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Molluscs on acid: gastropod shell repair and strength in acidifying oceans

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ABSTRACT: The importance of 'top-down' regulation of assemblages by predators is well documented at a variety of spatial and temporal scales on rocky-shores. Predators have consumptive and non-consumptive impacts on their prey; however, much remains to be discovered about how climate change may affect predator-prey interactions and processes related to these interactions. We investigated the effect of predicted near-future ocean acidification on a molluscan defence mechanism: shell repair. We simulated non-consumptive damage by a durophagous (shell crushing) predator to 2 common intertidal gastropod species: *Austrocochlea porcata* and *Subninella undulata*. Our data show a stark contrast in the response of these 2 gastropods to simulated ocean acidification; *A. porcata* exhibited a depressed shell repair rate, compromised shell integrity and reduced condition. These 3 critical attributes for survival and protection against predators were all severely affected by ocean acidification. In contrast *S. undulata* was unaffected by ocean acidification. These results suggest that if atmospheric CO_2 levels continue to rise, and ocean pH subsequently drops, then less resistant species such as *A. porcata* may face increased predation pressure and competition from more successful taxa within the same community. This could affect predator-prey relationships, with the potential to cascade through intertidal communities.

KEY WORDS: Climate change · Predation · Shell strength · Shell growth · pH · Ocean acidification

INTRODUCTION

The impact of predicted climate change on organisms has been investigated for decades; however, marine scientists are only beginning to understand how the acidification of the world's oceans might affect marine life (Dupont & Pörtner 2013). By the end of this century, ocean acidification, due to elevated partial pressure of carbon dioxide (pCO_2) levels from anthropogenic emissions, is expected to reduce the global mean surface pH (currently around 8.2) by up to 0.5 pH units (Caldeira & Wickett 2005), as well as diminish the saturation of 2 calcium carbonate ($CaCO_3$) species: aragonite and calcite (Kleypas et al. 2005). Additionally, cooler mid-high latitude environments will experience relatively rapid undersaturation of aragonite, placing these marine zones under greater threat than low latitude systems (Caldeira & Wickett 2005, Kleypas et al. 2005). This altered marine chemistry has the potential to reduce or disrupt calcification in marine organisms, threatening shell-forming taxa such as molluscs (Byrne et al. 2009, Gaylord et al. 2011, Lischka et al. 2011). However, the effect of elevated pCO_2 on key components of consumer-prey interactions has been tested for only a few species (Landes & Zimmer 2012, Allan et al. 2013, Poore et al. 2013). As predation is one of the key processes controlling population dynamics and structuring communities in

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marine ecosystems (Paine 1966, Sih et al. 1985, Harley 2011, Knights et al. 2012), understanding the effect of future acidification on predator-prey associations is important.

In the intertidal environment, durophagous (shell crushing) crabs are dominant predators, preying on a range of gastropod species (Chilton & Bull 1984, Moody & Aronson 2007). However, a large proportion of crab attacks fail, inflicting damage to the shells of intertidal molluscs (Vermeij 1982a), exposing vulnerable soft tissue to the threat of further predation and abiotic stress (Blundon & Vermeij 1983). The shell repair process re-establishes the function and integrity of shells, increasing the survival of prey (Blundon & Vermeij 1983). This repair strategy appears to have been highly successful throughout geological time, including in current climatic conditions, with more than 20% of individuals showing evidence of shell repair in some modern species populations (Vermeij et al. 1981, D. W. Coleman unpubl. data). In addition, the integrity (strength) of repaired shells is equivalent to undamaged shells (Salgëback 2005). Given the potential for near-future elevated CO_2 environments to compromise shell calcification (Kleypas et al. 2005, Kroeker et al. 2013), the effectiveness of this repair process may be under threat.

