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Habitat effects of macrophytes and shell on carbonate chemistry and juvenile clam recruitment, survival, and growth

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ABSTRACT

Adverse habitat conditions associated with reduced seawater pH often, but not always, negatively affect bivalves in early life history phases. Improving our understanding of how habitat-specific parameters affect clam recruitment, survival, and growth could assist natural resource managers and researchers in developing appropriate adaptation strategies for increasingly acidified nearshore ecosystems. Two proposed adaptation strategies, the presence of macrophytes and addition of shell hash, have the potential to raise local seawater pH and aragonite saturation state and, therefore, to improve conditions for shell-forming organisms. This field study examined the effects of these two substrate treatments on biological and geochemical response variables. Specifically, we measured (1) recruitment, survival, and growth of juvenile clams (*Ruditapes philippinarum*) and (2) local water chemistry at Fidalgo Bay and Skokomish Delta, Washington, USA, in response to experimental manipulations. Results showed no effect of macrophyte or shell hash treatment on recruitment or survival of *R. philippinarum*. Contrary to expectations, clam growth was significantly greater in the absence of macrophytes, regardless of the presence or absence of shell hash. Water column pH was higher outside the macrophyte bed than inside at Skokomish Delta and higher during the day than at night at Fidalgo Bay. Additionally, pore-water pH and aragonite saturation state were higher in the absence of macrophytes and the presence of shell. Based on these results, we propose that with increasingly corrosive conditions shell hash may help provide chemical refugia under future ocean conditions. Thus, we suggest adaptation strategies target the use of shell hash and avoidance of macrophytes to improve carbonate chemistry conditions and promote clam recruitment, survival, and growth.

1. Introduction

The absorption of anthropogenic carbon dioxide (CO_2) into seawater results in decreased pH, reduced availability of carbonate ions, and lower saturation states of the biominerals organisms use to construct shells and skeletons (Caldeira and Wickett, 2003; Doney et al., 2009; Feely et al., 2004). Studies examining the biological effects of these chemical changes, termed ocean acidification (OA), indicate that bivalves in early developmental stages are most vulnerable to OA (e.g., Gazeau et al., 2013; Kroeker et al., 2013; Parker et al., 2013). Known negative impacts include increased energy demands, impaired neurological functioning, altered behavior, and shell dissolution which can reduce growth and survivorship (Green et al., 2013; Kurihara, 2008; Waldbusser et al., 2015). Although adequate food supply can offset additional energetic costs caused by environmental stress (Hettinger et al., 2013a; Melzner et al., 2011; Parker et al., 2013), a recent study found that the initiation of feeding is delayed when pCO_2 is elevated (Waldbusser et al., 2015). Energetic deficits in early life-history stages may affect bivalve population dynamics either through a reduction in successful recruitment to adult populations (e.g., Melzner et al., 2011; Parker et al., 2013) or through negative carry-over effects that may impair the fitness of adult populations (Hettinger et al., 2013b).

Under moderate carbon emission projections, pH is expected to decline by 0.2–0.3 units by 2100 (IPCC, 2014). Therefore, resource managers are seeking strategies to ameliorate the impacts of OA on culturally, economically, and ecologically-important marine organisms such as bivalves (Rau et al., 2012; WABRPOA, 2012). Because habitat structure in coastal environments can influence survival and growth of

