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Native and exotic oysters in Brazil: Comparative tolerance to hypercapnia

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ABSTRACT

Environmental hypercapnia in shallow coastal marine ecosystems can be exacerbated by increasing levels of atmospheric CO$_2$. In these ecosystems organisms are expected to become increasingly subjected to pCO$_2$ levels several times higher than those inhabiting ocean waters (e.g.: 10,000 µatm), but still our current understanding on different species capacity to respond to such levels of hypercapnia is limited. Oysters are among the most important foundation species inhabiting these coastal ecosystems, although natural oyster banks are increasingly threatened worldwide. In the present study we studied the effects of hypercapnia on two important oyster species, the pacific oyster *C. gigas* and the mangrove oyster *C. brasiliana*, to bring new insights on different species response mechanisms towards three hypercapnic levels (ca. 1,000; 4,000; 10,000 µatm), by study of a set of biomarkers related to metabolic potential (electron transport system - ETS), antioxidant capacity (SOD, CAT, GSH), cellular damage (LPO) and energetic fitness (GLY), in two life stages (juvenile and adult) after 28 days of exposure.

Results showed marked differences between each species tolerance capacity to hypercapnia, with contrasting metabolic readjustment strategies (ETS), different antioxidant response capacities (SOD, CAT, GSH), which generally allowed to prevent increased cellular damage (LPO) and energetic impairment (GLY) in both species. Juveniles were more responsive to hypercapnia stress in both congeners, and are likely to be most sensitive to extreme hypercapnia in the environment. Juvenile *C. gigas* presented more pronounced biochemical alterations at intermediate hypercapnia (4,000 µatm) than *C. brasiliana*. Adult *C. gigas* showed biochemical alterations mostly in response to high hypercapnia (10,000 µatm), while adult *C. brasiliana* were less responsive to this environmental stressor, despite presenting decreased metabolic potential.

Our data bring new insights on the biochemical performance of two important oyster species, and suggest that the duration of extreme hypercapnia events in the ecosystem may pose increased challenges for these organisms as their tolerance capacity may be time limited.

1. Introduction

Shallow coastal marine ecosystems are major contributors in global carbon dioxide (CO$_2$) cycling, functioning as both sinks and sources of atmospheric CO$_2$ (Frankignoulle et al., 1998). The CO$_2$ flux between air and water in these ecosystems has received increasing attention under the eminence of global climate change (Cai, 2011; Feely et al., 2010). In brackish and marine waters pCO$_2$ levels can be naturally high (up to 10,000 µatm), in comparison to that of open ocean seawater (400 µatm). This fact raises the question of how the increase of atmospheric CO$_2$ levels expected for the upcoming decades (IPCC, 2013) may further exacerbate high pCO$_2$ levels in seawater of these ecosystems, and how this may affect resident biota (Tomanek et al., 2011; Melzner et al., 2013).

Organisms inhabiting shallow marine water bodies are known to possess compensation mechanisms to withstand elevated pCO$_2$ in seawater (hypercapnia), to prevent deleterious effects of acidification of tissues and body fluids that affect physiological fitness (Burnett, 1997). However, such mechanisms are time limited and may lead to negative energetic trade-offs (Sokolova et al., 2012), alterations in acid-base balance (Lindinger et al., 1984), as well as alterations of oxidative status (Tomanek, 2015; Matoo et al., 2013). Among these faunal inhabitants, bivalves are generally less tolerant to elevated levels of hypercapnia than vertebrates (Melzner et al., 2009), despite possessing adaptive mechanisms to thrive in constantly fluctuating environmental parameters (Ringwood and Keppler, 2002). They can partially compensate for hypercapnia-induced acidosis (Burnett, 1997), through mechanisms such as shell dissolution to increase internal bicarbonate

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levels (Shirayama and Thornton, 2005; Lannig et al., 2010) and metabolic adjustment (e.g. metabolic arrest, shifts in metabolic pathways) (Michaelidis et al., 2005; Lannig et al., 2010).