Mid-latitude temperate marine waters surround the southeast coast of Australia, supporting a diversity of gastropod grazers, often in high abundance. Duraphagous crabs including the black-fingered crab *Ozius truncatus* (Edwards 1834) have been identified as dominant predators on small gastropods and inflict characteristic damage patterns on their shells (Chilton & Bull 1984, authors' pers. obs.). In this study, we focus on how ocean acidification affects shell repair in gastropods after a simulated unsuccessful predatory attack. We assessed this in 2 common gastropods: a trochid, *Austrocochlea porcata* (Adams 1853) and a turbinid, *Subninella undulata* (Lightfoot, 1786). Both species are extremely abundant, and show high levels of shell damage and repair on intertidal rocky reefs (D. W. Coleman unpubl. data). Additionally, they may also be under threat from ocean acidification given the high aragonite:calcite ratios in their shells (98.65:1.35% and 98.2:1.8% in *S. undulata* and *A. porcata,* respectively) and the sensitivity of aragonite to dissolution at high pCO_2 concentrations (Orr et al. 2005). We tested the hypothesis that reduced pH would affect the rate of shell repair, changes in shell thickness, shell integrity (strength), gastropod condition and $CaCO_3$ polymorph composition relative to control (current) conditions.

MATERIALS AND METHODS

Study species and artificial damage

Austrocochlea porcata and *Subninella undulata* were collected in the Illawarra region on the New South Wales south coast (Towradgi reef: 34° 23′ 11″ S, 150° 54′ 54″ E). Both species are common Australasian endemic molluscs in the intertidal environment with broad distributions in temperate and sub-tropical Australia (http://seashellsofnsw.org.au, accessed on 31 August 2013). Field populations of both species show a high incidence of shell repair following unsuccessful attacks by predators: more than 20% of *A. porcata* and 25% of *S. undulata* show evidence of aperture repair (D. W. Coleman unpubl. data). To minimise the confounding influence of size variation, only *A. porcata* with a maximum length (ML), i.e. from tip of apex to the shell lip/aperture of 17 ± 2 mm and *S. undulata* measuring 26 ± 2 mm ML were collected. Hence our focus was on adults of these species. Approximately 7 ± 1 mm^2 of shell was removed from the aperture of *A. porcata* while 10^2 ± 1 mm^2 was removed from the larger species *S. undulata*. Damage was inflicted to simulate typical 'peel' damage inflicted to the shell aperture by the durophagous crab *Ozius truncatus* as observed in laboratory and field specimens. The snails were held in a vice and needle-nose pliers used to break the shell aperture. All individuals were quarantined for 48 h to ensure they were alive and behaving normally before being randomly allocated to treatments.

Experimental conditions

Experiments were carried out in 3 large recirculating seawater tables (3 × 1.5 × 0.25 m) with sump tanks of equal size totalling 520 l per system. Two acidification treatments were applied based on Intergovernmental Panel on Climate Change pH (pCO_2) predictions for 2100 and 2050 (IPCC 2007): pH 7.7 (~840 ppm) and pH 7.9 (~560 ppm), respectively. A control treatment, with pH 8.2 (~380 ppm), simulated present-day conditions. Seawater collected from the ocean (pH 8.2) was acidified, using a RedSea pro CO_2 system and a TUNZE™ Model 7074/2 pH controller, to the desired level within the rearing system. pH was recorded weekly and remained relatively constant in all treatments for the duration of the experiment.

Water temperature was maintained at 20°C for all treatments with 10% water changes performed weekly in addition to constant filtration and oxy-

genation to maintain >90% oxygen. Salinity was maintained at 35 to 37‰ using distilled water. These temperature and salinity values represent ambient conditions for this region during the experimental period (May 2009).

Water samples were taken at the beginning, middle and end of the experiment to determine total alkalinity (using the Gran plot calculation method). Aragonite (Ω_{ar}) and calcite (Ω_{ca}) saturation levels and pCO_2 were calculated using CO2SYS (Pierrot et al. 2006).

A. porcata were maintained in experimental aquaria for 95 d while the more rapidly growing *S. undulata* were held for 65 d. Food sources included 50 g of fresh *Ulva* spp. and boulders with micro and macro algae cover. This was replaced twice each week. Subsets of snails were periodically removed from the experimental conditions at several end points for the measurement of shell repair rate, shell strength and $CaCO_3$ polymorph composition.

