of anthropogenic carbon in the region's nearshore coastal ocean waters to be greater than 2% of the total dissolved inorganic carbon. This seemingly small increase has lowered the median saturation state of the coastal upwelled waters by ~0.5 units (Harris et al. 2013) and reduces the ability to buffer natural fluctuations on short time scales (Pacella et al. 2018). It is the amplification of the natural conditions from a changing baseline CO_2 that upended the region's oyster hatcheries and because improving the carbonate chemistry has restored a large majority of the previously lost production capacity (Barton et al. 2015).

In a longer geologic perspective, our current understanding of the rates of change in marine chemistry due to increasing anthropogenic CO_2 are unparalleled in at least the past 1 million years from direct measures of CO_2 in ice cores (Higgins et al. 2015) and from the past 66 million years using various proxies (Zeebe et al. 2016). Importantly, it is not the absolute amount of CO_2 in the atmosphere that is the section regarding ocean acidification; the increase is faster now than any of the earth's natural systems can counter or buffer that change (Hönisch et al. 2012). In fact, very recent research on the impact of the Chicxulub meteor that is attributed with causing the mass extinction at the Cretaceous–Paleogene boundary (66 million years ago) has been found to have caused similarly ''rapid'' acidification of the world's oceans (Henehan et al. 2019). The acidification event that occurred was estimated to have been 0.25 pH units decrease over less than 1,000 y, with the result of an equally rapid decline in calcified foraminifera in the fossil record (Henehan et al. 2019). Although the cause of the shift in ocean acid–base chemistry was not believed to be chemically identical to the current anthropogenic source of acidification, the rate of change is within the bounds of what is currently happening. Estimates put the change in oceanic pH at about 0.1 unit in the past 200 y; much of this change occurring in the last 50–70 y, with more rapid changes predicted with our current projections of CO_2 emissions. Acknowledging this geologic perspective on ocean acidification should elicit a pause to recognize since the fall of the dinosaurs, the animals we have in our oceans have never experienced a baseline shift in chemistry such as is currently happening.

The following is intended to provide a simple primer on carbonate chemistry, and, in particular, how it related to ocean acidification. Others have provided a far more comprehensive treatment of this topic (Zeebe & Wolf-Gladrow 2001); here, the intent is simply to remind the readers of some of the basics. The late Lars Gunar Sillen noted that the ocean's chemistry on geologic timescales results from a balance between acids leaking from the earth's interior and the basic weathering products from rocks on land, maintaining the pH of the ocean at a slightly basic condition. Thus, the reason we focus so much on carbonate chemistry is that it is the acid–base system in greatest concentration in the ocean and with active changes in speciation in the pH range of typical marine waters. In other words, other acid–base systems do not really matter much in most marine waters. Therefore, it is critical to note pH is technically only an indicator of the acid–base status of water; a function of the relative concentrations of linked acid and base systems, which are driven by natural (and anthropogenic) processes. So while one frequently sees plots of pH on an *x*-axis and the concentrations of inorganic carbon species on a *y*-axis (a Berjjum plot), it is incorrect to infer that pH is driving the distribution of the dissolved inorganic carbon species (dissolved CO_2, bicarbonate, and carbonate ions). The only cases where a system other than the dissolved inorganic carbon system is altering pH in significant ways is where other acids or bases are added to the system in large quantities, such as what appears to have happened from the meteor impact 66 million years ago (Henehan et al. 2019). It would be incorrect, however, to not recognize other systems will alter the acid–base status, but in most cases, only in small degrees relative to the carbonic acid system. So, returning to Dr. Sillen's note, then the pH of the ocean varies roughly as the ratio of CO_2 and carbonate ion (CO_3^{2-}) varies, on daily time scales from photosynthesis/respiration and calcification/dissolution

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of calcium carbonate, to geologic time scales from volcanism and weathering.

