



# Seawater acidification affects the physiological energetics and spawning capacity of the Manila clam *Ruditapes philippinarum* during gonadal maturation



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## ABSTRACT

Ocean acidification is predicted to have widespread implications for marine bivalve mollusks. While our understanding of its impact on their physiological and behavioral responses is increasing, little is known about their reproductive responses under future scenarios of anthropogenic climate change. In this study, we examined the physiological energetics of the Manila clam *Ruditapes philippinarum* exposed to CO<sub>2</sub>-induced seawater acidification during gonadal maturation. Three recirculating systems filled with 600 L of seawater were manipulated to three pH levels (8.0, 7.7, and 7.4) corresponding to control and projected pH levels for 2100 and 2300. In each system, temperature was gradually increased ca. 0.3 °C per day from 10 to 20 °C for 30 days and maintained at 20 °C for the following 40 days. Irrespective of seawater pH levels, clearance rate (CR), respiration rate (RR), ammonia excretion rate (ER), and scope for growth (SFG) increased after a 30-day stepwise warming protocol. When seawater pH was reduced, CR, ratio of oxygen to nitrogen, and SFG significantly decreased concurrently, whereas ammonia ER increased. RR was virtually unaffected under acidified conditions. Neither temperature nor acidification showed a significant effect on food absorption efficiency. Our findings indicate that energy is allocated away from reproduction under reduced seawater pH, potentially resulting in an impaired or suppressed reproductive function. This interpretation is based on the fact that spawning was induced in only 56% of the clams grown at pH 7.4. Seawater acidification can therefore potentially impair the physiological energetics and spawning capacity of *R. philippinarum*.

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## 1. Introduction

Rapidly increasing anthropogenic CO<sub>2</sub> emissions are resulting in ocean acidification and global warming. These environmental changes may have serious consequences for a variety of marine organisms. For example, elevated seawater pCO<sub>2</sub> levels, and the associated reductions in pH, are predicted to affect essential physiological processes (e.g., acid-base regulation, oxygen transport, and metabolic rate), ultimately affecting growth and reproduction, and even survival in extreme cases (Pörtner et al., 2004; Orr et al., 2005; Doney et al., 2009; Kroeker et al., 2013). While our current understanding of the impact of future global climate change scenarios on overall individual organism performance is increasing, to date, relatively little is known about the potential for multigenerational adaptation of marine biota to such persistent environmental changes (Somero, 2010; Kelly and Hofmann, 2013). However, such knowledge is crucial to predict how marine ecosystems

will be altered in the context of global climate change (Dupont and Pörtner, 2013).

The potential for fecundity loss is one of the most serious consequences of future global climate change scenarios and may affect the long-term sustainability of individual populations (Parmesan, 2006; Pörtner, 2008; Berg et al., 2010). Despite species-specific differences, a reduction in fecundity is likely to reflect an increase in the energetic costs required to compensate for ocean acidification impacts. This interpretation is consistent with the observations of Stumpp et al. (2012), according to which increased energetic costs resulted in significantly reduced gonadal development in adult sea urchins (*Strongylocentrotus droebachiensis*) when exposed to 2840 µatm pCO<sub>2</sub>. According to Podolsky and Moran (2006), females under increased stress such as that predicted under climate change scenarios may respond through increasing maternal energetic investment-per-offspring (e.g., increasing egg size) in order to favor larval performance. However, to ensure survival, they must allocate a large amount of energy to accommodate these stressful challenges (Wingfield and Sapolsky, 2003), consequently limiting the energy available for reproductive processes (Petes et al., 2008).

Reproduction is energetically expensive and is therefore inevitably compromised under stressful conditions. Bibby et al. (2008), for

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example, demonstrated that exposure to elevated  $p\text{CO}_2$  between 1160 and 3316  $\mu\text{atm}$  alters the reproductive condition of blue mussels (*Mytilus edulis*), forcing them to reabsorb their gametes as an energy-saving or survival strategy. Impaired or suppressed reproduction can have serious detrimental consequences for recruitment and population dynamics and, in the most extreme cases, species persistence (Berg et al., 2010). Therefore, predicting the long-term severity of ocean acidification on the reproductive success of marine organisms is crucial for gaining a better understanding of the energetic trade-offs between stress resistance and reproduction (Petes et al., 2008; Sokolova et al., 2012).

The Manila clam, *Ruditapes philippinarum*, is an ecologically and economically significant molluscan species, widespread in intertidal and shallow subtidal habitats. This species is extensively cultivated and forms the largest and oldest aquaculture industry in China, Japan, and Korea (Zhang and Yan, 2006; Uddin et al., 2012). For aquaculture purposes, this species has been introduced on the west coast of North America and in European countries (e.g., Portugal, Italy, France, and Spain) and has subsequently spread rapidly (Gosling, 2003). In all regions, *R. philippinarum* has proven readily adaptable to various coastal environments and its sustainability for aquaculture practices has been demonstrated (Drummond et al., 2006; Zhang and Yan, 2006; Dang et al., 2010).