Measuring shell repair rate

To determine whether acidification would affect the accretion of new shell, growth of fresh shell was measured as an estimate of shell repair rates in each treatment. After artificial damage, 15 *A. porcata* and 20 *S. undulata* were tagged using Selleys Knead It Aqua and 8 × 4 mm Hallprint tags. The amount of new shell accreted was measured in millimetres from the break-interface (margin where shell was removed) extending down to the calcifying edge. During each sampling period, the maximum length of new shell produced between these 2 margins was taken as the shell growth measurement. The demarcation between old and newly accreted shell was very clear and could be measured using Vernier calipers with high precision (0.05 mm). Shell growth was recorded every 5 d for each species over a period of 55 d for *A. porcata* and 30 d for *S. undulata*. At the end of both these respective periods, the shell aperture was fully repaired; further growth consisted of thickening of the repaired shell. We present data for the most extreme (pH 7.7) and control (pH 8.2) conditions for this variable.

Quantifying shell thickness

Snails were anaesthetised for 30 min in a freezer at −20°C and then the body tissue was removed using forceps. The shells were then cross-sectioned perpendicular to the mid-section of the outer growing edge, using a diamond saw. The cross-section was photographed (using Motic Images Plus 2.0) and shell thickness was determined at 5 points, 1.5 mm apart, along the cross-section of the repaired shell segment. The average of these measurements was termed the repaired shell thickness. Estimates of shell thickness were made once after 95 d (n = 20) days for *A. porcata* due to its slower repair rate, and at 25 (n = 8), 45 (n = 20) and 65 d (n = 20) days for *S. undulata*.

Determining shell strength

The crushing force required to break the shell was assessed with a 1 t compression-testing machine (Instron) (Fig. 1). Snails were anaesthetised for 30 min in a freezer at −20°C and then body tissue was removed using forceps. Empty shells were set in a high strength plaster (Dental Plaster, Boral™). As the strength of the regrown shell section was of interest, the outer shell lip was set as the first point of contact with the Instron compression plate (Fig. 1). Each shell was set in such a way that the compression force would contact the shell ~5 mm from the growing edge. Shell strength was measured as the maximum downward force in Newtons (compression load) required to fracture the outer lip. A 5 mm s^{-1} compression head speed was used; similar speeds have been used on other gastropod species for strength meas-

Fig. 1. Testing shell strength. Image shows the Instron testing machine used to measure shell strength and a close-up of the compression plate and its contact surface with the shell aperture of *Subninella undulata*

urements (Buschbaum et al. 2007). *A. porcata* was measured once after 95 d (n = 28) as this species repaired at a slower rate, whilst *S. undulata* was sampled at 25 (n = 8), 45 (n = 20) and 65 d (n = 20).

Condition index calculations

Assuming that shell repair would incur a metabolic cost, at the conclusion of the experiment we predicted the deteriorated condition of snails exposed to stress from reduced pH, with a condition index (CI_{weight}), following the method of Hickman & Illingworth (1980). Snails were anaesthetised in a freezer at −20°C prior to weight measurements. Snails were then defrosted, allowed to partially dry for 1 h, weighed (whole weight), then cracked to remove tissue from shell, and then the shell weighed. The soft tissue was dried for 48 h at 50°C to obtain a dry weight. These values were used to calculate the CI_{weight} from the following equation:

$$CI_{weight} = \frac{100 \times \text{dry tissue weight (g)}}{\text{Whole weight (g)} - \text{shell weight (g)}} \quad (1)$$

$CaCO_3$ polymorph composition

We estimated the percent aragonite and calcite compositions within repaired shell sections to determine whether increased CO_2 influenced the ratio of these 2 $CaCO_3$ polymorphs in the 2 gastropod species. X-ray diffraction (XRD) was used to analyse the ratio of $CaCO_3$ polymorphs. Pieces of repaired shell material (5 to 10 mm^2) were ground into a talc consistency and placed into a Spellman DF3 XRD generator in conjunction with a Phillips Goniometer. To reduce the reversion of aragonite to calcite due to heating during grinding, acetone was used to keep the material cool (Davies & Hooper 1963). XRD output was analysed in Sirpquant V.3.1 (Sietronics). Samples from each treatment and control were analysed after 95 d (*A. porcata*) and 65 d (*S. undulata*) in each treatment.