Extensive research on the impacts of seawater acidification on marine bivalves have been published (for reviews see Parker et al., 2013; Gazeau et al., 2014), however most studies focus on the effects of projected CO_2 levels for open ocean waters (up to 1,000 μatm by year 2100) (IPCC, 2013), while the effects of seawater acidification on organisms inhabiting shallow coastal ecosystems has been comparatively overlooked, even though in these systems pCO_2 can reach significantly higher levels (between 400 and 10,000 μatm) (Frankignoulle et al., 1998; Cai, 2011; Noriega and Araujo, 2014; Evans et al., 2013). Considering predictions for increased hypercapnia in shallow coastal systems (Melzner et al., 2013), competitive advantages between species may be altered (Byers, 2002), and zoogeographical shifts in species distribution may occur (Somero, 2010). Therefore, it is important to understand different species ability to cope with such stressors in a changing environment (Parker et al., 2013).

Oysters are important ecosystem engineers in estuarine systems worldwide, providing a variety of ecosystem services and holding a high socio-economic value (Grabowski et al., 2012). However, natural oyster reefs have become severely impacted at a global level due to human pressure and need to be protected (Beck et al., 2011). *Crassostrea brasiliana* is the most important native oyster species occurring in Brazilian estuaries, and is mainly harvested from natural populations, presenting a high socio-economic value, and is especially important for local extractivist communities (Mendonça and Machado, 2010; Neto et al., 2013). *Crassostrea gigas*, a non-native species to Brazil and virtually distributed all over the world, is currently cultured in the southern state of Santa Catarina, and accounts for over 90% of the national oyster aquaculture production (Melo et al., 2010). Since the natural occurrence of *C. gigas* in Brazil has already been registered (Melo et al., 2009), special concerns must be risen in order to understand how the increased frequency of climate change related events (e.g. hypercapnia) may influence different species, and shift competitive advantages towards each other.

Hence, the present study aimed to assess how two important oyster species currently harvested in Brazil, the mangrove oyster *Crassostrea brasiliana*, and the pacific oyster *Crassostrea gigas*, respond to hypercapnic conditions by assessment of a suit of biochemical markers, bringing new insights on how native and non-native oysters species may perform in an acidified estuary.

2. Methods

2.1. Species collection and experimental setup

Crassostrea brasiliana specimens were collected from submerged oyster racks in the Cananéia estuary (25°00′29.50″S 48°01′29.35″W) in the Extractive Reserve of the Mandira (SE Brazil). *Crassostrea gigas* individuals were obtained from the Laboratory of Marine Molluscs of the University of Santa Catarina (SE Brazil). Juvenile and adult specimens of both species were selected for laboratory exposures. Average shell height of *C. brasiliana* and *C. gigas* juveniles was 4.0 ± 0.8 cm and 4.2 ± 0.2 cm respectively. Average shell height of adults was 7.2 ± 0.4 cm for *C. brasiliana*, and 7.8 ± 0.3 cm for *C. gigas*.

Experiments took place during April and May 2015 and were performed in separate for each species. Acclimation to laboratory conditions followed one week prior to the beginning of exposures. During this period, juvenile and adult specimens were maintained in separate tanks, in recirculated artificial seawater (Ocean Fish – Prodac®) (pH 7.8; temperature 24 °C, salinity 25) and daily fed with AlgaMac Protein Plus® (10^9 cells L^{-1} initial cell density). After acclimation, oysters were randomly distributed into testing systems, consisting of 50 L aquaria with individual filters and circulation pumps (total seawater flow of 500 L^{-1}). Each condition was replicated in three separate aquaria, and aquaria were stocked with 4 adults and 8 juveniles each (12 adults and 24 juveniles per condition). Three different hypercapnia levels were tested 1,000 (pH 7.8), 4,000 (pH 7.4) and 10,000 (pH 7.0) μatm pCO_2. Hypercapnia levels were selected based on maximum pH recorded during summer (i.e.: pH 7.85) in submerged oyster beds in the Cananéia estuary (Miraldo and Valenti, unpublished data), high hypercapnia pH 7.0 (10,000 μatm pCO_2) based on reported $pCO2$ in estuarine systems worldwide (Cai, 2011), and an intermediate hypercapnia level pH 7.4 (4,000 pCO_2) to assess transient changes between low and extreme hypercapnia, and values reported for hypoxic estuaries (Melzner et al., 2013).

