



Long-term mesocosms study of the effects of ocean acidification on growth and physiology of the sea urchin *Echinometra mathaei*



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ABSTRACT

Recent research on the impact of ocean acidification (OA) has highlighted that it is important to conduct long-term experiments including ecosystem interactions in order to better predict the possible effects of elevated $p\text{CO}_2$. The goal of the present study was to assess the long-term impact of OA on a suite of physiological parameters of the sea urchin *Echinometra mathaei* in more realistic food conditions. A long-term experiment was conducted in mesocosms provided with an artificial reef in which the urchins principally fed on algae attached to the reef calcareous substrate. Contrasted pH conditions (pH 7.7 vs control) were established gradually over six months and then maintained for seven more months. Acid–base parameters of the coelomic fluid, growth and respiration rate were monitored throughout the experiment. Results indicate that *E. mathaei* should be able to regulate its extracellular pH at long-term, through bicarbonate compensation. We suggest that, within sea urchins species, the ability to accumulate bicarbonates is related to their phylogeny but also on the quantity and quality of available food. Growth, respiration rate and mechanical properties of the test were not affected. This ability to resist OA levels expected for 2100 at long-term could determine the future of coral reefs, particularly reefs where *E. mathaei* is the major bioeroder.

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1. Introduction

Over the last century, human activities have produced large amounts of CO_2 through fossil fuel burning, intensive agriculture and deforestation. Changes in ocean surface water chemistry (pH and carbonate saturation decrease) has been evidenced and unequivocally linked to the rise of atmospheric CO_2 concentration (IPCC, 2013). This raised concerns about the possible impact of these changes on marine organisms.

Responses of organisms to ocean acidification (OA) greatly differ according to taxa (e.g. Wittmann and Pörtner, 2013). Due to their low metabolism and poor osmoregulation abilities, sea urchins have been considered as victims of OA (Dupont et al., 2010; Melzner et al., 2009; Pörtner et al., 2004). However, studies carried out so far

produced contrasted results. Some adult sea urchins appear to be able to maintain the pH of their coelomic fluid (the main extracellular fluid compartment in echinoderms) when facing a decrease of the seawater pH (Dupont and Thorndyke, 2012; Calosi et al., 2013; Collard et al., 2013, 2014; Moulin et al., 2014; Stumpp et al., 2012; Uthicke et al., 2014). On the contrary, other studies reported an incomplete or ineffective extracellular pH regulation (Catarino et al., 2012; Kurihara et al., 2013; Miles et al., 2007; Spicer et al., 2011). Organisms which cannot avoid extracellular acidosis could be directly affected by OA (Fabry et al., 2008; Melzner et al., 2009; Pörtner et al., 2004; Pörtner, 2008). For those which regulate their extracellular pH, the energetic cost of proton elimination or buffering could modify the allocation of the resources within the organism, leading to reduced calcification and somatic or gonad growth. Indeed, several authors observed a decreased growth when sea urchins were submitted to elevated $p\text{CO}_2$ (Albright et al., 2012; Courtney et al., 2013; Holtmann et al., 2013; Shirayama and Thornton, 2005; Stumpp et al., 2012; Wolfe et al., 2013) while in

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other studies, no effect was reported (Kurihara et al., 2013; Moulin et al., 2014; Uthicke et al., 2013, 2014). Regarding energy allocation to the reproductive organs, it seems that OA leads to a gonad growth decrease and/or a gametogenesis delay (Kurihara et al., 2013; Siikavuopio et al., 2007; Stumpff et al., 2012; Uthicke et al., 2013) but, in some cases, it is only evidenced when temperature is increased in combination with the reduction in seawater pH (Uthicke et al., 2014). When dealing with energy related effects, crucial aspects are the duration of the experiment and the provided food. Until now, only three studies conducted long-term experiments (over 6 months, Dupont et al., 2013; Kurihara et al., 2013; Shirayama and Thornton, 2005). All three reported significant effects either on growth or reproductive output although the latter was modulated according to acclimatization duration (Dupont et al., 2013). Indeed, in this last study, after a four months exposition to elevated $p\text{CO}_2$, the energy allocated to reproduction was decreased but not after a 16 months acclimatization. This highlights the need for more long-term studies. Moreover, previous studies exposed sea urchins brutally to increased $p\text{CO}_2$ levels whereas gradual acclimatization will better mimic future OA. Furthermore, in all studies carried out so far on postmetamorphic sea urchins, food was supplied *ad libitum* and used algae were not submitted to OA before being provided to sea urchins. Yet, the biochemical composition and palatability of algae may be affected by OA (e.g. Borell et al., 2013; Poore et al., 2013). Asnaghi et al. (2013, 2014) reported more severe effects of OA on *Paracentrotus lividus* when fed non-calcified algae instead of calcified algae *Corallina* and OA is known to significantly reduce growth of coralline algae (Kuffner et al., 2008).

Therefore, the goal of the present study was to assess the impact of OA at long-term on a suite of physiological parameters of a sea urchin not fed *ad libitum*. The sea urchin *Echinometra mathaei* was submitted during six months to a gradual pH decrease until reaching a moderate OA level (pH 7.7). Sea urchins were then maintained at the targeted pH for seven more months. Sea urchins were placed in replicated mesocosms provided with an artificial reef consisting of hermatypic scleractinians and reef calcareous substrate with its diverse communities of algae as principal food. The growth, the carbonate chemistry of the coelomic fluid (pH, dissolved inorganic carbon and total alkalinity) and the respiration rate of sea urchins were monitored throughout the experiment. Biomechanical resistance of the skeleton was also tested at the end of the experiment to assess the test's robustness to fish predation.