Statistical analysis

We used 1-way ANOVA to compare among means for thickness, strength, condition and $CaCO_3$ polymorph data (GMAV5, University of Sydney). A Students *t*-test was used to compare treatment means for shell repair rate data (JMP V.9.0). Prior to analysis we calculated Cochran's C to test the assumption of homogeneity of the variances, while normality was assessed using Shapiro-Wilks tests (JMP V.9.0). We used SNK tests for post-hoc comparison among means.

RESULTS

Shell repair rate

The shell repair rate at elevated pCO_2 differed markedly between the 2 gastropod species (Fig. 2). Accretion of new shell in *Austrocochlea porcata* was significantly reduced at pH 7.7 ($t_{42} = 4.68$, $p < 0.0001$) compared to the control treatment (Fig. 2A). After 55 d, the daily shell accretion for *A. porcata* was 0.08 ± 0.007 mm d^{-1} (mean ± SE) at pH 8.2, which was

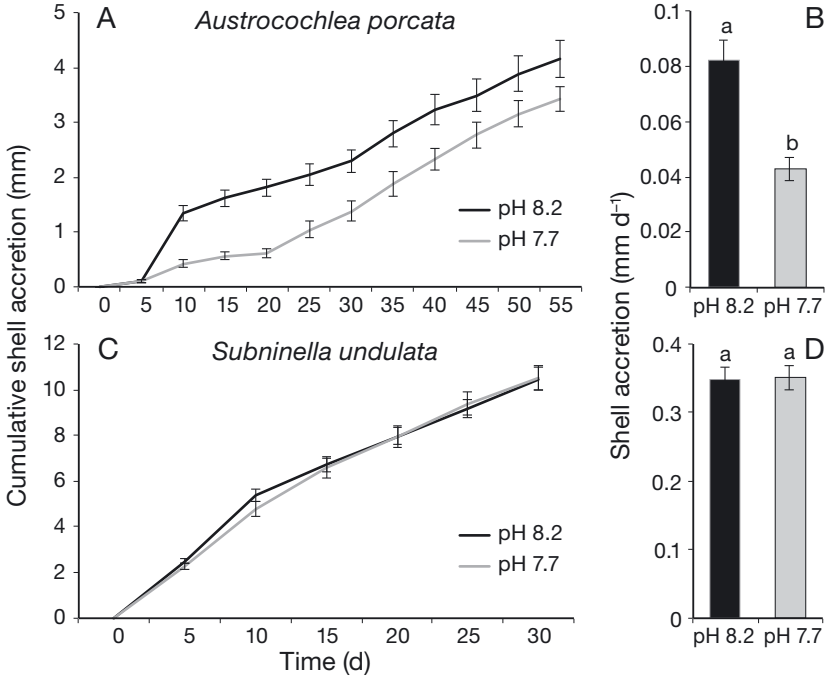

Fig. 2. Repair rates of gastropod shells following artificial shell damage and exposure to modified pH (7.7) in comparison with control conditions (pH = 8.2). (A,C) Cumulative shell accretion (mm) over time and (B,D) shell accretion per day (mm) for (A,B) *Austrocochlea porcata* (n = 20) and C,D) *Subninella undulata* (n = 15). Values are mean ± SE. Different letters above columns in panels (B) and (D) indicate significant statistical difference ($p < 0.05$)

Table 1. Analysis of variance of shell response variables: shell thickness, strength, snail condition and $CaCO_3$ composition, in response to increasing pCO_2 (pH 8.2, 7.9 and 7.7) for *Austrocochlea porcata* and *Subninella undulate,* after 95 and 65 d respectively. Significant values ($p < 0.001$) are shown in **bold**