To achieve targeted hypercapnia levels, food grade CO_2 was diffused into each aquarium (conditions pH 7.4 and pH 7.0) through bubble-counter CO_2 diffusers, at gas releasing rates that were pre-established for each condition, and regulated through six-needle valves (ISTA Products®) allowing for constant and stable gas flow (Duarte et al., 2015). During the entire experimental procedures, pH of each tank was measured and checked three times per day (Hanna Instruments®). After acclimation to laboratory conditions, oysters that were exposed to intermediate and high hypercapnia (pH 7.4 and pH 7.0 respectively) were progressively acclimated to hypercapnia by −0.2 pH units per day until targeted pH values were achieved. This procedure added 4 extra days of acclimation time to each testing group.

After pH equilibration in testing aquaria, exposures carried on for 28 days. During this period water parameters (temperature, dissolved oxygen, salinity) were daily monitored (YSI Pro plus®). Faecal debris were removed prior to feeding (AlgaMac Protein Plus®) 5 days a week, giving partial water renewals of 5%. Oysters were checked for mortality on a daily basis. Water samples were collected every week, prior to total water renewals to determine total alkalinity (TA) for each aquarium by potentiometric titration (Gran, 1952) with an automatic titrator (Mettler Toledo®). Determined TA for each aquarium was plotted against pH, temperature and salinity average values measured during each week on CO2SYS software, to determine carbonate system variables (Robbins et al., 2010), using dissociation constants K1 and K2 from Mehrbach et al. (1973) refit by Dickson and Millero (1987) and KSO_4 from Dickson (1990) (Table 1).

At the end of the experiment (28 days), oysters were frozen at −80 °C until further analysis.

Table 1
Carbonate system physicochemical parameters for pH experiments (mean ± SD; n = 4). Measured pH, and determined total alkalinity (A_t) from weekly water sampling (Temperature 24.5 °C ± 0.3, salinity 25.5, and 77% dissolved oxygen). Partial CO_2 pressure (pCO_2), bicarbonate (HCO_3^-) and carbonate ion concentrations (CO_3^{2-}), and saturation states of calcite (ΩCal) and aragonite (ΩAg), calculated with CO2SYS software (Robbins et al., 2010).

	Condition	pH	A_t (μmol. Kg^{-1})	pCO_2 (μatm)	HCO_3^-(μmol.kg^{-1})	CO_3^{2-}(μmol.kg^{-1})	ΩCal	ΩAra
C. gigas	pH 7.8	7.78 ± 0.03	2,087 ± 88	1,182 ± 76	1937 ± 99	69.0 ± 6.3	1.8 ± 0.2	1.1 ± 0.1
	pH 7.4	7.38 ± 0.02	2,679 ± 115	3,927 ± 305	2591 ± 113	37.5 ± 2.1	1.0 ± 0.1	0.6 ± 0.04
	pH 7.0	7.01 ± 0.04	2,881 ± 107	10,101 ± 862	2840 ± 105	17.7 ± 1.9	0.5 ± 0.05	0.3 ± 0.03
C. brasiliana	pH 7.8	7.78 ± 0.02	1,919 ± 109	1,068 ± 66	1764 ± 101	63.6 ± 5.2	1.7 ± 0.14	1.1 ± 0.09
	pH 7.4	7.38 ± 0.04	2,508 ± 175	3,751 ± 423	2428 ± 170	34.4 ± 4.1	0.9 ± 0.1	0.6 ± 0.07
	pH 7.0	7.00 ± 0.04	2,789 ± 105	9,992 ± 1010	2751 ± 104	16.7 ± 1.5	0.4 ± 0.04	0.3 ± 0.03

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