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Variation in the effects of ocean acidification on shell growth and strength in two intertidal gastropods

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ABSTRACT: Many marine organisms rely on calcified hard parts to resist predation, and ocean acidification (OA) affects calcification negatively. However, calcification-related consequences may manifest in variable and/or cryptic ways across species. For example, shell strength is a primary defense for resisting shell-crushing predation, yet the consequences of OA on such biomechanical properties cannot be assessed visually. We exposed 2 species of intertidal gastropods common to the west coast of North America (the black turban snail *Tegula funebralis* and the striped dogwhelk *Nucella ostrina*) to OA (pH decreased by ~0.5 units) and predation cues for 6 mo, then measured both shell growth and strength. Shell growth in *T. funebralis* was significantly depressed under OA and in the presence of predation cues (declines of 83 and 63%, respectively). Shells produced by OA-exposed *T. funebralis* were also 50% weaker. In contrast, shell growth of *N. ostrina* was unaffected by OA, yet its shells were still 10% weaker. These findings highlight the potential for both different and easily overlooked responses of organisms to seawater acidification. Moreover, such results raise the possibility of ensuing shifts in consumption rates and rankings of prey items by shell-crushing predators, leading to shifts in the balance of species interactions in temperate shoreline communities.

KEY WORDS: Mollusca · Biomechanics · Seawater pH · Predation · *Tegula funebralis* · *Nucella ostrina*

1. INTRODUCTION

Ocean acidification (OA) from human-induced CO_2 emissions has negative effects on many marine organisms, leading to impaired physiological performance, modified species interactions, and potential ecosystem disturbances (Kroeker et al. 2014, Sanford et al. 2014, Gaylord et al. 2015). For example, marine taxa that precipitate calcified shells, such as molluscs, may experience increased vulnerability to shell-crushing predation under OA (Orr et al. 2005, Hendriks et al. 2010, Gazeau et al. 2013). This trend could also be exacerbated by the fact that shell-crushing predators, such as crabs, appear to be less susceptible to seawater acidification (Amaral et al. 2012, Kroeker et al. 2013, 2014, although see Coffey et al. 2017). Increased costs of calcification, therefore, may have important implications for gastropods and other molluscs that use their shells to deter shell-crushing (durophagous) predation.

Durophagy has been a common method of predation since the Palaeozoic (Vermeij et al. 1981, Alexander & Dietl 2003, Leighton 2011). Molluscs, such as gastropods, are therefore dependent on their shells as

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an important defense against predation (Palmer 1979, Vermeij et al. 1981, Alexander & Dietl 2003). Mollusc shells have varying amounts of organic matrix, and, regardless of microstructural differences, have little ability to bend before catastrophic breakage/shattering occurs (Wainwright et al. 1976). Although such structures are strong and rigid, they remain vulnerable to compressive and tensile forces exerted by shell-crushers. For example, durophagous crabs are capable of exerting large forces with their shell-crushing chelae (Taylor 2000). Additionally, crabs often apply methods of force-pulsing on mollusc shells, wherein the crab repeatedly point-loads the shell and creates material fatigue through propagation of microfractures, thereby increasing the likelihood of shell failure (Boulding & LaBarbera 1986). However, force-pulsing methods require predators to expend more time and energy (Boulding & LaBarbera 1986, Miller & LaBarbera 1995), and the existence of repair scars on shells documents the occurrence of unsuccessful attacks (Molinaro et al. 2014, Stafford et al. 2015).

Complicating efforts to understand predator–prey interactions involving molluscs is the issue that molluscs demonstrate a variety of plastic responses that may increase the search time, and/or force, time, and energy that a durophagous predator must spend handling the shell (Kroeker et al. 2014). Morphological changes to the shell generally enhance resistance to predation (Zipser & Vermeij 1978), but often require additional shell calcification. For example, gastropods may increase shell ornamentation or thickness under threat of predation (Appleton & Palmer 1988, Avery & Etter 2006). Some gastropods are also capable of making changes to their general morphology that increases their shell strength (Bourdeau 2012), which could be critical if calcium carbonate becomes limited.

In addition, behavioural changes from exposure to predation cues may cause animals to attenuate their foraging activities and can thereby reduce growth (Appleton & Palmer 1988, Chivers & Smith 1998, Trussell et al. 2003). Because smaller molluscan shells are typically weaker (Currey & Hughes 1982), they are more vulnerable to shell-crushing predation. Organisms exposed to both OA and predation might therefore experience reduced growth that would make them critically vulnerable to predation. However, seawater acidification disrupts antipredatory fleeing responses to sea stars in some gastropods (Jellison et al. 2016). The potentially mixed effects of both OA and predation risk on both gastropod shell growth and plastic shell responses are poorly understood, as there has been only one other long-term study in which gastropods were exposed to both OA and predator cues (Landes & Zimmer 2012).

Responses to OA, such as changes to shell integrity, may be relatively inconspicuous, yet important. In the case of shelled gastropods, for instance, experiments that quantify OA effects on behaviour, shell growth, or shell thickness (Landes & Zimmer 2012, Kroeker et al. 2014, Jellison et al. 2016) provide valuable information about predation risk. However, these studies may also remain incomplete, as size is not the only metric or shell property by which prey resist durophagy. Shell strength, while less conspicuous and more difficult to measure, provides a more accurate metric, as it can be used to directly assess resistance to shell crushing. Thus, although researchers often assume stasis in susceptibility to predation when shell growth appears resilient to OA (Gazeau et al. 2013, Kroeker et al. 2013, Lord et al. 2017), shell strength could also be affected. For example, some species of gastropod exposed to acidification exhibit no change in growth, yet experience increased shell dissolution (Nienhuis et al. 2010), which would presumably have a negative effect on shell strength. Most biomechanical studies that examine the impacts of OA on shell strength are limited to bivalves (Welladsen et al. 2010, Gaylord et al. 2011, Fitzer et al. 2015), with few including gastropods (Amaral et al. 2012, Coleman et al. 2014, Leung et al. 2017a), indicating that there is strong value in conducting further tests of shell strength in a broader array of calcifying taxa, such as gastropods, which are abundant and diverse constituents of coastal food webs.