Source	*Austrocochlea porcata*					*Subninella undulata*				
	df	MS	*F*	p	n	df	MS	*F*	p	n
Shell thickness										
pH treatment	2	52113	2.57	0.085	20	2	11555	0.60	0.553	20
Error	57	20265				57	6916			
Integrity										
pH treatment	2	71.5	11.1	**<0.001**	28	2	5147	1.80	0.174	20
Error	81	6.4				57	2854			
Condition										
pH treatment	2	81.9	15.8	**<0.001**	20	2	8.9	1.55	0.221	20
Error	57	5.2				57	5.8			
$CaCO_3$ composition										
pH treatment	2	1.04	0.35	0.708	6	2	0.01	0.29	0.754	6
Error	15	2.94				15	0.02			

double the rate recorded for this species at pH 7.7 (0.04 ± 0.004 mm·d^{-1}) (Fig. 2B). In contrast, shell regrowth in *Subninella undulata* was unaffected by elevated pCO_2 ($t_{57} = -0.090$, $p = 0.929$), with a mean ± SE repair rate of 0.35 ± 0.01 mm d^{-1} across both treatments (Fig 2C,D).

Shell thickness

We did not detect significant differences in shell thickness for *A. porcata* following ~3 mo of repair (95 d) (Table 1, Fig. 3A). In contrast, *S. undulata* shells from the lowest pH treatment (pH 7.7) were significantly thicker than shells at both pH 8.2 and pH 7.9 after 25 ($F_{2,21} = 4.70$, $p = 0.0205$) and 45 d ($F_{2,57} = 11.01$, $p < 0.0001$) of repair (Fig. 4A). However, shell thickness was similar across all treatments after 65 d of exposure (Table 1, Fig. 4A).

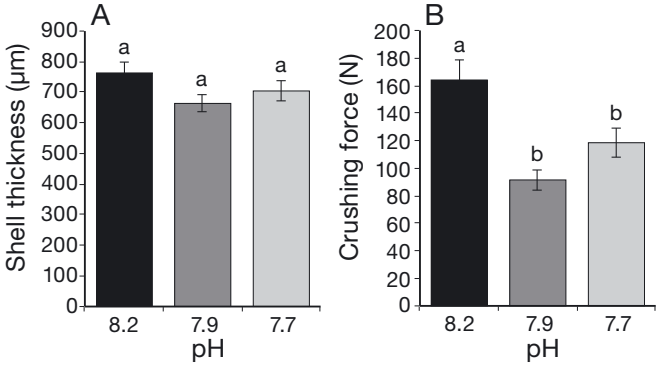

Fig. 3. Thickness and strength of *Austrocochlea porcata* shells (n = 28) after repair in CO_2-enriched seawater. (A) Shell thickness (µm) and (B) shell strength (measured as crushing force [N] required to cause fracture) after 95 d exposure to modified pH (7.7, 7.9) and in control pH conditions (8.2). Values are mean ± SE. Different letters above columns indicate significant statistical differences ($p < 0.05$)

Shell strength

The strength of *A. porcata* shells were significantly reduced when repaired in both pH 7.7 and pH 7.9 treatments after a 95 d repair period (Table 1). Shells of *A. porcata* held in the lowest pH were on average 28% weaker than those held in the control conditions (Fig 3B). In contrast, we failed to detect any evidence of compromised shell strength for *S. undulata* shells when repaired at low pH (Fig. 4B). Shell resistance to crushing in *S. undulata* increased steadily over the 65 d of our experiment, and no changes among treatments were detected after 25 ($F_{2,21} = 2.23$, $p = 0.132$), 45 ($F_{2,57} = 3.02$, $p = 0.057$) or 65 d (Table 1, Fig. 4B). Although non-significant, shells repaired at the lowest pH required the greatest crushing force after longer exposure times. Compared to the control, shells in the lowest pH (7.7) treatment were on average 16 and 10% stronger after 45 and 65 d, respectively.

