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Review

Effects of CO_2-driven sediment acidification on infaunal marine bivalves: A synthesis

Jeff C. Clements [a,b,*], Heather L. Hunt [b]

[a] Department of Health Management, Atlantic Veterinary College, University of Prince Edward Island, 550 University Avenue, Charlottetown, Prince Edward Island C1A 4P3, Canada
[b] Department of Biological Sciences, University of New Brunswick, 100 Tucker Park Road, PO Box 5050, Saint John, New Brunswick E2L4L5, Canada

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ABSTRACT

While ocean acidification (OA) effects on marine organisms are well documented, impacts of sediment acidification on infaunal organisms are relatively understudied. Here we synthesize CO_2-driven sediment acidification effects on infaunal marine bivalves. While sediment carbonate system conditions can already exceed near-future OA projections, sediments can become even more acidic as overlying seawater pH decreases. Evidence suggests that infaunal bivalves experience shell dissolution, more lesions, and increased mortality in more acidic sediments; effects on heavy metal accumulation appear complex and uncertain. Infaunal bivalves can avoid negative functional consequences of sediment acidification by reducing burrowing and increasing dispersal in more acidic sediments, irrespective of species or life stage; elevated temperature may compromise this avoidance behaviour. The combined effects of sediment acidification and other environmental stressors are virtually unknown. While it is evident that sediment acidification can impact infaunal marine bivalves, more research is needed to confidently predict effects under future ocean conditions.

Contents

1. Introduction

While a variety of habitats exist throughout the world's oceans, the majority of the ocean bottom is covered in loose sediments (Snelgrove, 1999). Soft-sediment habitats are large contributors to ecosystem functioning in marine coastal areas (Gattuso et al., 1998). These habitats also house a substantial amount of marine biodiversity both above (epifaunal) and below (infaunal) the sediment surface, including a suite of deposit- and suspension-feeding bivalves. Infaunal marine bivalves can play important ecological and economic roles in the areas in which they reside. Bivalves have long been known to be important structuring agents in benthic freshwater and marine ecosystems (Rex, 1981, Vaughn and Hakenkamp, 2001, Strayer and Malcolm, 2007).

* Corresponding author at: Department of Health Management, Atlantic Veterinary College, University of Prince Edward Island, 550 University Avenue, Charlottetown, Prince Edward Island C1A 4P3, Canada.
E-mail address: jefferycclements@gmail.com (J.C. Clements).

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Their calcium carbonate shells supply other organisms with a refuge from predators and various other stressors, and can provide suitable substrate for the settlement and attachment of various epibionts. Additionally, their feeding activity can direct solute and particle transport and affect the larval settlement of numerous benthic organisms (Ertman and Jumars, 1988, Gutierrez et al., 2003). Through the uptake and release of carbon dioxide (CO_2) and calcium (Ca) during shell production and dissolution respectively, bivalves also play a vital role in the cycling of these elements within their communities, making them, and other hard-shelled molluscs, important in shaping the dynamics of the benthic marine habitats in which they reside (Green, 1980). Infaunal bivalves are socioeconomically important as well (e.g. soft-shell clams, *Mya arenaria*, and northern quahogs, *Mercenaria mercenaria* in northeastern North America). Given that infaunal marine bivalves provide important ecological services in marine habitats and are important socioeconomically in coastal areas, it is necessary to understand the biological and environmental processes that can influence their ecology, as well as current and future risks to their well-being.

Ocean acidification is one potential threat to infaunal marine bivalves. Ocean acidification is a predictable outcome of elevated atmospheric CO_2 concentrations, whereby the dissolution of atmospheric CO_2 into the oceans results in a decrease in surface ocean pH (Doney et al., 2009). It is well known that ocean acidification poses a threat to marine molluscs, including a suite of infaunal and epifaunal marine bivalves (see review by Gazeau et al., 2013). However, such effects are typically described only in the context of water column acidification, even though infaunal species reside below the sediment-water interface and are exposed to drastically different pH and carbonate system conditions in the sediment (see Section 2).