While the potential for significant ecological and economic impacts of future scenarios of anthropogenic environmental change on *Mytilus* species has been widely recognized (Michaelidis et al., 2005; Range et al., 2012; Navarro et al., 2013; Múgica et al., 2015; Wang et al., 2015), *R. philippinarum* has received relatively little attention. Recent studies have shown that sediment acidification due to  $\text{CO}_2$  leakage from sub-seabed storage greatly facilitates heavy metal bioaccumulation in *R. philippinarum* (e.g., Rodríguez-Romero et al., 2014; Basallote et al., 2015). In a study of its close relative, *Ruditapes decussatus*, Range et al. (2011) hypothesized that increased survival of clams exposed to elevated  $p\text{CO}_2$  of 3702  $\mu\text{atm}$  may be associated with a delay in their reproductive processes. This hypothesis is supported by the observation of reduced energy acquisition (i.e., feeding activity) in *R. decussatus* exposed to the same  $p\text{CO}_2$  level of 3702  $\mu\text{atm}$  (Fernández-Reiriz et al., 2011). However, despite its ecological and cultural significance, the reproductive performance of *R. philippinarum* in the context of global climate change, to the best of our knowledge, has not yet been investigated. Considering the available data from previous studies and the highly variable environments clams inhabit, it is conceivable that clam reproduction may respond plastically to increasing environmental stress, potentially allocating energy for reproduction to costly physiological defenses, that in extreme cases, translates to impaired or suppressed reproductive function. An improved understanding of the reproductive response of *R. philippinarum* under future climate change scenarios is therefore crucial for evaluating its population dynamics.

The aim of the present study was to experimentally evaluate the potential effect of seawater acidification on the physiological energetics of *R. philippinarum* during gonadal maturation. For this purpose, reproductive control was a prerequisite. Out of all environmental parameters, temperature is considered the major forcing and timing factor in the regulation of marine bivalve gonadal development and spawning cycles (Gosling, 2003). In the Yellow Sea, for example, sea surface temperature (SST) ranges from 3.2 °C in February to 25.2 °C in August. Uddin et al. (2012) observed that the onset of gametogenesis in female Manila clams was initiated in February when the SST is 3.2 °C. Clams in the early developmental stage were dominant in March (7 °C) and April (12 °C). Ripe clams were first observed in May (17 °C) and the proportion of clams in the ripe stage rapidly increased to 56.5% in July (22 °C). The first spawning clams were observed in May and, in August and September, spawning activity reached its annual peak when SST ranged between 25.6 and 24.7 °C.

A continuous energy supply is essential for the continuous ripening of gonads, i.e., clams need to actively filter more food. Accumulating

evidence suggests that the feeding activity of many bivalves is positively related with temperature up to an optimum, beyond which it declines sharply (e.g., Sobral and Widdows, 1997; Guzmán-Agüero et al., 2013). The thermal optimum for *R. philippinarum* is 20 °C (Han et al., 2008). Therefore, in the present study, we adhered to a previously established protocol for artificial induction of gonadal maturation as follows: (1) progressive temperature increases from 10 to 20 °C within 30 days (ca. 0.3 °C per day) and (2) over the following 40 days maintaining a constant temperature of 20 °C. After 70 days of artificial ripening, clams were then induced to spawn by thermal shock. During the experiment, physiological energetics were measured in terms of key physiological parameters: energy acquisition (from ingestion and digestion), energy expenditure (from respiration and ammonia excretion), and energy budget (i.e., scope for growth). In addition, spawning rate was utilized as an estimation of clam reproductive response at the end of the experiment.

## 2. Materials and methods

### 2.1. Adult collection and maintenance

Wild-type adult *R. philippinarum* specimens (32.2 ± 2 mm shell length) were collected from the intertidal shores of Liangshui Bay (39°04'14.41" N, 122°01'47.70" E), Liaodong Peninsula, Northeast China, in April 2014. Environmental conditions at the sample collection site were as follows: temperature 8.6 °C, salinity 32.4, and pH (total scale) 8.18. Clams were transported to an aquarium facility where they were allowed to acclimate to laboratory conditions for 2 weeks prior to experimentation. Clams were held in recirculating seawater that mimicked natural conditions. Temperature, salinity, pH, and light:dark cycles were maintained at constants of 9 °C, 32, 8.1, and 12 h:12 h, respectively. They were fed twice daily with an equal mixture of the microalgae *Chaetoceros muelleri*, *Nitzschia closterium*, *Chlorella vulgaris*, and *Isochrysis galbana* to fulfill their nutritional requirements for gonadal development. Furthermore, given that food availability may counteract the influence of ocean acidification on marine bivalves (Thomsen et al., 2012), a constant food supply (ca. 20,000 cells/mL) was maintained over the duration of the experiment. In the present study, histological analysis indicated that 63% of clams were in the early developmental stage prior to experimentation.

### 2.2. Experimental setup

To assess the influence of seawater pH, three separate, but identical, recirculating systems were established, as outlined in Fig. 1. Each system comprised three exposure chambers (i.e., three replicates), a filter chamber, a temperature-controlling chamber, and a gas mixing chamber, and each held a total volume of ca. 600 L seawater. In these experimental systems, elevated seawater  $p\text{CO}_2$ , and the associated reduced pH, were maintained by vigorously bubbling pure  $\text{CO}_2$  gas into the gas mixing chamber and monitored using a digital pH controller. Gas flow was adjusted using a mass flow controller. At the same time, a constant rate of fresh air was supplied into the gas mixing chamber. After ca. 36 h of equilibration, the whole system reached a steady state. Two low pH conditions, 7.7 and 7.4, were successfully established, corresponding to the predicted levels for 2100 and 2300 (Caldeira and Wickert, 2003), respectively. The control system was bubbled with ambient air only. Temperature targets in each system were controlled in the temperature controlling chamber using a digital temperature regulator.

Clams were randomized into three groups and assigned into either the control or experimental system at a density of 150 individuals per exposure chamber. During the subsequent 2 weeks, they were acclimated to the experimental conditions; temperature was kept at a constant level of 10 °C and pH was slowly adjusted to target levels (ca. 0.5 pH unit per day). Over the following 30 days (from May 1st to 30th, 2013), clams were subjected to increasing temperature regimes. In all

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