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Physiological energetics of the thick shell mussel *Mytilus coruscus* exposed to seawater acidification and thermal stress

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HIGHLIGHTS

- Combined effects of pH and temperature on the mussel are investigated.
- Thermal stress impairs the energy budget of mussels.
- The mussels are tolerant to seawater acidification based on scope for growth.

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ABSTRACT

Anthropogenic CO_2 emissions have caused seawater temperature elevation and ocean acidification. In view of both phenomena are occurring simultaneously, their combined effects on marine species must be experimentally evaluated. The purpose of this study was to estimate the combined effects of seawater acidification and temperature increase on the energy budget of the thick shell mussel *Mytilus coruscus*. Juvenile mussels were exposed to six combined treatments with three pH levels (8.1, 7.7 and 7.3) × two temperatures (25 °C and 30 °C) for 14 d. We found that clearance rates (CRs), food absorption efficiencies (AEs), respiration rates (RRs), ammonium excretion rates (ER), scope for growth (SFG) and O:N ratios were significantly reduced by elevated temperature sometimes during the whole experiments. Low pH showed significant negative effects on RR and ER, and significantly increased O:N ratios, but showed almost no effects on CR, AE and SFG of *M. coruscus*. Nevertheless, their interactive effects were observed in RR, ER and O:N ratios. PCA revealed positive relationships among most physiological indicators, especially between SFG and CR under normal temperatures compared to high temperatures. PCA also showed that the high RR was closely correlated to an increasing ER with increasing pH levels. These results suggest that physiological energetics of juvenile *M. coruscus* are able to acclimate to CO_2 acidification with a little physiological effect, but not increased temperatures. Therefore, the negative effects of a temperature increase could potentially impact the ecophysiological responses of *M. coruscus* and have significant ecological consequences, mainly in those habitats where this species is dominant in terms of abundance and biomass.

1. Introduction

The combustion of fossil fuels by human is increasing carbon dioxide (CO_2) at a rapid rate with an increase of 100 ppm from the industrial revolution and today stands at 390 ppm (Caldeira and Wickett, 2003; IPCC, 2007). The dissolution of CO_2 in the oceans has dramatically altered the inorganic carbon chemistry of seawater by reducing the saturation of CO_3^{2-} and the pH (Feely et al., 2004). It is now unequivocally accepted that an increase in atmospheric CO_2 is causing global climatic changes, with noticeable increases in global mean temperatures and ocean acidification (OA) (Caldeira and Wickett, 2003; IPCC, 2007).

The global average surface temperature has increased by approximately 0.7 °C during the last century (Hansen et al., 2006) and a continued rising by between 1.8 °C and 4 °C by the end of the 21st century is predicted (IPCC, 2007). Temperature is a key factor that can influence animal physiological responses (Pörtner and Knust, 2007; Sara et al., 2011) and is, therefore, one of the most important factors determining the fundamental niche of a species (Hofmann and Todgham, 2010; Pörtner, 2010; Ezgeta-Balić et al., 2011). Beyond the borders of the thermal window marine invertebrates form internal (systemic) hypoxia (hypoxemia) with significant reductions in aerobic capacity, metabolic rate and scope for growth (Pörtner, 2002a,b; Pörtner and Knust, 2007). Marine bivalves, representing a reliable model to: (i), investigate

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adaptations to highly fluctuating environmental variance (Davenport and Davenport, 2005) and (ii), forecast the distribution and abundance of coastal biodiversity in the context of climate change (Helmuth et al., 2010), are particularly sensitive to external temperature changes, thus the effects of temperature on energy budgets were frequently studied (Wilbur and Hilbish, 1989; Helmuth et al., 2010; Sara et al., 2008, 2011).

The oceans have dissolved up to 50% of CO_2, leading to decreases in both pH and carbonate ions (e.g., Feely et al., 2004; Orr et al., 2005). The pH of the ocean surface is already nearly 0.1 units lower than the values from preindustrial epoch (Orr et al., 2005) and it is predicted to decrease by 0.4 units by the end of this century and nearly 0.8 units within the next 300 years (Caldeira and Wickett, 2003, 2005; Orr et al., 2005). A growing body of evidence indicates that OA impacts physiology, growth and reproduction in many marine species (e.g., Caldeira and Wickett, 2003; Pörtner et al., 2004; Michaelidis et al., 2005; Orr et al., 2005; Berge et al., 2006; Fabry et al., 2008; Kurihara, 2008; Pörtner, 2008; Doney et al., 2009; Melzner et al., 2009; Miller et al., 2009; Parker et al., 2009; Kroeker et al., 2010; Fernández-Reiriz et al., 2011; Gazeau et al., 2013). A rise in pCO_2 levels can induce changes in the extracellular acid–base balance that can produce metabolic disturbances, adversely affecting relevant processes, such as calcification, metabolism, growth and fitness (Fabry et al., 2008; Melzner et al., 2009). Many marine calcifying organisms have exhibited negative responses to high pCO_2, such as disorder in metabolic rates (Thomsen and Melzner, 2010), reduction of food uptake (Dupont and Thorndyke, 2010; Fernández-Reiriz et al., 2011) and alteration in calcification and development (Ross et al., 2011). However, adverse effects are not necessarily universal, with different species demonstrating different sensitivities to OA (Gutowska et al., 2008; Kroeker et al., 2010; Hendriks et al., 2010; Sanders et al., 2013). These previous studies showed important variability in the responses, among species, populations, and life stages (reviewed by Doney et al., 2009; Hendriks et al., 2010; Kroeker et al., 2010; Hofmann et al., 2010; Gazeau et al., 2013). Our current understanding of the effect of future OA on the physiological and ecological fitness of marine organisms is incomplete.