Whereas we have established pH as being an indicator of acid–base status, alkalinity often confounds those wading into carbonate chemistry and ocean acidification research. Total or titration alkalinity is simply the ability of the system to resist changes to pH from addition of acids. In the most precise definition, alkalinity is the sum of the charges of conjugate bases of weak acids with a pK (dissociation constant) greater than 4.5 (Dickson 1981). In other words, they have a propensity to accept protons in natural waters (and thus limit decreases in pH). In most marine waters, this means bicarbonate plus two times carbonate, plus the minor contribution of borate, with bicarbonate making the largest total contribution to the total alkalinity. As total alkalinity increases, the effect of increasing CO_2 on pH decreases, and thus, in part probably why the reef-forming bivalves called rudists were able to evolve during the Cretaceous period (and a majority of other calcium carbonate minerals were formed), when atmospheric CO_2 was generally far more elevated than today. It is estimated that the ocean's total alkalinity may have been twice the current levels during the Cretaceous (Zeebe 2001). A greater understanding of buffering capacity or resisting changes in carbonate chemistry highlights some current research that has demonstrated the effect of increasing anthropogenic carbon on the ability of marine waters to buffer natural fluctuations on seasonal (Kwiatkowski & Orr 2018, Landschutzer et al. 2018) and daily (Pacella et al. 2018) timescales. Although the increase in anthropogenic carbon does not directly alter total alkalinity, it does reduce the buffering efficacy (by reducing the number of carbonate ions), and thus amplifying natural fluctuations. Both Kwiatkowski and Orr (2018) and Pacella et al. (2018) estimated this reduction in buffering efficiency from increasing baseline CO_2 will lead to a more rapid change in the poorest chemistry conditions relative to changes in average conditions.

A remaining carbonate chemistry parameter that is notable is the saturation state of calcium carbonate: the corrosivity of water to that mineral. Under current rates of change in CO_2, the decline in pH and saturation state (noted by Ω) are coupled in their decline; under less rapid changes in CO_2, rates of rock weathering can keep up delivering more carbonates to the ocean, and Ω may, therefore, be stable or even increase, with rates of CO_2 increasing more akin to what has happened in the geologic past (Hönisch et al. 2012). The current rates of acidification have already caused significant changes in Ω and moved parts of the ocean that are already natural elevated in CO_2 closer to being corrosive (Harris et al. 2013, Feely et al. 2016). Shell-forming (calcium carbonate) organisms have generally been implicated as being most vulnerable to OA (Kroeker et al. 2013); the exact mechanisms for the physiological impacts of OA on biocalcification continue to be debated (*sensu* Cyronak et al. 2016, Waldbusser et al. 2016a). Saturation state is correlated with the ratio of bicarbonate to protons (the substrate and potential inhibitor of calcification), called SIR, so work is still needed to tease apart these variables more cleanly. It is also quite possible that there will not be a singular answer to this question, as OA appears to have multiple modes of action on bivalve larvae (Waldbusser et al. 2015). A more holistic understanding of physiological mechanisms or better designed research will help the community better understand physiological mechanisms for OA impacts on marine organisms.

Carbonate chemistry may seem elusive to some; however, biological responses to changes in carbonate chemistry, and ultimate ecosystem effects are even more challenging to constrain. History demonstrates that the current rate ocean acidification will likely have significant effects on a great many marine organisms, and myriad laboratory experiments and some field studies demonstrate this to be true. Exceptions always occur. Biology may and will find some ways to compensate for these disturbances to the chemical habitat in which they reside. Resilience may come through rapid evolution due to strong selection pressure of the environment *via* genetic adaptation or by selective breeding promoting lines that appear to have more capacity to cope with change (Durland et al. 2019). In other cases, some species may already contain traits (presumably evolved for other reasons) to allow them to thrive in a new environment (Waldbusser et al. 2016b) *via* exaptation. These potential bright spots do not alleviate us from the global responsibility to protect and sustainably manage our marine resources, nor to understand the extent and types of impacts we should anticipate.

The articles published in this section on ocean acidification impacts on shellfish come from a group of shellfish biologists whom are exploring some of the more challenging questions our community faces. These studies provide the more subtle nuance and insight needed to understand the responses of organisms, the mechanisms for possible recovery or resistance to OA, and the application of techniques that the industry may use as they continue to face and adapt to this ever-increasing section for aquaculture.

