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Ocean acidification does not impact shell growth or repair of the Antarctic brachiopod *Liothyrella uva* (Broderip, 1833)

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ABSTRACT

Marine calcifiers are amongst the most vulnerable organisms to ocean acidification due to reduction in the availability of carbonate ions for skeletal/shell deposition. However, there are limited long-term studies on the possible impacts of increased pCO_2 on these taxa. A 7 month CO_2 perturbation experiment was performed on one of the most calcium carbonate dependent species, the Antarctic brachiopod *Liothyrella uva*, which inhabits the Southern Ocean where carbonate ion saturation levels are amongst the lowest on Earth. The effects of the predicted environmental conditions in 2050 and 2100 on the growth rate and ability to repair shell in *L. uva* were tested with four treatments; a low temperature control (0 °C, pH 7.98), a pH control (2 °C, pH 8.05), mid-century scenario (2 °C, pH 7.75) and end-century scenario (2 °C, pH 7.54). Environmental change impacts on shell repair are rarely studied, but here repair was not affected by either acidified conditions or temperature. Growth rate was also not impacted by low pH. Elevated temperature did, however, increase growth rates. The ability of *L. uva* to continue, and even increase shell production in warmer and acidified seawater suggests that this species can acclimate to these combined stressors and generate suitable conditions for shell growth at the site of calcification.

1. Introduction

Increasing CO_2 levels from anthropogenic activities over the past 250 years have altered our oceans through warming and also acidification (Caldeira and Wickett, 2003, 2005; IPCC, 2013; Orr et al., 2005). This latter process has received much attention recently with the chemical implications now being fairly well described, although the biological and ecological consequences are less well described (Gattuso et al., 2013; Wittmann and Pörtner, 2013). However, there is a consensus that marine calcifying organisms are the most susceptible animal group to ocean acidification because the predicted reduction in the availability of carbonate ions will make it more difficult and more energetically expensive for shell production (Byrne, 2011; Byrne and Przeslawski, 2013; Doney et al., 2009; Watson et al., 2012). To date studies have reported varied responses of calcifying organisms to future predicted pH levels with an increasing number of studies indicating that some species are tolerant (Havenhand and Schlegel, 2009; Parker et al., 2012; Ries et al., 2009). However, it must be recognised that the majority of experiments have been conducted on relatively short time scales so the ability of organisms to acclimate or adapt is largely unknown (Byrne, 2011; Byrne and Przeslawski, 2013; Gattuso et al., 2013; Wittmann and Pörtner, 2013). Longer term studies are increasing though, which are providing insights into how organisms are coping with acidifying oceans (Form and Riebesell, 2012; Kelly et al., 2013; Pandolfi et al., 2011; Pespeni et al., 2013).

The fastest rates of change in carbonate chemistry are expected in the Southern Ocean (Caldeira and Wickett, 2005; McNeil and Matear, 2008). CO_2 is more soluble in cold water (Revelle and Fairbridge, 1957) resulting in naturally low carbonate ion saturation levels compared to temperate and tropical regions. Acid–base coefficients are also more sensitive in cold temperatures making this high latitude region a forerunner of biological ocean acidification impacts for other oceans (Fabry et al., 2009). Furthermore, the absence of shell-crushing predators, such as crabs, lobsters and heavily jawed fish (Aronson et al., 2007) and the difficulty of extracting Ca^{2+} from seawater at low temperature (Aronson et al., 2007; Harper, 2000) have resulted in Antarctic species generally having thin, weakly calcified shells (Vermeij, 1978; Watson et al., 2012). This, added to the low physiological rates of Antarctic marine species (Peck et al., 2007), especially low metabolic rates (Peck and Conway, 2000), slow growth rates (Arntz et al., 1994), delayed reproduction (Meidlinger et al., 1998) and high longevity (Pearse et al., 1991), indicates that these organisms are likely to be amongst the most vulnerable species worldwide to acidifying oceans. Although there are several studies on the potential impacts of this aspect of climate change on the larval stage of Antarctic calcifying

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organisms (see review by Byrne (2011)), there are limited studies on adults (Cummings et al., 2011; McClintock et al., 2009), and the longest of these lasted for 4 months.