Although considerable effort in OA research has aimed to identify common patterns across taxa and environments (Gazeau et al. 2013, Kroeker et al. 2014, Gaylord et al. 2015), species-level variation can be equally relevant to understanding the ecological consequences of acidification (Sanford et al. 2014). For example, in rocky intertidal habitats along the northeastern Pacific, the gastropods *Tegula funebralis* (Trochoidea) and *Nucella ostrina* (Muricoidea) are common prey for shell-crushing predators such as crabs. However, the 2 gastropods have different shell microstructure and composition, responses to predation, life histories, and ecological roles. *T. funebralis*, a grazer, has a nacreous (columnar aragonite plates/crystals) shell and periostracum (Geller 1982), while *N. ostrina*, a barnacle and mussel drill, has an outer homogenous calcite layer and inner cross-lamellar aragonite layer with no periostracum (Watabe 1988, Avery & Etter 2006). While calcite is more resistant to dissolution, nacre is mechanically stronger than both

calcite and other forms of aragonite (Watabe 1988). Behaviourally, both species flee the water when exposed to predation cues (Jacobsen & Stabell 2004, Mach & Bourdeau 2011), but several species of *Nucella*, including *N. ostrina*, also respond to predation cues morphologically in the form of shell thickening/inducible defenses (Appleton & Palmer 1988, Pearson 2004), as well as changes in shape (Bourdeau 2012). However, past studies have indicated that there may not be a true induced defense in *N. ostrina*, and instead, the species may simply reduce its growth when exposed to predation cues (Bourdeau 2011). One could therefore imagine a scenario where the 2 species display different growth or calcification responses to OA that would make one species comparatively more or less vulnerable to durophagous predation. Any changes to the vulnerability of one species over the other under seawater acidification could potentially lead to changes in their favourability to predators, shifts in the rankings of prey by predators, and alterations to the strengths of associated trophic links in food webs (Kroeker et al. 2014).

Here, we addressed such issues of variability among species and the potential for overlooked responses, such as shell strength in gastropods, by exposing 2 species of intertidal gastropods from the west coast of North America to both seawater acidification (decreased pH of ~0.5 units) and predation cue for 6 mo. We measured both shell growth and strength as proxies for resistance to durophagy, and considered the implications of the responses that these 2 species exhibit.

2. MATERIALS AND METHODS

2.1. Specimens

To explore the potential ecological implications of OA on gastropods threatened by durophagous predation, juveniles (small individuals) of both *Tegula funebralis* and *Nucella ostrina* were collected from the northern side of Horseshoe Cove in the Bodega Marine Reserve (BMR) near Bodega Bay, California (38° 19′ 0″ N, 123° 04′ 14″ W) in November and December 2016 in accordance with BMR regulations. Collected gastropods were acclimated to laboratory conditions at Bodega Marine Laboratory for at least 3 wk. Initial shell height and width of each gastropod was measured using digital calipers (height and width of *T. funebralis* and *N. ostrina*, respectively: 6.14 ± 0.70 and 7.77 ± 0.81 mm; 12.06 ± 1.43 and 7.95 ± 0.98 mm), and 160 individuals of each species most similar in size were selected for subsequent experiments (see Table 2 & Table S1 in the Supplement at www.int-res.com/articles/suppl/m626p109_supp.pdf).

2.2. Methods

To compare the effects of both OA and predation cues on shell growth, the experiment was divided into 4 water treatments: (1) ambient water, no conspecific cue; (2) ambient water, injured conspecific cue present; (3) low pH water, no conspecific cue; and (4) low pH water, injured conspecific cue present. Gastropods were divided randomly into 32 groups of 10 individuals (16 groups species^{-1}). Each group was randomly assigned to a 10 l tank (n = 2 species × 4 treatments × 4 replicate tanks treatment^{-1} = 32 tanks total; Fig. S1). The growing edge of each gastropod shell was marked with a thin line of coloured nail polish, which provided individuals with unique identifying tags and allowed easy determination of growth during the experiment (see Fig. 2).

Water conditions for each of the 4 treatments were controlled, monitored, tested, and reset every 24 h for 185 d. Once a day, each tank was filled with 7 l of water from 1 of 4 source (sump) tanks: 2 replicate ambient tanks, and 2 replicate low pH tanks (Fig. S1). This volume was sufficient to maintain animal health and minimize shifts in seawater chemistry due to respiration. Water was acquired from the laboratory seawater supply, and was dual filtered to 30 then 5 µm. The 'low pH' water treatments were created daily through direct chemical manipulation via an equimolar addition of 1 M hydrochloric acid (HCl) and 1 M sodium bicarbonate ($NaHCO_3$) (Jellison et al. 2016), which increased dissolved inorganic carbon (DIC) while maintaining alkalinity and reproduced the chemical changes caused by the addition of CO_2, as specified by international standards (Riebesell et al. 2010). Water for the 'ambient' treatments was left unchanged to reflect the natural daily and seasonal changes experienced by organisms around Bodega Bay, including a period of upwelling with naturally lower water pH in the spring months. 'Low pH' conditions approximated a drop of 0.5 pH units (pH_{total}), as determined using the software CO2Calc (Robbins et al. 2010). Each of the 32 tanks was placed in a flow-through seawater table which acted as a temperature bath (mean ± SD: 12.26 ± 1.00°C; Fig. S1, Table S2). TidbiT® temperature loggers, which recorded temperature every 15 min, were placed in tanks on opposite corners of the seawater table to confirm temperature did not differ

across the table and that any spatial segregation between pH or cue treatments would have minimal effects on the results (Fig. S1, Table S2). After each experimental tank was filled with the appropriate water each day, an airtight lid was placed on the tanks to prevent off-gassing of the low pH treatments. There was enough headspace for the gastropods to leave the water, allowing for the possibility of an anti-predatory 'fleeing' response for those exposed to the injured conspecific cue. An airline was placed at the bottom of each tank (<1 bubble s^{-1}) to provide water circulation and prevent a temperature or pH cline from developing. In these respects, each tank imitated a tide pool, a common environment for both species (Jellison et al. 2016) (Fig. S1).

To examine the effects of predation threats, treatments also included a 'no cue' control, as well as a 'cue' condition in which an injured conspecific was used to signal the threat of predation, as both species respond to injured conspecific cues (Jacobsen & Stabell 2004, Mach & Bourdeau 2011). An extra individual of each species was crushed using a pair of pliers, and the dead gastropod was then mixed with 100 ml of seawater and left for 5 to 10 min. Crushing a conspecific was used as a proxy for the chemical effluent simulated by crab-crushing predation, as other methods of predation (e.g. being consumed by a sea star) do not usually result in a shell being crushed. While a combined crab and crushed conspecific cue might elicit a stronger response (Appleton & Palmer 1988), the use of a crushed conspecific cue alone was used as a more conservative, generalized fear response that would be generated by crushing predation, regardless of the predator's identity (e.g. *Cancer productus* or *Romaelon antennarium*) or diet (e.g. Scherer & Smee 2016). A 10 ml aliquot of the 'dead snail' effluent water was then pipetted into each of the appropriate tanks. This cue was added 3 times wk^{-1} to appropriate tanks.