Most studies published in this section focus on bivalves, perhaps in part because in general bivalves (and molluscs) have been found to be less resistant to acute effects of ocean acidification in laboratory studies. Unfortunately, our crustacean friends have been studied far less. Glandon et al. help to fill this gap with results from multistressor experiments (temperature and acidification) on blue crab respiration. The authors found that under a 30-day acclimation period, respiration did not respond to elevated temperature or $P_{CO2;}$ however, short-term thermal shock experiments did find a nearly doubling in respiration rate relative to similar temperature treatment in the acclimation study. An important conclusion of the study is that although these blue crabs seem very capable of acclimating to more gradual changes, the understanding of how acute weather-scale changes may affect estuarine organisms is still lacking. Examining the more subtle behavioral responses of three different phyla, Clements and Comeau conducted a quantitative and qualitative review of 34 studies on prey responses to acidification. The authors found negative behavioral responses in bivalve molluscs and malacostracan crustaceans, positive responses in cephalopods, and no response in gastropods and echinoids. A fascinating component of these types of nonlethal effects of acidification exposure is the potential role for highly conserved (across the animal kingdom) neurotransmitter interference, with γ-aminobutyric acid ($GABA_A$) function being affected. Another looming question from this work is: How may these behavioral responses propagate into population or ecosystem scale effects?

Venkataraman et al. present results of a carryover study of adult exposure effects on larvae. Although there are now conflicting studies to date whether adult bivalve exposure may precondition larvae to perform better under acidification, the authors demonstrate that a 7-wk exposure of adult Pacific

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oysters results in fewer larvae surviving to the D-hinge stage nearly 4 mo later. Given the well-documented ocean acidification impacts on the Pacific oyster industry in the U.S. Pacific Northwest, the authors highlight the need to carefully consider adult exposure in aquaculture operations, as well as the broader ecosystem scale implications should these findings hold true for other species.

Delving deeper into physiological mechanisms, two of the studies presented here examine the internal fluids or conditions within bivalves relative to changes in water chemistry. *Gray et al*. proffer the question whether brooding oysters prepare their young for a future high CO_2 world by the simple fact that in the brooding chamber, early larvae must tolerate some potentially harmful levels of acidification due to metabolism. The authors find that pH in the brooding chamber of the European flat oyster is correlated with seawater pH, but is always lower, and pH declines rapidly in the brooding chamber once ventilation ceases. But, a better characterization of the complete carbonate chemistry of brooding chambers and evolutionary advantages of brooding versus broadcast spawning bivalves are needed. In a similar vein, Cameron et al. explored changes in extra pallial fluid pH and calcification under temperature and acidification in the King scallop. Whereas the authors found that pH did change with seawater pH, those changes were not consistent across different temperatures, and suggest regulation of extra pallial fluid pH could not explain entirely how the scallops were maintaining calcification under elevated CO_2. Interestingly, higher temperatures seemed to mitigate acidification effects, suggesting that this species may be resilient to climate change impacts.

The final three articles in the section are more directly related to aquaculture and stakeholder interests. The emerging green-lipped mussel hatchery effort to bolster declining natural recruitment of the species in New Zealand has been an overwhelming success story. Fundamental work is, however, needed (and perhaps now easier given hatchery supply of larvae) to understand how to alter hatchery chemistry for improved larval production. Ragg et al. provide results from a study examining larval survivorship under six levels of saturation state, at both the D-hinge and later veliger stages. The authors provide a lot of results to unpack, but the really interesting findings were moderate levels of buffering appeared to improve growth and survivorship, and acidification treatments or over-buffering had very deleterious effects. In addition, these effects, if applied during early larval development, resulted in significant decreases in later larvae held in control conditions, demonstrating a very significant carryover effect from the early larval exposure. In a study of blue mussel attachment mechanics to aquaculture ropes, George et al. found that conditions infrequently experienced by mussels in farmed conditions could contribute to ''fall-off'' effects, given some of the conditions experienced in late summer in their system. Mechanistic studies are always so satisfying; the authors examined the actual plaque hardening associated with byssal thread attachment. In their experimental conditions, the very lowest of pH conditions experienced within the farmed mussels would delay hardening of the plaque adhesives, and transient hypoxia events could temporarily weaken plaques, even after fully cured. In a second submission, Clements and Comeau explore the use of a noninvasive biosensor, high-frequency, noninvasive electromagnetic-based biosensors, to detect valve-gaping responses in marine bivalves. The authors provide a review of the development and application of the technology, with current limitations. One aspect the authors note is the potential to use these sensors on shellfish in aquaculture settings; however, they note the limited studies to date find valve gaping to be generally insensitive to moderate changes in carbonate chemistry. The authors lead one to think more deeply about approaches for aquaculture operations to take advantage of their target species as sentinels in an early warning system.

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