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Insights from sodium into the impacts of elevated pCO_2 and temperature on bivalve shell formation

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ABSTRACT

Ocean acidification and warming are predicted to affect the ability of marine bivalves to build their shells, but little is known about the underlying mechanisms. Shell formation is an extremely complex process requiring a detailed understanding of biomineralization processes. Sodium incorporation into the shells would increase if bivalves rely on the exchange of Na^+/H^+ to maintain homeostasis for shell formation, thereby shedding new light on the acid-base and ionic regulation at the calcifying front. Here, we investigated the combined effects of seawater pH (8.1, 7.7 and 7.4) and temperature (16 and 22 °C) on the growth and sodium composition of the shells of the blue mussel, *Mytilus edulis*, and the Yesso scallop, *Patinopecten yessoensis*. Exposure of *M. edulis* to low pH (7.7 and 7.4) caused a significant decrease of shell formation, whereas a 6 °C warming significantly depressed the rate of shell growth in *P. yessoensis*. On the other hand, while the amount of Na incorporated into the shells of *P. yessoensis* did not increase in acidified seawater, an increase of Na/Ca_{shell} with decreasing pH was observed in *M. edulis*, the latter agreeing well with the aforementioned hypothesis. Moreover, a combined analysis of the shell growth and sodium content provides a more detailed understanding of shell formation processes. Under acidified conditions, mussels may maintain more alkaline conditions favorable for calcification, but a significant decrease of shell formation indicates that the mineralization processes are impaired. The opposite occurs in scallops; virtually unaffected shell growth implies that shell mineralization functions well. Finding of the present study may pave the way for deciphering the mechanisms underlying the impacts of ocean acidification and warming on bivalve shell formation.

1. Introduction

Rapidly increasing anthropogenic CO_2 emissions are not only resulting in ocean warming, but also ocean acidification (OA) and altered seawater carbonate chemistry (Doney et al., 2009). These changing environmental conditions may have widespread implications for marine biota, especially bivalve mollusks (Kroeker et al., 2010; Rodolfo-Metalpa et al., 2011; Hendriks et al., 2015). There is mounting evidence that OA can impair the capacity of marine bivalves to produce their shells, leading to reduced calcification and growth rates (Gazeau et al., 2013; Kroeker et al., 2013; Waldbusser et al., 2014; Milano et al., 2016) and, in extreme cases, decalcification and mortality (McClintock et al., 2009; Gazeau et al., 2013). Furthermore, the negative effects of OA on shell mineralization may have significant functional and ecological implications. Reduced shell mechanical properties may increase the susceptibility to predation and, ultimately, alter the predator-prey dynamics in marine ecosystems (Gaylord et al., 2011; Schalkhausser et al., 2013; Kroeker et al., 2014).

OA does not act in isolation but usually interacts with other environmental stressors, specifically temperature (Pörtner and Farrell, 2008; Kroeker et al., 2013). The interactive effects of OA and temperature, which can be antagonistic or synergistic, may shape highly variable responses of marine bivalves to near-future climate change scenarios. For example, elevated temperature, within the thermal tolerance window, may alleviate the detrimental effects of OA on bivalve shell formation (Parker et al., 2009; Ko et al., 2014; Li et al., 2016) and, conversely, may exacerbate these threats (Hiebenthal et al., 2013; Schalkhausser et al., 2013; Li et al., 2015). Evidently, predicting the impacts of elevated pCO_2 and temperature on marine bivalves is fraught with great difficulty given the complexity and diversity of the responses observed. Therefore, it becomes critical to gain a better understanding of the processes and mechanisms determining their sensitivity and resilience to ocean acidification and warming.

Biomineralization of bivalve shells takes place in the extrapallial fluid (EPF), a thin film of liquid between the outer mantle epithelium (OME) and the calcifying shell (Wheeler, 1992). Bivalve mollusks can elevate the pH of the EPF to facilitate inorganic $CaCO_3$ precipitation (Crenshaw and Neff, 1969). For example, the oyster *Crassostrea gigas* appears to alkalinize the EPF by ca. 0.23 pH unit during the growing season (Wada and Fujinuki, 1976). Over a tidal cycle, the formation of shell

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