The gastropods were given sufficient food to prevent competition among individuals. *T. funebralis* were fed small pieces of the macroalgae *Pelvetiopsis limitata*, *Mastocarpus papillatus*, and *Ulva lactuca*. *N. ostrina* were fed barnacles (*Balanus glandula* and *Chthamalus dalli*) attached to small rocks that were cleaned of all other organisms and any adherent sediment or debris. Food was refreshed as needed (usually once per week) and to avoid any additional effects of pH on the food source.

To ensure tight control of water conditions, temperature, dissolved oxygen, salinity, and pH (mV) of the 4 sumps were recorded each day using a YSI ProPlus sensor (Table S2), that was in turn calibrated against spectrophotometric pH measurements made on the total scale (Table S2). Temperature data from the YSI were comparable to the TidbiT® data. Daily bottle samples were taken from each sump for analysis of total alkalinity using a Metrohm 855 Robotic Titrosampler to ensure that the addition of HCl and $NaHCO_3$ had not changed the alkalinity (Table S2). An additional water sample was pulled weekly from each sump, and pH was determined using an Ocean Optics Jaz Spectrometer (Table S2). Spectrometer pH and alkalinity data were run through CO2Calc to determine the *in situ* pH and pCO_2.

After 6 mo (180 and 185 d for *N. ostrina* and *T. funebralis*, respectively), a final set of height and width measurements were taken for each gastropod individual to determine differences in growth among treatments over the course of the experiment (see Fig. 2, Tables 2 & S1). Specimens were then prepared for the second experiment to measure any differences in shell strength between the 4 treatments. The gastropods were euthanized by placing them in a freezer (–18°C). Freezing is a common, humane method of euthanasia not known to affect shell structure (A. R. Palmer pers. comm) and is comparable to other studies of shell strength in gastropods (Coleman et al. 2014). After 24 h, the gastropods were then thawed and the body tissue was carefully removed using small forceps. Shells were air-dried for several weeks prior to biomechanical tests. In certain species, material properties of dried shells can differ modestly from those of wet shells; however, the focus of the current experiment was on relative changes across size and species as a function of pH treatment.

A primary goal of measuring shell strength was to determine whether OA might weaken shells sufficiently to be crushed outright by crabs. After weighing each shell using a scale to 0.0001 g accuracy, 20 specimens were randomly selected from each of the 4 treatments for use in biomechanical tests. Dental plaster was poured into 1 cm tall × 2.5 cm wide cups and the gastropods were partially embedded in the plaster as it dried (Fig. 1). Shells were aligned with the axis of coiling perpendicular to the dental plaster, and the apertural lip facing vertically towards the upper plate of an Instron® universal testing system (Fig. 1), similar to another OA study (Coleman et al. 2014). The shell orientation ensured that experimental growth would be the primary source of contact with the Instron®, and roughly simulated the orientation in which a crab would first pick up a gastropod to attempt a static crush (Zipser & Vermeij 1978).

Each shell was crushed to total failure (any fracturing of the shell above the body whorl, indicating the

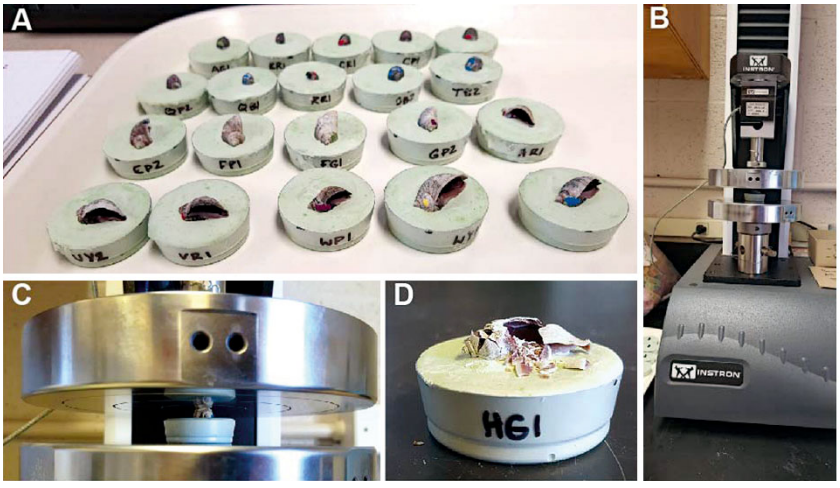

Fig. 1. Instron® crushing tests: (A) prepared specimens, placed in dental plaster plugs, aligned using a protractor, and positioned with the outer apertural lip facing the upper plate of the Instron® and the axis of coiling parallel to the dental plaster/Instron® plates. (B) Instron® universal testing system with a prepared shell between the plates. The upper plate was placed immediately above the highest point of the shell and then lowered at a constant speed until the point of total shell failure. (C) A specimen of *Nucella ostrina* during a crushing trial. The orientation of the shell roughly simulated the manner in which a crab would initially attempt a static crush of the shell (squeezing the sides of the shell). (D) A specimen of *N. ostrina* after crushing. Shells were crushed to the point of total failure, which was a consistent popping or blow-out of the apex/spire in both species

gastropod would be unable to survive the crush). Shells of both species broke in a consistent manner (a distinct 'popping' or 'blow out' of the spire and/or apex). The force to induce total failure of the shell was recorded (maximum compression load, N) (Table S3). After initial analyses, p-values for *N. ostrina* tests were nearly significant ($p = 0.06$), so an additional 10 *N. ostrina* from each treatment were crushed to ensure sample size was not limiting statistical power (Table S3).