Gastropod condition

We observed a significant reduction in the condition index for *A. porcata* in both pH 7.9 and 7.7 compared to the control after 3 mo exposure (Table 1). The average condition index for snails in pH 8.2 was

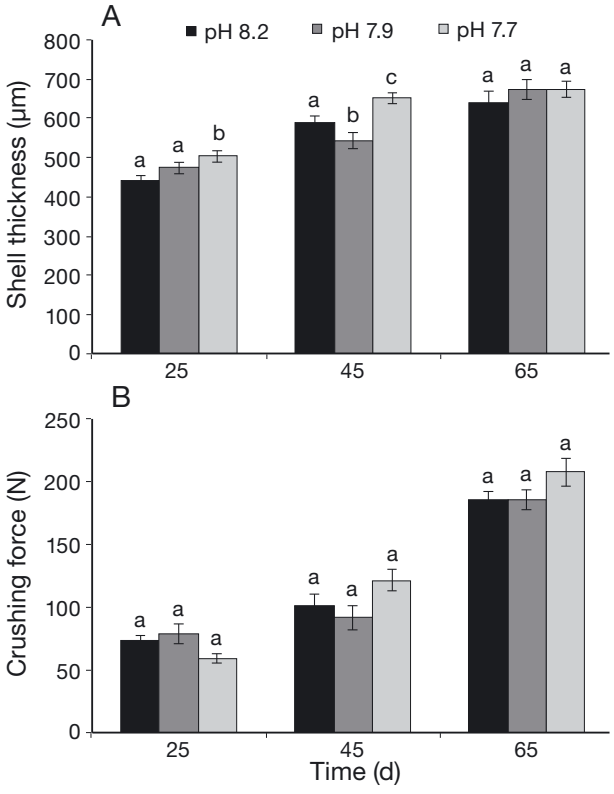

Fig. 4. Thickness and strength of *Subninella undulata* shells after repair in CO_2-enriched seawater. (A) Shell thickness (µm) and (B) shell strength (measured as crushing force [N] required to cause fracture) after 25 (n = 8), 45 (n = 20) and 65 d (n = 20) exposure to modified pH (7.7, 7.9) and in control ph conditions (8.2). Values are mean ± SE. Different letters above columns indicate significant statistical differences ($p < 0.05$)

around 3 units higher compared with both pH 7.9 and pH 7.7 (Table 2). We did not observe a significant reduction in condition index among the pH treatments for *S. undulata* (Table 1). There was however a clear loss of a large amount of the protective organic periostracal layer from the older shell sections in individuals of this species exposed to the high pCO_2 treatments (Fig 5).

$CaCO_3$ polymorph composition

Elevated pCO_2 concentration had no significant effect on the ratio of aragonite to calcite in the repaired shell material of both species (Table 1). Shell aragonite and calcite levels varied by a maximum of 0.6% among all treatments for *A. porcata* (Table 2). *S. undulata* shells contained slightly higher aragonite to calcite ratios than *A. porcata*, however there was only a 0.1% difference among treatments (Table 2).

DISCUSSION

Prey species with efficient anti-predator adaptations may have an ecological advantage over more vulnerable prey (Bengston 2002), especially when exposed to the additional environmental stress associated with a changing climate (Allan et al. 2013). We show contrasting responses during shell repair in 2 herbivorous gastropod species exposed to pCO_2 conditions anticipated in a near-future ocean. Under predicted ocean acidification scenarios for the end of the 21st century the trochid gastropod *Austrocochlea porcata* showed significant deteriorations in 3 critical responses: shell repair rate, shell structural integrity and snail condition. We interpret the decline in shell

Table 2. Snail condition and shell $CaCO_3$ composition for *Austrocochlea porcata* and *Subninella undulata* after exposure to increasing pCO_2 (pH 8.2, 7.9 and 7.7). Errors are ± 1 SE

