



Sodium provides unique insights into transgenerational effects of ocean acidification on bivalve shell formation



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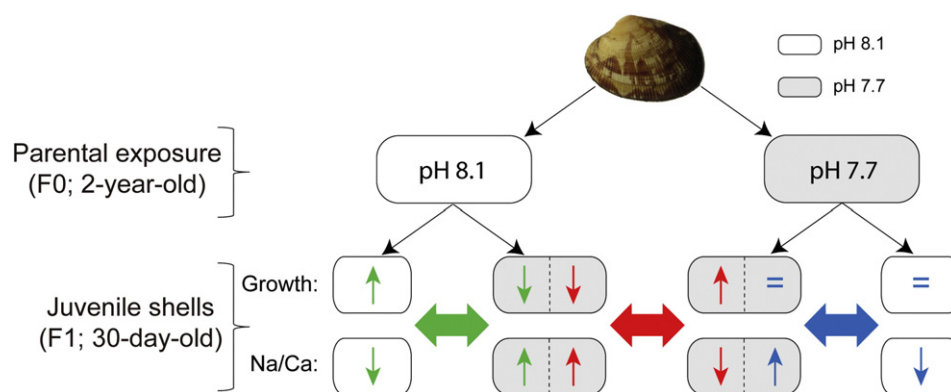
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HIGHLIGHTS

- Transgenerational effects alleviate the impacts of high CO₂ on bivalve shell formation.
- At pH 7.7, Na/Ca_{shell} decreases significantly following transgenerational exposure.
- Na/Ca_{shell} sheds new light on the mechanisms for such acclimation.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:

Received 11 July 2016

Received in revised form 11 October 2016

Accepted 25 October 2016

Available online 4 November 2016

Editor: D. Barcelo

Keywords:

Bivalve shells

Ruditapes philippinarum

Sodium-to-calcium

Ocean acidification

Transgenerational effects

ABSTRACT

Ocean acidification is likely to have profound impacts on marine bivalves, especially on their early life stages. Therefore, it is imperative to know whether and to what extent bivalves will be able to acclimate or adapt to an acidifying ocean over multiple generations. Here, we show that reduced seawater pH projected for the end of this century (i.e., pH 7.7) led to a significant decrease of shell production of newly settled juvenile Manila clams, *Ruditapes philippinarum*. However, juveniles from parents exposed to low pH grew significantly faster than those from parents grown at ambient pH, exhibiting a rapid transgenerational acclimation to an acidic environment. The sodium composition of the shells may shed new light on the mechanisms responsible for beneficial transgenerational acclimation. Irrespective of parental exposure, the amount of Na incorporated into shells increased with decreasing pH, implying active removal of excessive protons through the Na⁺/H⁺ exchanger which is known to depend on the Na⁺ gradient actively built up by the Na⁺/K⁺-ATPase as a driving force. However, the shells with a prior history of transgenerational exposure to low pH recorded significantly lower amounts of Na than those with no history of acidic exposure. It therefore seems very likely that the clams may implement less costly and more ATP-efficient ion regulatory mechanisms to maintain pH homeostasis in the calcifying fluid following transgenerational acclimation. Our results suggest that marine bivalves may have a greater capacity to acclimate or adapt to ocean acidification by the end of this century than currently understood.

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1. Introduction

During the past 250 years, atmospheric carbon dioxide (CO₂) concentrations have increased by nearly 40% due to human activities (Doney et al., 2009). Approximately one third of anthropogenic CO₂ emissions has entered the oceans, reducing ocean pH and driving unprecedented changes in seawater carbonate chemistry (IPCC, 2013). This phenomenon, termed ocean acidification (OA), is predicted to have widespread implications for calcifying organisms (Orr et al., 2005; Hendriks et al., 2010; Bach, 2015). Juvenile specimens are particularly vulnerable to lower pH levels (Kroeker et al., 2013). There is ample evidence that OA may impair the ability of pelagic larvae and early juveniles to produce their skeletal structures, leading to developmental delay and high mortality (e.g., Kurihara, 2008; Parker et al., 2009; Stumpp et al., 2013; Waldbusser et al., 2014).

Profound effects of OA occurring at one stage of life may generate negative or positive carry-over effects in subsequent life stages. For example, Hettinger et al. (2012, 2013) found that OA had detrimental effects on larval growth and survival of tank-grown specimens of the Olympia oyster, *Ostrea lurida*, and these effects persisted into the juvenile stage and continued for another four months even when they were transferred to the natural environment. In contrast, positive carry-over effects have been observed in the bay scallop, *Argopecten irradians*, and the hard clam, *Mercenaria mercenaria* (Gobler and Talmage, 2013). Juveniles of both species reared at elevated pCO₂ during larval development grew faster under natural conditions compared to those exposed to ambient pCO₂ (= current ocean pH of 8.1). Given that many calcifying species such as mollusks have complex life cycles, it is essential to investigate carry-over effects during all life stages. Furthermore, it is relevant to know if such carry-over effects can possibly persist into the next generation (Ross et al., 2016). Such information is critical for understanding whether marine biota will be able to acclimate and/or adapt to long-term OA exposure.