Rhychonelliform brachiopods are potentially the most calcium carbonate dependent group of marine animals because their calcareous skeleton and other support structures makes up over 90% of their dry mass (Peck, 1993, 2008). They have locally also been important organisms in shallow water communities, providing a habitat for a diverse range of epifauna including encrusting sponges and algae (Barnes and Peck, 1996), for the last 500 million years surviving several geological periods where the pH has fluctuated. Ocean pH has declined in the past 250 years at a rate of at least an order of magnitude faster than has occurred for millions of years (Doney and Schimel, 2007; Doney et al., 2009). Despite this, only two studies have addressed the potential climate change impacts on extant brachiopods (McClintock et al., 2009; Peck, 2008) and only the former investigated ocean acidification effects where significant dissolution in *Liothyrella uva* (our target taxon) valves was found after only 14 days in pH 7.4 conditions. However, only empty valves were used so the biological response and ability of *L. uva* to compensate for the impacts of future pH conditions therefore remain to be investigated.

L. uva (Broderip, 1833) is a large (maximum recorded length is 55 mm), epifaunal, sessile, suspension-feeding terebratulide brachiopod with a circumpolar distribution (Peck et al., 2001). It is found down to 300 m and is highly abundant in habitats protected from anchor ice and ice scour with reported densities up to 3000 individuals per m^2 (Foster, 1974; Peck et al., 2001). *L. uva* is typically found attached singly or in clumps to vertical and overhanging rocks around the South Orkney Islands, the Antarctic Peninsula and Peter I Island (Foster, 1974). Previous growth studies on *L. uva* have recorded slower growth rates than temperate rhychonelliform brachiopods and it can live for over 55 years (Peck and Brey, 1996). It also has a limited tolerance to elevated temperature, surviving up to 4.5 °C (Peck et al., 2001).

The shell is essential to the existence of *L. uva*, providing protection from predators and preventing any encounters with harmful substances and the loss of body fluids (Harper et al., 2012). Any environmental insult negatively impacting the production, maintenance and/or repair of their shell could thus prove fatal. *L. uva* also becomes naturally damaged and their shells require repairing in the environment (Harper et al., 2009). Given this, and the current focus on ocean acidification, the aims of this study were to determine how shell growth rates and the frequency of shell repair following damage in *L. uva* were affected in a 7 month experiment using predicted mid and end century pH levels.

2. Materials and methods

2.1. Sampling collection

Specimens of *L. uva* (Broderip, 1833) were hand collected by SCUBA divers from Trolval Island, Ryder Bay, Antarctica (67° 35.44′ S, 68° 12.44′ W) at 15–25 m depth in May 2012. Animals remained in their conspecific clumps with only the pedicle of the central brachiopod attached to the cliff face being cut ensuring that the majority of specimens were not damaged during collection. Environmental conditions in Ryder Bay at 15–25 m depth consist of seawater temperatures that range from −1.8 to +1.0 °C, however, temperatures rarely exceed +0.5 °C (Clarke et al., 2008), the pH range is 8.04–8.10 (McNeil and Matear, 2008) and salinity is 33.0–34.0 (Clarke et al., 2008). Brachiopods were kept underwater during the short transportation from the sampling site to the marine laboratory in Rothera and in recirculating aquaria (0.0 ± 0.5 °C) whilst being transported back to the UK. Specimens remained in an ambient recirculating seawater system in the UK in similar conditions for a further two weeks to habituate to aquarium conditions before the experiment began.