2.3. Analyses

To determine the effects of both pH and predation cues on shell growth, generalized linear mixed models (GLMMs) were used, with sumps and tanks as random effects, and pH and predation cue as fixed effects. Separate tests were run for both height and width of each species, using the change in size measured from the beginning and the end of the experiment as the measure of growth (Table S1). For each set of growth measurements, 4 GLMMs were fit (all had sumps and tanks as random effects): a null model with only random effects; a pH-only model; a cue-only model; and a full mixed model with both pH and cue as fixed effects (Table S4). For *T. funebralis*, gamma distributions with a log-link function were used given that the data were skewed to zero, as many *T. funebralis* specimens did not grow (skew >1). To accommodate the gamma distribution, which does not handle zero data, half of the smallest growth increments were added to all zero data (0.005 mm), which is a common data transformation for addressing this problem (Berry 1987). For *N. ostrina*, a Gaussian distribution was used, as the data were roughly normally distributed (Shapiro-Wilk test for normality, $p > 0.05$). The best fit model for each growth series was determined as the model with the lowest Akaike's information criterion (AIC) value (Table S4). Models were ranked from best to worst (1–4). Log-likelihood ratio tests were conducted to determine which models were statistically distinguishable from the null and from each other. All GLMM models and log-likelihood ratio tests were conducted using the 'lme4' package in R v.3.4.4, and the models were plotted and checked using the 'DHARMa' package (Fig. S2).

Shell strength (maximum force recorded at the point of shell failure) was analyzed using 2-way ANCOVAs to determine the effects of pH and cue on shell strength, with dry shell mass as a covariate of the response variable (maximum crushing force). A Shapiro-Wilk test for normality and a Levene's test for homogeneity of variances were also conducted to confirm the data met the model assumptions. To test whether any spatial segregation of treatments or tanks influenced our results, additional 2-way ANCOVAs were run on tank averages. All ANCOVA analyses were conducted using the XLSTAT program for Microsoft Excel.

Due to logistical constraints concerning tank access, the cue treatments for both species were positioned on one side of the seawater table. The spatial segregation of cue/no-cue treatments caused certain aspects of the experiment to be pseudoreplicated (side of the water table confounded with cue treatment). While we acknowledge this segregation may cause challenges for completely unambiguous interpretation of the results, it is important to note that in all other respects, experimental conditions were

carefully controlled, leading to no obvious differences between the 2 sides of the table (the table was only about 60 cm wide, and tanks were placed less than 5 cm apart). For example, the temperature loggers placed in tanks on opposite corners of the sea table (including a cue and no-cue tank) were indistinguishable (Table S2), and seawater flow was perpendicular to the placement of all tanks.

3. RESULTS

3.1. Shell growth

Shell growth of *Tegula funebralis* decreased significantly under low pH conditions and in the presence of predation cues, with log-likelihood ratio tests indicating that a full mixed effects model including pH, cue, and their interaction as fixed effects significantly outperformed all other models (log-likelihood test, $p < 0.0001$) (Figs. 2B,C,D,I,J, 3A & 4A, Tables 1 & S4). In particular, *T. funebralis* reared under low pH grew 83% less than when in ambient treatments (log-likelihood test, width $p = 0.001$) (Tables 1, 2, S1 & S4), with 17 individuals raised under low pH not growing at all (Figs. 3A & 4A, Table S1), and most experiencing dissolution resulting in pitting and small holes around the apex (Fig. 2C,D,I,J). Injured conspecific cues also had a significant effect on shell growth, as *T. funebralis* exposed to cue grew 63% less than those not exposed to cue (log-likelihood test, width $p = 0.0085$) (Figs. 2B,D, 3A & 4A, Tables 1, 2, S1 & S4). There was likely a significant interaction between pH and cue, possibly due to a zero-boundary effect, as pH reduced growth such that cue could not decrease growth additively in mixed treatments (there could not be growth less than zero) (Figs. 3A & 4A).

In contrast, shell growth in *Nucella ostrina* was not affected by pH, as pH models were indistinguishable from the null (log-likelihood test, width $p = 0.6008$) (Figs. 2G,H, 3B & 4B, Table 1). Instead, both cue models (height and width) performed the best, indicating that only the injured conspecific cue significantly affected growth in *N. ostrina* (log-likelihood tests, $p < 0.0001$), with cue-exposed specimens growing 34% less than those not exposed to cue (Figs. 2F,H, 3B & 4B, Tables 1 & S4), consistent with previous reports (Bourdeau 2011, Lord et al. 2017). Similar to Bourdeau (2011), there was no evidence