	Austrocochlea porcata		*Subninella undulata*	
	% aragonite:calcite	Condition index	% aragonite:calcite	Condition index
pH 8.2	95.1:4.9 ± 0.9	25.9 ± 0.5	98.9:1.1 ± 0.05	34.5 ± 0.5
pH 7.9	95.4:4.6 ± 0.47	22.5 ± 0.5	99.0:1.0 ± 0.09	35.9 ± 0.4
pH 7.7	95.7:4.3 ± 0.7	22.3 ± 0.5	98.9:1.1 ± 0.03	35.2 ± 0.5

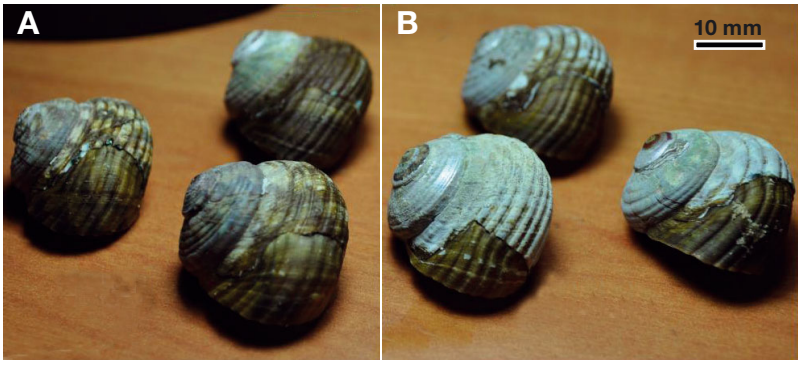

Fig. 5. Repaired gastropod shells at current and forecast near-future pH levels. *Subninella undulata* exposed to (A) pH 8.2 and (B) pH 7.7 for 65 d. Individuals reared in the most acidic conditions show loss of the protective periostracum layer following artificial damage, with the exception of the repaired shell section

regeneration rate and shell strength as indicative of compromised calcification under conditions predicted in a near-future ocean whilst the loss in condition may be a consequence of increased metabolic cost with reduced pH (Wood et al. 2008). In contrast, the turbinid *Subninella undulata* was unaffected by the same acidification scenarios for all response variables. The buffering capacity of the thick organic periostracum of this species may confer a level of protection not seen for *A. porcata* (Neves et al. 2007). The findings of this experiment, which used a single water table for each pH treatment should be interpreted cautiously, but we highlight that outcomes for the 2 future ocean scenarios (2050 and 2100) showed a high level of consistency.

Ocean acidification research has increased exponentially in recent years, particularly in relation to laboratory based studies (Dupont & Pörtner 2013). These studies generally involve short-term exposure periods with healthy individuals of a specific life stage, for example larval fish (Bignami et al. 2013), early developing molluscs (Parker et al. 2011, Davis et al. 2013) and fertilisation in echinoderms (Byrne et al. 2010). This is under the assumption that injured individuals are not commonly encountered in populations (Blundon & Vermeij 1983). However, many individuals of a diverse range of taxa are damaged or injured at some stage in their life cycle due to unsuccessful attacks by predators or other factors (Vermeij 1982c). This is particularly apparent in marine molluscs as they leave evidence of these episodes in their shells (Vermeij 1982a, Cadee 1999). Consequently, it is apparent that non-lethal shell damage and subsequent shell repair can account for large proportions of populations of calcifiers (Vermeij et al. 1981, Cadee 1999, D. W. Coleman unpubl. data). Until now, the impact of ocean acidification on shell damage and repair was unknown.

The shell repair process incurs significant metabolic cost to marine calcifiers, with the speed of regeneration critical to survival (Zisper & Vermeij 1980). We show that the repair process in *A. porcata* is vulnerable to increased pCO_2. In particular, snail condition and repair rate deteriorated at lower pH levels (pH 7.7). Lischka et al. (2011) found a parallel response in undamaged polar pteropods, with reduced shell increments at high pCO_2 levels. Similarly, reductions in shell growth and weight have also been found for a subtidal conch (*Strombus lubuanus*) following 6 mo exposure to an increase of only 200 ppm pCO_2 (Shirayama & Thornton 2005). In addition to reduced shell growth, raised CO_2 caused deterioration in the condition of *A. porcata*. Wood et al. (2008) reported a similar response in ophiuroid brittlestars during arm regeneration: brittlestars exposed to raised pCO_2 experienced significant loss of muscle mass.