Abbreviations: RSG, recruitment survival and growth

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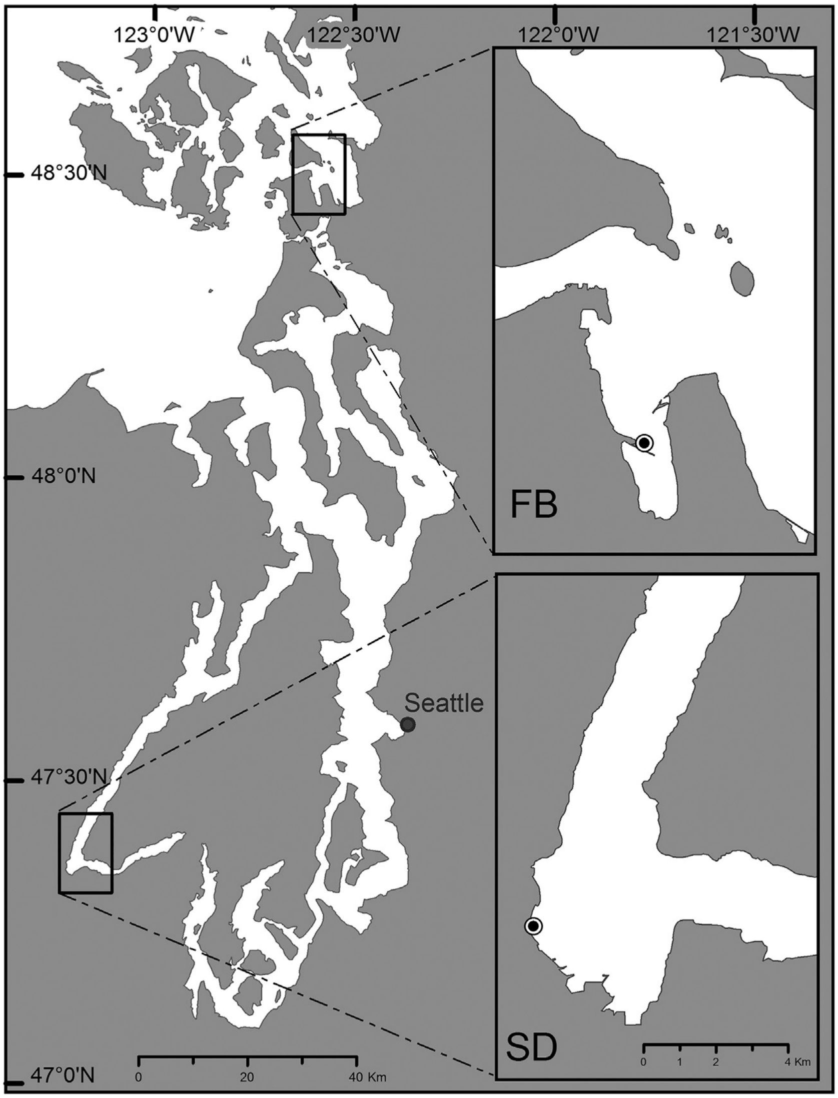

Fig. 1. Map of study sites (◉) in Fidalgo Bay (FB) and Skokomish Delta (SD), Washington, USA.

juvenile invertebrates (McDevitt-Irwin et al., 2016; Walters and Wethey, 1996), two habitat modifications have been proposed to mitigate future OA impacts on clams. The first strategy is the addition of shell hash (broken shell) to intertidal clam beds (Billé et al., 2013; Rau et al., 2012; WABRPOA, 2012). Beach coarsening with crushed shell and gravel is known to promote natural recruitment and growth in hardshell clams by increasing substrate stability and interstitial space as well as protecting juvenile clams from predation (Ruesink et al., 2014; Thompson, 1995; Toba et al., 1992). The presence of crushed shell may also increase total alkalinity locally, neutralizing CO_2 in the overlying water and increasing biomineral saturation states in sediment pore-water (Green et al., 2013, 2009). Although some laboratory and field experiments on juvenile clams have found higher recruitment and survival in sediment with crushed shell (e.g., Clements et al., 2016; Green et al., 2009), other research has found no difference in recruitment or survival between gravel versus shell-enhanced plots (Ruesink et al., 2014; Toba et al., 1992). These differing results suggest that both sediment grain size and sediment pH can influence clam abundance; however, sediment pH may become increasingly important as organisms are exposed to more extreme carbonate chemistry conditions.

A second OA adaptation strategy is the restoration or introduction of photoautotrophs, such as seagrass and macroalgae (collectively termed macrophytes), near shellfish beds (Billé et al., 2013; Hendriks et al., 2015; WABRPOA, 2012). While the structural presence of emergent macrophytes provides shelter for bivalves from predators and desiccation (Coleman and Williams, 2002; Peterson et al., 1984), recent studies suggest macrophytes may also act as a chemical refuge for calcifying organisms. Via photosynthesis, macrophytes exhibit the ability to draw down CO_2 in seawater and increase pH and aragonite saturation state ($\Omega_{aragonite}$), potentially enhancing the calcification processes of co-existing organisms (Buapet et al., 2013; Hendriks et al., 2014; Unsworth et al., 2012). However, the effectiveness of this phytoremediation as an OA adaptation technique for bivalves remains unclear. The magnitude of any buffering effect caused by aerobic photosynthesis within a macrophyte bed is likely to be site specific and would depend on a variety of factors, including structural parameters of the bed, local hydrodynamics, and aerobic respiration, (Cryonak et al., 2018; Hendriks et al., 2014). Moreover, studies investigating the effects of macrophyte presence on clam growth have reported conflicting results (e.g., Everett, 1994; Irlandi and Peterson, 1991; Tsai et al., 2010).

While there is limited research investigating the independent effects of these two potential OA adaptation strategies (i.e., adding shell hash to a beach or restoring macrophyte populations near clam beds), to our knowledge, even fewer studies have integrated the two strategies (but see Ruesink et al., 2014), and no studies have examined their combined effects on both bivalve performance and local seawater chemistry. Therefore, we designed a field experiment that incorporated these two strategies as substrate treatments to investigate their effect on clam