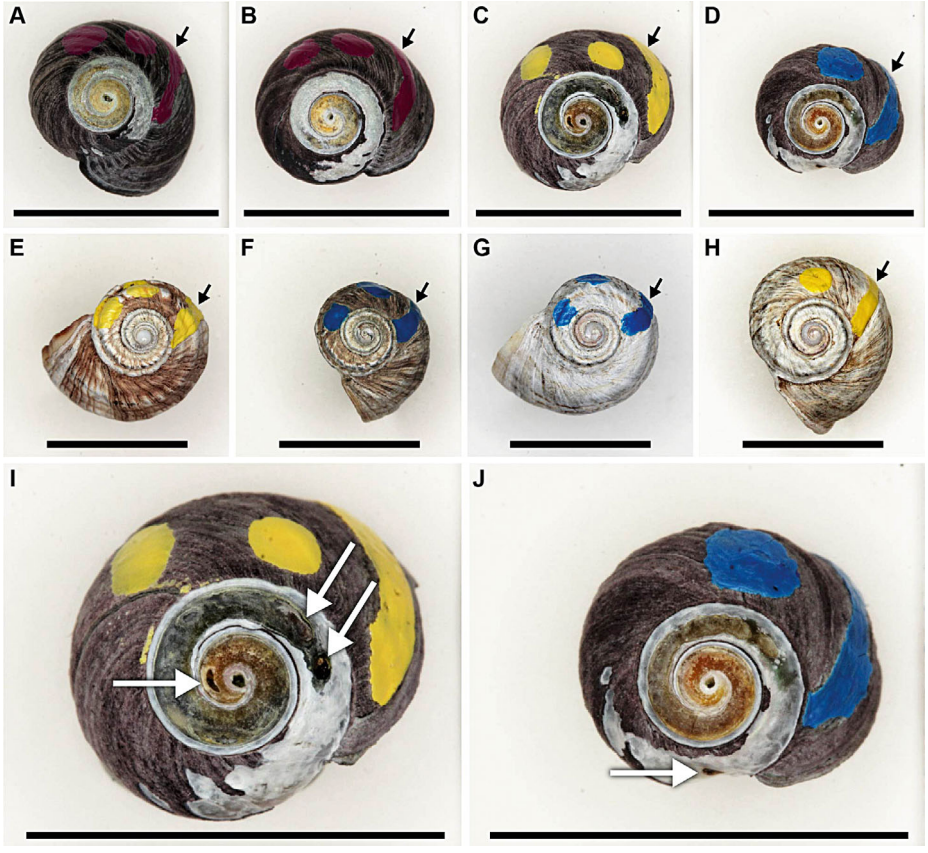

Fig. 2. Apical views of representative gastropods from each of the 8 experimental treatments. Black arrows: nail polish lines along the body whorl indicating the leading edge of the shell and thus the gastropod's size at the beginning of the experiment. All subsequent growth (clock-wise from the nail polish line) indicates growth during the 6 mo experimental treatment. Nail polish was aligned at approximately the same angle for each specimen to allow easy visual comparison of shell growth. Colour and extra dots were used for specimen identification. *Tegula funebralis*: (A) ambient, no cue; (B) ambient, cue; (C) low pH, no cue; (D) low pH, cue. *Nucella ostrina*: (E) ambient, no cue (F) ambient, cue; (G) low pH, no cue; (H) low pH, cue. (I) and (J) are expanded images of (C) and (D), respectively. White arrows: dissolution and pitting of *T. funebralis* shells experienced under low pH treatments (often resulting in holes). Scale bar = 1 cm

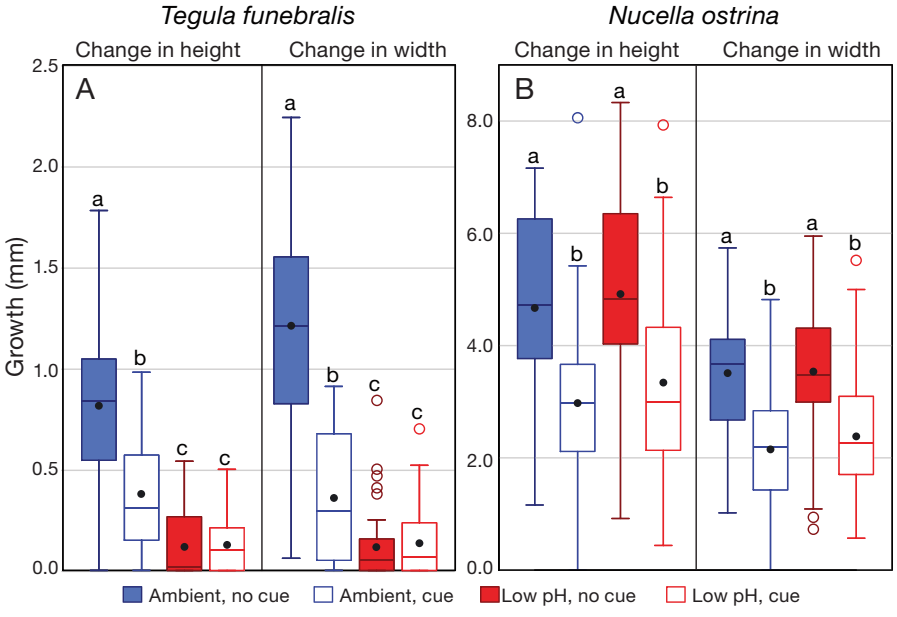

Fig. 3. New shell growth of (A) *Tegula funebralis* and (B) *Nucella ostrina* over the 185 d experiment. Note that *y*-axes differ between panels (*N. ostrina* grew faster than *T. funebralis*). Data are from Table S1 in the Supplement. Each legend item indicates a treatment group (n = 40 species^{-1}). Boxes: upper and lower quartiles; central lines: medians; black circles: means; whiskers: min./max. data; open circles: outliers. Different letters above boxes indicate groups that differ significantly

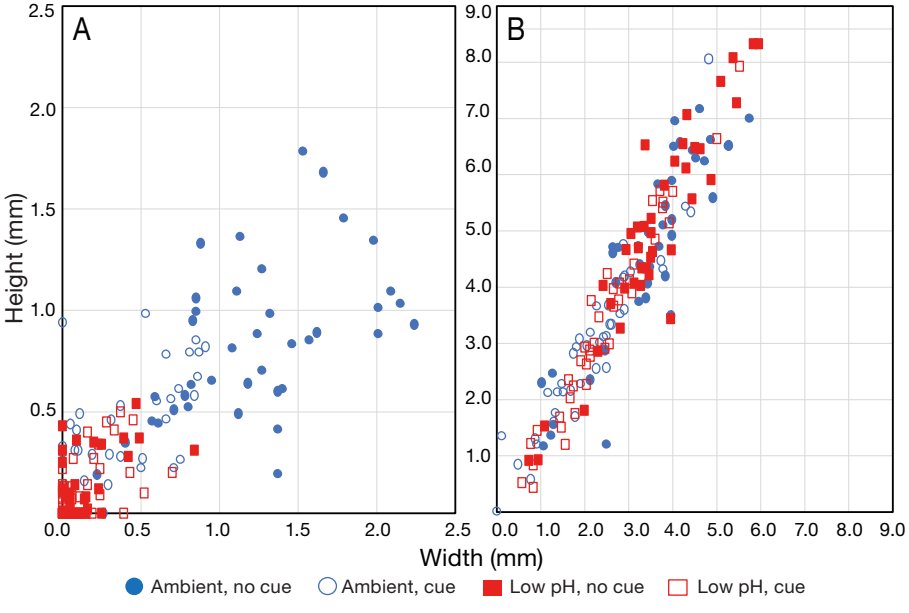

Fig. 4. New shell growth of (A) *Tegula funebralis* and (B) *Nucella ostrina* over the 185 d experiment. Note that *y*-axes differ between panels. Data are from Table S1 in the Supplement. Each legend item indicates a treatment group (n = 40 species^{-1}). Color indicates pH treatment. Solid shapes: treatments without a cue; open shapes: treatments with a cue. Scatterplots do not indicate any discernable changes to exterior shell morphology (height and width) caused by any of the experimental treatments

of shell thickening (mass-to-size ratios between treatments were indistinguishable) (Tables 2 & S3) or changes to morphology (Fig. 4) indicative of an induced defense, despite inducible defenses often being observed for the genus (Appleton & Palmer 1988, Pearson 2004, Bourdeau 2011, 2012).

Note that for all models for both species, the defined random effects (sumps and tanks) had standard deviations close to zero (all <1; Table S4), indicating that these random effects had no appreciable effect on growth. As the residual error was also generally low, the results are not likely a function of any potential artefacts due to tank or treatment placement, and most of the explanatory power for changes in growth can be safely attributed to the differences between treatments.