Despite meriting considerable research effort in recent years, the biological impacts of OA have been mostly considered in isolation (Byrne, 2011). Interactive effects of OA and temperature are still poorly understood (Pörtner, 2008; Lannig et al., 2010; Fang et al., 2014). Although scarce, some recent studies have shown that the effects of CO_2 could be modified by high temperatures (Parker et al., 2009). Duarte et al. (2014) investigated the combined effects of OA and temperature increase on *Mytilus chilensis* and found that mussels are able to overcome increased temperatures, but not increments of CO_2 levels. As global warming and OA are occurring concomitantly and the responses of the organisms exposed to these environmental stressors are widely variable, the combined effects must be evaluated extensively in bivalves. Consequently, more studies are necessary to better understand how the interaction between temperature and OA affects both the individual organisms and the whole ecosystem.

Measurements of the different physiological rates of bivalves (clearance, ingestion, absorption, respiration, excretion) can be integrated to determine the net energy balance (difference between the energy absorbed from the ingested food and the energy lost in respiration and excretion), which is commonly referred to the "Scope for Growth" (SFG) (Bayne and Widdows, 1978; Widdows and Hawkins, 1989; Smaal and Widdows, 1994; Fernández-Reiriz et al., 2012). This physiological index, besides being a good predictor of the growth rate (Bayne et al., 1979), is also a good indicator of the condition and fitness of organisms (Widdows, 1985) and a precise and sensitive index of the environmental conditions (Widdows, 1985; Albentosa et al., 2012). Being one of the main approaches to model bivalve growth, SFG has been successfully used in a range of bivalve species exposed to varying environmental conditions (Albentosa et al., 2012; Fernández-Reiriz et al., 2012; Duarte et al., 2014). Environmental temperature is a primary controlling factor in a host of physiological processes, including feeding and growth, that are extremely relevant to many ecosystem level functions (Fry, 1971). Bivalve molluscs have a limited capacity for acid–base regulation due to the lack of developed ion-exchange and nonbicarbonate mechanisms (Melzner et al., 2009). The extracellular alterations caused by exposure to elevated pCO_2 are likely to affect processes such as energy partitioning and metabolism (Pörtner, 1987; Melzner et al., 2009). The feeding physiology and energetic balance in bivalves are affected by various environmental factors, such as pH and temperature (Newell et al., 1977; Beiras et al., 1995; Fernández-Reiriz et al., 2011, 2012; Guzmán-Agüero et al., 2013; Duarte et al., 2014). The SFG approach provides an instantaneous estimate of the energy status of a given animal and also insights into the physiological components underlying observed growth rate changes (Smaal and Widdows, 1994; Han et al., 2008). Despite its relevance, SFG has rarely been used in the evaluation of the combined effects of OA and temperature on the physiology of marine organisms. Therefore, it is necessary to conduct specific studies to delineate the SFG of ecologically or commercially relevant species under OA and thermal stress.

The potential for significant ecological and economic impacts of OA on bivalves has been explicitly recognized (Fabry et al., 2008; Fernández-Reiriz et al., 2011). However, there has been little investigation on the influence of temperature and OA on the physiology of *Mytilus coruscus*. *M. coruscus* is an important economic shellfish, widely distributed in the eastern coast of China, and especially cultured as an important aquaculture species along the coastal waters of Zhejiang province (Chang and Wu, 2007; Liao et al., 2013). During the last few decades, due to the overexploitation of wild resources of this species, it has been difficult to meet the market demands, particularly within the Yangtze River Delta area (Chang and Wu, 2007). As a common calcifier inhabiting coastal ecosystem, *M. coruscus* attaches to hard substrates in subtidal zones and forms extensive subtidal beds that play an important ecological role, affecting the community structure of the associated macrofauna. Therefore, this species is a key organism for studying the biological impacts of OA and warming, with great significance in ecology and aquaculture. Despite its importance, less information is available on the ecophysiology of *M. coruscus* apart from a few reports on its larval metamorphosis and settlement (Yang et al., 2014a,b). As an important aquaculture species in coast area of east China, it is necessary to study the feeding physiology of *M. coruscus* under global change scenario.

The aim of this study was to investigate the combined effects of OA and temperature lasting for 14 d on the physiological processes in juvenile thick shell mussels *M. coruscus*. The physiological responses of the mussels were measured in terms of key physiological parameters, including clearance rate (CR), absorption efficiency (AE), respiration rate (RR), ammonia excretion rate (ER), oxygen to nitrogen (O:N) ratio and scope for growth (SFG). Such data are crucial for the management of populations of commercially exploited bivalves, and potentially useful as predictive indicators of changes in coastal biodiversity of East China Sea caused by OA and temperature elevation.

2. Materials and methods

2.1. Biological material and acclimation procedure

Samples of juvenile mussels *M. coruscus* (27 ± 2 mm shell length, 68.0 ± 4.5 mg dry tissue weight) were collected from a mussel raft at Shengsi island of Zhejiang Province (30° 33′ 00.945″ N, 121° 49′ 59.757″ E), China during September 2013 (water temperature: 24.5 °C; salinity: 25.0‰; and pH: 8.11). Before being used for ecophysiological experimentation, they were held in fiber-glass tanks (500 l) equipped with a filtering system and air supply in the Shanghai Ocean University Shellfish Laboratory. The conditions mimicked the Shengsi island environment encountered in September: temperature, salinity, pH and oxygen content were kept constant at 25 °C, 25‰, 8.1 and 7–8 mg O_2 l^{-1}. Mussels were fed daily twice with the microalgae