Following damage, rapid shell repair and overall animal condition are important factors in ensuring long-term survivorship. However it is also critical that shells regain structural integrity after damage (Blundon & Vermeij 1983). Strong shells are a fitness advantage for molluscs (Currey & Hughes 1982); rapid adaptation to thicker and architecturally diverse shells in response to predators is evident for many taxa (Vermeij 1982b, Fisher et al. 2009). Given the challenges that ocean acidification will present to calcifiers there have been a surprisingly small number of studies testing the effect of ocean acidification on integrity of undamaged molluscan shells; however, results are consistent in suggesting a trend towards reduced shell strength in response to lower pH conditions (Bibby et al. 2007, Hall-Spencer et al. 2008, Welladsen et al. 2010). Under current climate conditions, repaired shells are structurally as strong as undamaged shells (Turra et al. 2005). However, in our study, shells of *A. porcata* were significantly weaker after 3 mo in both acidification treatments, suggesting that near-future acidification may incur a significant cost to shell strength for this species and perhaps many other molluscan taxa. In contrast, *S. undulata* experienced small increases in both shell thickness and strength, suggesting that this species may be more resilient to ocean acidification due to calcification compensation under acidification stress. Other calcifying species including barnacles and brittlestars also show compensatory calcification under high pCO_2 conditions (Wood et al. 2008, McDonald et al. 2009). Over long time frames *S. undulata* may be affected by acidified conditions due to a clear loss of the periostracum on existing shell (Fig. 5). This protective organic layer slows the rate of shell dissolution and prevents entry of bioeroding organisms that may further compromise shell integrity (Mao Che et al. 1996, Kardon 1998).

We present evidence of striking species-specific outcomes in the face of elevated pCO_2. The variation in the impacts of pCO_2 on different taxa has been emphasised by recent reviews (Byrne & Przeslawski 2013, Kroeker et al. 2013). A decline in fitness of one species under unfavourable conditions may modify competitive strength (Willett 2010) or increase predation intensity (Vance 1979). These effects may cascade through the entire assemblage (Peacor & Werner 2000, Trussell et al. 2003). Poore

et al. (2013) report deterioration in the fitness of the herbivorous amphipod *Peramphithoe parmerong* when exposed to warming and reduced pH and suggest reduced plant-herbivore interaction strength as a result of the raised susceptibility of algal tissue to herbivores. Conversely, Landes & Zimmer (2012) consider that although the fitness of a predatory crab and its prey can change with acidification, it does not necessarily result in a drastic change in the predator-prey interaction. These highly species-specific effects on predator-prey dynamics under future acidification could arise from a variety sources; these could include changes in per capita feeding rates, changed abundances of predators or prey, changed distributions of predators or prey, modified predator behaviour, and altered prey defences (e.g. Allan et al. 2013). Thus, the influence of climate change stressors on species and their interactions is likely to differ on a case-by-case basis (Byrne & Przeslawski 2013). This will make drawing inferences from one system and applying to another a very real challenge.

This study presents the first investigation into the effect of ocean acidification on molluscan shell repair. We highlight the vulnerability of the calcification process to ocean acidification in an ecologically important gastropod *A. porcata.* The contrasting outcomes in shell repair for 2 ecologically and physiologically similar species may have important implications for interactions among species and the structure of rocky shore assemblages. These findings suggest that within this century, the balance in intertidal communities may change as more resilient species gain an advantage over those less tolerant of increased pCO_2. The challenge for ecologists will be to understand how species respond to these changes in combination with other climate change stressors such as temperature and ultraviolet radiation (Byrne 2011, Byrne & Przeslawski 2013, Davis et al. 2013, Dupont & Pörtner 2013), and to identify the effects on a range of processes, life stages and species-interactions in ecologically realistic settings. Further, understanding the likelihood of acclimation, or adaptation across generations, represents a significant challenge to ecologists.

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