For cue treatments, when exposed to cue effluent, both species left the water within ~10 min. Individuals often hid, clustered, or remained above the water even after 24 h. While it was not possible to measure how often gastropods returned to the water, casual observation throughout the experiment suggests that gastropods exposed to cue spent less time in the water. Lack of induced shell thickening or changes in morphology (Fig. 4) indicates that, similar to *T. funebralis*, cue-exposed specimens of *N. ostrina* simply grew less.

3.2. Shell strength

While the 2 species demonstrated very disparate results in terms of growth, with *T. funebralis* shell growth strongly impacted by pH but *N. ostrina* being unaffected, biomechanical tests indicated both species experienced reduced shell strength when exposed to pH (Table 3). However, the effect size was different,

Table 1. Growth generalized linear mixed models (tank and sump as random effects; null model includes only random effects) and log-likelihood (Pr > Chi-sq) comparisons of models used to determine the effects of pH and cue on shell growth. Models were ranked (1–4 = best–worst) based on Akaike's information criterion (AIC) scores (lower AIC scores were considered better models). Detailed results/reports of each model can be found in Table S4 in the Supplement. BIC: Bayesian information criterion

Tegula funebralis							*Nucella ostrina*						
Model Rank	Effect(s)	AIC	BIC	LogLik	Deviance	df resid	Model Rank	Effect(s)	AIC	BIC	LogLik	Deviance	df resid
MIXED MODELS													
Height													
1	pH × Cue	−92.2	−70.7	53.1	−106.2	153	1	Cue only	621.4	636.8	−305.7	611.4	155
2	pH only	−87.5	−72.2	48.8	−97.5	155	2	pH × Cue	625.1	646.6	−305.5	611.1	153
3	Cue only	−75.2	−59.8	42.6	−85.2	155	3	Null	635.4	647.7	−313.7	627.4	156
4	Null	−73.9	−61.6	40.9	−81.9	156	4	pH only	637.1	652.4	−313.5	627.1	155
Width													
1	pH × Cue	−69.6	−48.0	41.8	−83.6	153	1	Cue only	502.4	517.7	−246.2	492.4	155
2	pH only	−54.8	−39.4	32.4	−64.8	155	2	pH × Cue	505.7	527.3	−245.9	491.7	153
3	Cue only	−50.8	−35.4	30.4	−60.8	155	3	Null	520.0	532.3	−256.0	512.0	156
4	Null	−45.9	−33.6	26.9	−53.9	156	4	pH only	521.8	537.1	−255.9	511.8	155
MODEL COMPARISONS													
Height													
Rank	Model	4	1	2	3		Rank	Model	3	2	4	1	
4	Null	–					3	Null	–				
1	pH × Cue	<0.0001	–				2	pH × Cue	0.0010	–			
2	pH only	<0.0001	0.0131	–			4	pH only	0.5736	0.0003	–		
3	Cue only	0.0698	<0.0001	1.0000	–		1	Cue only	<0.0001	0.8443	<0.0001	–	
Width													
Rank	Model	4	1	2	3		Rank	Model	3	2	4	1	
4	Null	–					3	Null	–				
1	pH × Cue	<0.0001	–				2	pH × Cue	0.0001	–			
2	pH only	0.0010	<0.0001	–			4	pH only	0.6008	<0.0001	–		
3	Cue only	0.0085	<0.0001	1.0000	–		1	Cue only	<0.0001	0.7255	<0.0001	–	

and *T. funebralis* experienced much greater reductions in shell strength from exposure to low pH than did *N. ostrina*. *T. funebralis* shells exposed to low pH were significantly (41%) weaker than ambient shells, regardless of size, failing at forces ~171 N less than those grown under ambient conditions (2-way ANCOVA: $F_{72,1}$ = 18.049, p < 0.0001; Fig. 5A, Table 3). Shell strength in *N. ostrina* was compromised by pH, despite resilient growth, with shells exposed to low pH being 9% weaker and failing at forces ~44 N less than ambient shells (2-way ANCOVA: $F_{112,1}$ = 6.591, p = 0.0116; Fig. 5B). This pattern also held when average values for each tank were used in the analyses (2-way ANCOVA: *T. funebralis*: $F_{8,1}$ = 7.119, p = 0.0280; *N. ostrina*: $F_{8,1}$ = 5.932, p = 0.0410; Table 3).

For both species, shell strength was significantly correlated with size (mass) (2-way ANCOVA: *T. funebralis*: r = 0.4140, $F_{72,1}$ = 20.670, p < 0.0001; *N. ostrina*: r = 0.460, $F_{112,1}$ = 87.949, p < 0.0001), with larger shells requiring more force to crush to total failure (breakage of the spire) (Fig. 5, Table 3). However, it is critical to reiterate that shells exposed to low pH failed at lower forces than did shells of the same size grown under ambient pH conditions (Fig. 5). Conspecific cues did not affect shell strength in either species, indicating cue simply reduced growth for both species (Table 3).

4. DISCUSSION

Reductions in shell growth and/or strength indicates increased vulnerability of both gastropod species to predation under OA. Independent of growth, shells of both *Tegula funebralis* and *Nucella ostrina* grown under low pH conditions were 'cryptically' vulnerable in that low pH shells were weaker than ambient pH shells of the same size (Fig. 5). A study that only examined shell growth might have concluded that *N. ostrina* was unaffected by OA, yet we demonstrated that simulated OA conditions reduced shell strength. Our results therefore indicate

Table 2. Summary data (means ± SD) for each treatment and analyses of shell growth and strength. Tank averages are also included for use in strength analyses (mass and max. load). Raw data measurements are available in Tables S1 (growth) and S3 (strength) in the Supplement