Sediment porewater is known to have a higher pH buffering capacity than seawater in the water column (Leclercq et al., 2002, Andersson et al., 2003). Consequently, it has been largely assumed that infaunal organisms are more resilient to the effects of ocean acidification (see Widdicombe et al., 2011 for review). Indeed, studies have shown that various infaunal organisms appear robust to changes in seawater pH and carbonate geochemistry, including polychaetes (Batten and Bamber, 1996, Widdicombe et al., 2009), nematodes (Widdicombe and Needham, 2007), sea urchins (Dashfield et al., 2008), and brittlestars (Wood et al., 2009). In contrast, owever, recent work has documented that sediment acidification can indeed impact infaunal organisms, with much of this work focusing on infaunal marine bivalves (Green et al., 2004, 2009, 2013, Clements and Hunt, 2014, Rodríguez-Romero et al., 2014, Clements et al., 2016). This suggests that a clearer understanding of the effects of sediment pH and carbonate chemistry on infaunal bivalves is necessary, particularly in light of the need to make predictions about the effects of ocean acidification on infaunal species. Consequently, a synthesis of current knowledge pertaining to the effects of sediment acidification on infaunal marine bivalves is warranted. Here we describe the drivers of sediment acidification and its links to ocean acidification, synthesize the biological effects of sediment acidification on infaunal marine bivalves, elucidate critical unknowns, and suggest directions for future research.

2. A primer on the drivers of CO_2-induced sediment acidification

In most marine systems, sediment porewater pH and carbonate saturation state (a measure of the capacity of seawater to precipitate calcium carbonate; saturation state is influenced by pH, temperature, salinity, and pressure; >1 = supersaturation, 1 = saturation, <1 = undersaturation) is usually much lower than that of overlying water (Northwest Atlantic: Hales et al., 1994, Hales and Emerson, 1996, Green and Aller, 1998, Green et al., 2009; California coast: Cai and Reimers, 1993). Sediment pH typically ranges from ~6.5–8.2 (Widdicombe et al., 2011; although conditions can exceed the extremes of this range), and sediments often exhibit strong gradients in pH and carbonate saturation state, with a steep and continual decrease in pH at the sediment surface until a depth at which the pH stabilizes (Figs. 1, 2A; Widdicombe et al., 2011). However, depth gradients do not always follow this particular pattern, as pH and carbonate saturation state can indeed increase with depth (see Green et al., 2004, 2009 for examples), particularly as overlying water pH decreases (Fig. 2A; Widdicombe et al., 2011).

Sediment pore-water pH and associated carbonate geochemical conditions are primarily controlled by the decomposition of organic matter by microbial fauna (Widdicombe et al., 2011). Given that microbes in the surface sediment are primarily aerobic respirators, they consume O_2 and produce CO_2 as they decompose large amounts of organic matter that can build up at the sediment surface. In poorly-oxygenated sediments, this CO_2 can build up and reduce surface-sediment pH (Fig. 2B). If aerobic respiration via organic matter decomposition contributes more to pH reduction than processes occurring in deeper sediments, surface sediment porewater pH and carbonate geochemistry may become more acidic than deeper sediments. As microbial activity slows down and/or as sediment reworking increases, sediments can most often recover to pre-decomposition pH conditions. As a result of these processes, considerable variation in surface-sediment pH can be observed, spanning across basic and acidic conditions (pH ~ 6.5–8.2; Widdicombe et al., 2011).

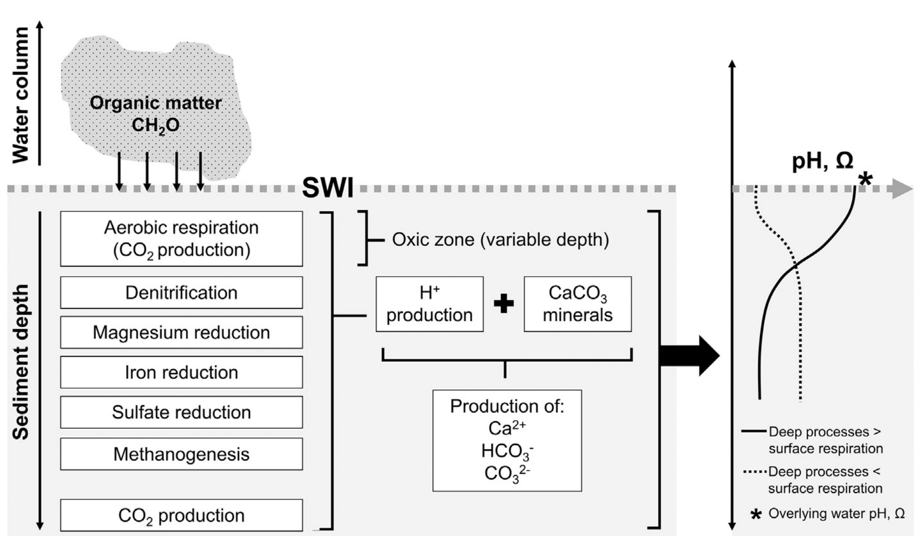

Fig. 1. Conceptual diagram of the diagenetic processes influencing sediment pH and carbonate chemistry. Modified from Widdicombe et al. (2011). SWI = sediment-water interface.

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