Environmental stress experienced by parents may alter the response of their offspring to harsh environmental conditions, a phenomenon known as transgenerational epigenetic effect (Youngson and Whitelaw, 2008). A growing body of evidence suggests that transgenerational effects, i.e., carry-over effects from parents to offspring, might confer environmental resilience to the offspring if they are subjected to the same environmental situation as their parents (Marshall, 2008; Marshall and Morgan, 2011; Ross et al., 2016). Such acclimation is of paramount importance for marine calcifiers to cope with OA as it can occur over much shorter time frames. Markedly increased growth rates, survival rates and fecundity in subsequent generations through transgenerational epigenetic effects have been reported from calcifying species with short generation times such as coccolithophores (Lohbeck et al., 2012) and copepods (e.g., Fitzer et al., 2012; De Wit et al., 2015; Thor and Dupont, 2015) that were exposed to elevated CO₂-levels. However, relevant studies on calcifiers with relatively long generation times such as bivalve mollusks are very limited (Ross et al., 2016). Parker et al. (2012, 2015) demonstrated positive transgenerational effects on growth and physiological performances of the Sydney rock oyster, *Saccostrea glomerata*, whereas the underlying mechanisms are still not fully understood (Gonalves et al., 2016).

Amongst others, shells provide protection against predators. However, OA may seriously impair physical properties of the shells (Beniash et al., 2010; Fitzer et al., 2014; Milano et al., 2016). In particular, the maintenance of larval and juvenile shell integrity becomes much more difficult when subjected to lowered seawater pH and saturation state (Fitzer et al., 2014; Waldbusser et al., 2014), thereby increasing the susceptibility of bivalves to predation (Kroeker et al., 2014). Since rapid juvenile growth after larval settlement and metamorphosis is the most important factor affecting molluscan recruitment success (Gosling, 2003), elucidating the mechanisms driving decreased shell growth under OA conditions can provide a better understanding of how OA will affect the recruitment and population dynamics of bivalves.

Following larval settlement and metamorphosis and the formation of the mantle tissue, the mineralization of juvenile and adult bivalve shells takes place in the extrapallial space (EPS) which is located between the outer mantle epithelium (OME) and the calcifying shell (Wheeler, 1992). During the growing season, bivalves can actively elevate the pH of the EPS, which facilitates the (inorganic) precipitation of CaCO₃, and stimulate the synthesis and secretion of organic matrix by the OME which in turn, governs the precipitation of CaCO₃ (Marin et al., 2012). Hence, the acid-base status of the EPS is a critical determinant of shell production. OA has been shown to lower the pH of the EPS due to the passive proton leakage (Thomsen et al., 2010; Heinemann et al., 2012). However, it is not yet clear whether and to what extent bivalves are able to actively remove these excessive protons to maintain alkaline conditions at the calcifying front, partly due to the technical challenge of continuous monitoring of the pH in the EPS. The search for a proxy that can record temporal changes of calcifying pH has therefore received growing interest. For example, Frieder et al. (2014) found that uranium-to-calcium ratios in shells of *Mytilus californianus* and *M. galloprovincialis* may fulfill this task as uranium exists almost exclusively as a group of multiple uranyl carbonate complexes whose relative abundances are strongly dependent on pH (Djogić et al., 1986). Likewise, the boron isotopic composition of *Mytilus edulis* shells (Heinemann et al., 2012) has been suggested as an alternative pH proxy (Klochko et al., 2006). Moreover, sodium-to-calcium ratio in shells will likely contribute to a better understanding of the specific mechanisms by which bivalves regulate the pH at the site of calcification (Zhao et al., 2017).

The Manila clam, *Ruditapes philippinarum*, is a eurythermal and euryhaline mollusk species that is worldwide distributed in estuarine and coastal waters (Gosling, 2003). It is also amongst the commercially most important species in global fisheries (FAO, 2012). Due to such ecological and economical significance, quantifying the influence of OA on *R. philippinarum* becomes imperative. A recent study has shown that OA can severely impair adult physiological energetics and spawning ability during reproductive conditioning (Xu et al., 2016). Spawning failure can lead to a significant reduction of larval supply. However, a fundamental challenge ultimately affecting larval recruitment and population maintenance of *R. philippinarum* lies in whether parental exposure will generate positive carry-over effects to their offspring, especially at the early life stages, thereby helping them to acclimate to OA. In the present study, we exposed adult clams to reduced seawater pH (7.7) during gonadal maturation and then compared the rate of shell growth of newly settled juveniles to those from parents were exposed to seawater pH 8.1. More specifically, we analyzed the sodium composition of the shells in order to gain a more detailed understanding of the underlying mechanisms. The results represent a first look at whether transgenerational acclimation of this species to OA would be expected.

2. Materials and methods

2.1. Adult collection and maintenance

Specimens of 2-year-old *R. philippinarum* (32 ± 2 mm shell length) were collected from the intertidal zone of Liangshui Bay (39°04'14.41" N, 122°01'47.70" E), Yellow Sea during April 2014. Seawater temperature, salinity and pH at Liangshui Bay varied between 1.2 and 23.8 °C, 30.8 and 32.8, and 7.98 and 8.26 in the year 2014, respectively (monthly variations see Fig. 1 in Supplementary material). Upon arrival in the laboratory, they were maintained in a 600-L tank with circulating seawater at temperature of 9 °C, salinity of 32 and pH 8.1 for a 2-week acclimation period. The acclimation conditions were comparable to those recorded at the sampling site and day of collection. During the acclimation and the following experimental period, seawater was taken from the storage tank (120 m³; Engineering Research Center of Shellfish Culture and Breeding in Liaoning Province, Dalian Ocean University) where

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