2.2. Experimental design

This study was conducted in a recirculating CO_2 microcosm adapted from Suckling et al. (in press) at the British Antarctic Survey (BAS), UK. Four treatments were used where two functioned as lowered pH treatments (pH 7.75 and pH 7.54) based on the IPCC 'business-as-usual' scenario of the predicted reduction of 0.3–0.5 pH units from the present day average of pH 8.05 in oceanic surface waters by 2100 (Table 1) (IPCC, 2013). The third was a pH control as the seawater remained at ambient pH (pH 8.05). As a concurrent 2 °C increase in temperature is expected to occur alongside this forecasted decrease in pH by the end of the century (Mitchell et al., 1998), these three systems were maintained at 2 °C throughout the experiment. The fourth remaining system was a temperature control which was held at the present-day average surface seawater temperature for Ryder Bay, 0 °C (Clarke et al., 2008). The average pH of this treatment was pH 7.98 which was slightly lower than, but close to, the pH of the pH control treatment probably as a result of the increased solubility of CO_2 and carbonates (CO_3^{2-}) in seawater at the lower temperatures.

The pH of the lowered pH treatments was altered by intermittently bubbling CO_2 gas through a ceramic diffuser to maintain the pH at the predetermined pH levels via a solenoid valve connected to an Aqua Medic pH controlled computer and glass electrode (with plastic shaft) system. The pH control had a similar set up but without the pH control system. An Aqua Medic Ocean Runner power head 2000 circulated the seawater in the mixing tank to ensure a constant pH. Seawater was then gravity fed from each mixing tank at a rate of 0.65 ± 0.03 L min^{-1} into the experimental tank. Seawater temperature was manipulated by the use of temperature-controlled laboratories. Air temperature was maintained at −2.5 °C in the laboratory with the pH control and both lowered pH treatments but the lifting pumps (Aqua Medic Ocean Runner 3500) and the mixing power heads (Aqua Medic Ocean Runner 2000) in each treatment's mixing tank caused the seawater temperature to raise to the desired ~2 °C, with minimal variability (Table 1). The temperature control treatment was situated in the main BAS aquarium where the air temperature was set at −1.5 °C and the absence of lifting and circulating pumps caused the seawater temperature to be maintained at ~0 °C.

Seawater temperatures (°C, Digital Testo 106) and pH_{NIST} (Aquamedic pH controlled computer and electrode system) were monitored and recorded daily. pH_{NIST} was also more accurately measured once a week with a temperature compensated HANNA bench top meter pH/ORP 115 v pH 21-01. Salinity (Tropical Marine Centre V2 Handheld refractometer), TCO_2 (mmol L^{-1}; Ciba Corning TCO_2 Analyzer 965, Olympic Analytical, UK) and nutrient content (silicate and phosphate; according to methods in Nickell et al. (2003)) of each treatment were also measured weekly. Twice a week, the Aqua Medic pH probes were calibrated with NIST certified pH buffers. Other carbonate system parameters, including the partial pressure of CO_2 (pCO_2) and the saturation values for calcite (Ω_C) and aragonite (Ω_A), were modelled from applying TCO_2 and pH_{NIST} data to the program CO2SYS (Lewis and Wallace, 1998) with refitted constants (Dickson and Millero, 1987; Mehrbach

Table 1
Mean (±SD) seawater parameters in all four treatments during the 7 month experiment which follow the format recommended by Barry et al. (2010). Values for pCO_2, Ω calcite and Ω aragonite were calculated from CO2SYS (Lewis and Wallace, 1998) with refitted constants (Dickson and Millero, 1987; Mehrbach et al., 1973).

Seawater parameter	Temperature control	pH control	pH 7.75	pH 7.54
pH_{NIST}	7.98 ± 0.02	8.05 ± 0.03	7.75 ± 0.03	7.54 ± 0.03
pCO_2 (μatm)	417 ± 15	365 ± 67	725 ± 133	1221 ± 179
Ω calcite	1.20 ± 0.10	1.49 ± 0.15	0.78 ± 0.11	0.50 ± 0.10
Ω aragonite	0.75 ± 0.06	0.94 ± 0.10	0.49 ± 0.07	0.32 ± 0.06
Temperature (°C)	−0.3 ± 0.1	1.7 ± 0.3	1.9 ± 0.4	2.2 ± 0.4
Salinity	35 ± 1	35 ± 1	35 ± 1	35 ± 1