Treatment		Tank no.	*Tegula funebralis*				*Nucella ostrina*			
			Growth (mm)		Strength		Growth (mm)		Strength	
			Height	Width	Mass (g)	Max. load (N)	Height	Width	Mass (g)	Max. load (N)
All tanks										
Ambient	No Cue	All	0.82 ± 0.40	1.21 ± 0.54	0.2001 ± 0.0612	453.1 ± 104.6	4.66 ± 1.72	3.46 ± 1.20	0.5997 ± 0.1787	499.7 ± 109.4
Ambient	Cue	All	0.38 ± 0.29	0.39 ± 0.32	0.1632 ± 0.0483	383.3 ± 118.1	2.97 ± 1.50	2.17 ± 1.10	0.5570 ± 0.2070	500.2 ± 134.4
Low pH	No Cue	All	0.12 ± 0.16	0.12 ± 0.18	0.1351 ± 0.0395	261.9 ± 109.0	4.96 ± 1.86	3.56 ± 1.20	0.6372 ± 0.2265	470.2 ± 149.5
Low pH	Cue	All	0.14 ± 0.15	0.14 ± 0.18	0.1282 ± 0.0383	231.8 ± 112.9	3.35 ± 1.74	2.46 ± 1.13	0.5022 ± 0.1459	441.7 ± 96.8
Individual tanks										
Ambient	No Cue	1	0.86 ± 0.37	1.53 ± 0.35	0.1915 ± 0.0553	390.2 ± 75.3	4.14 ± 1.95	3.58 ± 1.36	0.6034 ± 0.1193	536.4 ± 64.2
		2	0.90 ± 0.36	1.59 ± 0.37	0.2312 ± 0.0658	544.1 ± 114.7	4.68 ± 1.54	3.72 ± 1.17	0.6988 ± 0.0896	530.5 ± 111.4
		3	0.59 ± 0.35	0.80 ± 0.56	0.1570 ± 0.0244	419.9 ± 96.7	4.10 ± 1.64	2.94 ± 1.21	0.4782 ± 0.2257	455.1 ± 136.1
		4	0.95 ± 0.46	0.91 ± 0.35	0.2207 ± 0.0754	485.2 ± 84.3	5.72 ± 1.44	3.61 ± 1.06	0.6158 ± 0.1887	475.2 ± 107.5
Ambient	Cue	5	0.58 ± 0.32	0.48 ± 0.36	0.1567 ± 0.0533	333.8 ± 105.1	2.25 ± 1.10	1.86 ± 0.87	0.4123 ± 0.1115	396.0 ± 49.4
		6	0.40 ± 0.26	0.33 ± 0.33	0.1326 ± 0.0278	295.3 ± 62.7	3.48 ± 1.36	2.58 ± 1.12	0.6753 ± 0.1283	558.3 ± 93.3
		7	0.33 ± 0.24	0.28 ± 0.33	0.2120 ± 0.0547	447.5 ± 150.1	3.20 ± 2.03	2.21 ± 1.47	0.5577 ± 0.3343	484.8 ± 189.2
		8	0.23 ± 0.25	0.35 ± 0.30	0.1514 ± 0.0099	456.6 ± 64.3	2.95 ± 1.30	2.02 ± 0.88	0.5646 ± 0.1151	546.9 ± 113.4
Low pH	No Cue	9	0.08 ± 0.14	0.18 ± 0.25	0.1332 ± 0.0306	229.6 ± 60.8	5.84 ± 1.10	4.17 ± 0.79	0.8196 ± 0.0616	527.1 ± 82.3
		10	0.14 ± 0.17	0.15 ± 0.16	0.1479 ± 0.0510	333.4 ± 125.8	5.36 ± 1.89	3.62 ± 1.20	0.5893 ± 0.2175	469.4 ± 150.7
		11	0.15 ± 0.15	0.08 ± 0.16	0.1507 ± 0.0447	268.0 ± 118.4	4.62 ± 2.54	3.43 ± 1.71	0.6137 ± 0.2913	496.3 ± 184.5
		12	0.10 ± 0.18	0.09 ± 0.15	0.1023 ± 0.0087	213.1 ± 124.5	4.01 ± 1.25	3.01 ± 0.71	0.5363 ± 0.1157	384.5 ± 110.8
Low pH	Cue	13	0.13 ± 0.11	0.18 ± 0.20	0.1152 ± 0.0320	294.3 ± 162.5	3.71 ± 1.12	2.63 ± 0.82	0.5613 ± 0.0842	483.1 ± 93.2
		14	0.15 ± 0.19	0.16 ± 0.11	0.1514 ± 0.0606	189.0 ± 123.1	5.00 ± 1.70	3.50 ± 1.27	0.6101 ± 0.1697	477.2 ± 108.0
		15	0.16 ± 0.19	0.11 ± 0.16	0.1254 ± 0.0116	233.5 ± 103.8	2.68 ± 1.44	1.97 ± 0.83	0.4295 ± 0.1171	400.8 ± 95.3
		16	0.11 ± 0.10	0.11 ± 0.22	0.1209 ± 0.0345	210.3 ± 21.6	2.02 ± 1.10	1.75 ± 0.70	0.4122 ± 0.1086	405.1 ± 64.1

that measures of shell strength are critical to properly assessing the vulnerability of calcifiers to OA. For example, a gastropod that may be of a size sufficient to avoid shell-crushing predation under ambient conditions may be vulnerable at low pH conditions, such as those predicted for the end of the 21st century (Orr et al. 2005).

Decreased shell growth under OA further compounds the effects of shells weakened by exposure to OA, making it more difficult for gastropods to grow to a size which would allow them to avoid shell-crushing predation, resulting in smaller individuals that are critically vulnerable to predators such as crabs. In addition, the presence of predators also reduces shell growth, as fearful gastropods spend less time foraging (Trussell et al. 2003), further compromising shell growth under future OA conditions. For example, mollusc shells typically require more force to fail than can be exerted by their predators (Boulding & LaBarbera 1986, Miller & LaBarbera 1995), yet 14 (of 40) of the *T. funebralis* grown under low pH and/or cue conditions failed at forces less than can be produced by predators such as *Cancer productus* (140–264 N; Taylor 2000) (Fig. 5A). Thus, OA could produce conditions where crabs could crush *T. funebralis* outright, instead of the usual force-pulsing or peeling methods which are more time consuming and have less guarantee of success (Zipser & Vermeij 1978). For instance, *C. productus* in the field take >9 min on average to peel an individual *T. funebralis* (L. R. Leighton unpubl. data). *T. funebralis* takes significantly more time to grapple and handle, with lower rates of success (>7 min, 61% success) than those for *N. ostrina* (2 min, 96% success), which can be crushed, rather than peeled (Mendonca et al. 2017). In contrast, a typical static crush can take <1 min (Mendonca et al. 2017). The combined effects of reduced shell strength and growth may therefore result in significantly decreased handling times for

Table 3. Two-way ANCOVA results of pH and cue treatments on shell strength. Maximum force (N) was used as the response variable for shell strength, and shell mass (g) was the covariable, used as a proxy for size. An additional set of ANCOVAs was run on average strength (N) and size (g) measurements for each tank. Shapiro-Wilk test for normality $p > 0.05$ for all ANCOVAs. Levene's test for homogeneity of variances $p > 0.05$ for all ANCOVAs