2. Materials and methods

2.1. Mesocosms design and seawater physico-chemistry

The complete description of the technical setup of the artificial reef mesocosms is presented in Leblud et al. (2014). Briefly, the study was conducted in two separated mesocosms (true replicates). Each mesocosm is composed of one main unit and two experimental aquaria. Both experimental aquaria were connected to the main unit and the water flow was the same for both aquaria ($800 \pm 50 \text{ mL min}^{-1}$). Water was recirculated between the main unit and each aquarium, so that the water from both aquaria was mixed in the main unit. This design allowed the maintenance of the same physico-chemical parameters in both aquaria. Only $p\text{CO}_2$ and pH differed: one aquarium was kept at control conditions (mean target pH in total scale, pH_T , 8.10) and the other was acidified by bubbling CO_2 , controlled by an IKS system (mean target pH_T 7.65). The contrasted conditions of pH were established gradually over six months (approximately -0.03 units of pH_T every two weeks) and then the targeted pH was maintained for seven more months. In our reference field site (La Saline fringing reef, Réunion Island,

$21^\circ 70'S$, $55^\circ 32'E$), pH increased between sunrise and zenith time on average by 0.18 units (± 0.05 , $N = 1344$, from 2011/05/10 to 2011/06/13, pH measured every 15 min, Cuet P., pers. Comm., see also Chauvin et al., 2011). From zenith to sunset, the pH decreased approximately by the same value. In order to get more realistic conditions in our mesocosms, daily variation of pH_T was maintained at a level similar to field values through community respiration/photosynthesis and change in the day/night pH setpoint of the control system (for data, see Leblud et al., 2014).

In each experimental aquarium, a temperature sensor (Aquastar, Germany) and a pH electrode (Aquastar, Germany) were connected to an IKS control system (IKS, Aquastar, Germany) which recorded the values every 20 s. Seawater samples were collected every other day and immediately filtered ($0.22 \mu\text{m}$ GSWP, Millipore). Total alkalinity (A_T) was measured by a potentiometric titration with 0.01 M HCl in NaCl 0.7 M following Dickson et al. (2007) and adapted for a smaller volume (25 mL). Each titration was automatically performed by computer using a Titronic Universal automatic titrator (SI Analytics, Germany), a C3010 multi parameter analyzer to record pH (Consort, Belgium) and a TW Alpha Plus autosampler (SI Analytics, Germany). Calibration was performed using certified reference seawater provided by A. G. Dickson (Scripps Institute of Oceanography, Dickson, batch 94). Once a day, the electromotive force (e.m.f.) was measured using a 827 pH Lab Metrohm meter (Switzerland) with a combined glass electrode (Metrohm 6.0228.010 with temperature sensor). The e.m.f. was then converted to pH_T using calibration curves of standard buffers of known pH, 2-aminopyridine/HCL (AMP) and tris/HCL (TRIS) (DelValls and Dickson, 1998; Dickson et al., 2007; DOE, 1994). Salinity and temperature were measured once a day using a conductivity meter pH/Cond 340i WTW (Germany). The intercalibration between these measures (pH_T and temperature) and those recorded by the IKS control system allowed recalculating the true 24 h cycle of pH and temperature and to adjust setpoints of the controllers. The $p\text{CO}_2$ was determined from A_T , pH_T , temperature and salinity data using the program R (R Core Team, 2013) and the package seacarb (Lavigne and Gattuso, 2012) (Lueker et al. (2000) constants for K1 and K2; Perez and Fraga (1987) constant for Kf; Dickson (1990) constant for Ks). Nutrients concentration were also determined throughout the experiment (see Leblud et al. 2014 for methods used).

2.2. Mesocosms community

Sea urchins (*E. mathaei* corresponding to *Echinometra* sp. B) were collected at Réunion Island in the Indian Ocean, from the back-reef of Saint-Pierre fringing reef ($21^\circ 33'S$, $55^\circ 47'E$). This zone, in major part covered with detritic sediment, is characterized by a low algae cover (coralline algae and encrusting pheophyta), a low coral cover (10–15%) and a high sea urchin density (ca. $30 \text{ individuals m}^{-2}$) resulting in low food availability and competition between sea urchins. The experimental community composition was similar to that in the field. In order to determine the species of *Echinometra* to which belonged the individuals used in this experiment, the color of the spine and the appearance of the milled ring as well as that of the skin on the peristome were chosen as criteria. Indeed, a study by Arakaki et al. (1998) assigned violet *Echinometra* presenting dark milled ring and dark skin on the peristome to the species *Echinometra* sp. B. Violet spines are specific to *Echinometra* sea urchins from Mauritius and Réunion Island as it is not found in Okinawa, Indonesia and other parts of the Pacific Ocean. Other *Echinometra* sea urchins were also collected: green *Echinometra* sea urchins with spines without white tips, with dark milled ring and dark skin on the peristome. They were also assigned to *Echinometra* sp. B (Arakaki et al., 1998). Therefore, violet

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