Effect(s)	*Tegula funebralis*					*Nucella ostrina*				
	SS	df	MS	*F*	p	SS	df	MS	*F*	p
Individual shells										
pH	179045.450	1	179045.450	18.049	**<0.0001**	54230.240	1	54230.240	6.591	**0.0116**
Cue	7604.150	1	7604.150	0.767	0.3842	18463.120	1	18463.120	2.244	0.1370
Mass	205056.650	1	205056.650	20.670	**<0.0001**	723664.730	1	723664.730	87.949	**<0.0001**
pH × cue	172.400	1	172.400	0.017	0.8955	2096.570	1	2096.570	0.255	0.6147
pH × mass	4698.520	1	4698.520	0.474	0.4935	4965.300	1	4965.300	0.603	0.4389
Cue × mass	458.350	1	458.350	0.046	0.8304	8.670	1	8.670	0.001	0.9740
pH × cue × mass	1139.440	1	1139.440	0.115	0.7357	8013.290	1	8013.290	0.974	0.3258
Within	714253.900	72	9920.000			921564.300	112	8228.000		
Total	1586311.100	79				1861381.900	119			
All shells per tank										
pH	21538.204	1	21538.204	7.119	**0.0280**	6655.959	1	6655.959	5.932	**0.0410**
Cue	1851.492	1	1851.492	0.612	0.4570	2119.721	1	2119.721	1.889	0.2070
Mass	119980.392	1	119980.392	38.658	**<0.0001**	27822.261	1	27822.261	24.797	**0.0010**
pH × cue	1385.911	1	1385.911	0.458	0.5180	106.572	1	106.562	0.095	0.7660
pH × mass	1718.783	1	1718.783	0.568	0.4730	496.104	1	496.104	0.422	0.5250
Cue × mass	452.211	1	452.211	0.149	0.7090	773.293	1	773.293	0.689	0.4310
pH × cue × mass	6205.456	1	6205.456	2.051	0.1900	561.588	1	561.588	0.501	0.4990
Within	24202.696	8	3025.337			8976.000	8	1122.000		
Total	177335.145	15				47511.498	15			

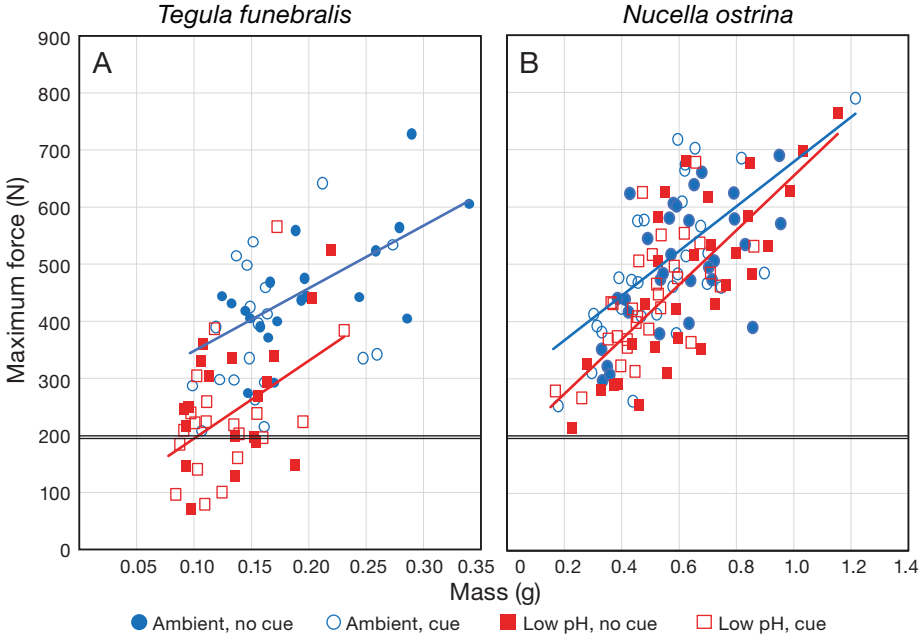

Fig. 5. Shell strength of (A) *Tegula funebralis* and (B) *Nucella ostrina* after experimental treatments. Note that *x*-axes differ between panels (*N. ostrina* grew larger than *T. funebralis* and therefore weighed more; *N. ostrina* specimens were approaching adult size at the end of the experiment). Mass of dried shells was a proxy for size. Maximum force values were recorded by the Instron® at total shell failure. Treatments are indicated by colour and shape (n = 20 and 30 for *T. funebralis* and *N. ostrina*, respectively). Blue (ambient) and red (low pH) trend lines indicate 95% confidence lines for pH treatments. Black line (200 N) indicates conservative crushing-force estimates for adult *Cancer productus* (Taylor 2000). As *N. ostrina* is often observed being crushed outright by crabs (e.g. Mendonca et al. 2017), this suggests that the maximum force values (*y*-axis), and subsequent interpretation, are conservative

durophagous predators (Leighton 2002), creating indirect ecological consequences wherein the per capita consumption rates of crabs on gastropods may increase (Kroeker et al. 2014).

Impaired strength and growth may also increase the vulnerability of gastropods by increasing the time required to reach a size refuge wherein resistance to durophagy is more likely. In particular, *T. funebralis* is a slow-growing species (Frank 1975). Over the course of the 6 mo experiment, 4 (of 80) *T. funebralis* from the ambient treatments did not grow, whereas 17 (of 80) from low pH treatments did not grow. De-

creased growth rates, coupled with impaired shell strength, therefore suggest that species such as *T. funebralis* may spend considerably more time in a critically vulnerable state. These effects would be even more pronounced in environments where gastropods experience greater predation risks.

In addition, many of the *T. funebralis* exposed to low pH developed small, complete holes through the shell near the apex (Fig. 2C,D,I,J). While apex abrasion is typical for *T. funebralis* (Geller 1982), it rarely produces overt holes, especially in juveniles. Holes present substantial weakness to shell-crushing predators, and may make affected individuals more detectable to chemosensitive predators (octopods, crabs, sea stars) even if the gastropod foot is retracted, suggesting strong ecological consequences for *T. funebralis* due to OA. Overall, the consequences of seawater acidification appear to be far more severe for *T. funebralis* than for *N. ostrina*.

The dissimilar effects of OA on 2 gastropods that co-exist in many of the same habitats signals the extensive implications of OA for coastal ecosystems. For instance, as *T. funebralis* experienced both reduced growth and shell integrity to a far greater extent than *N. ostrina*, it is conceivable that the per capita consumption rate of crabs feeding on *T. funebralis* populations might increase relative to *N. ostrina*, especially if the weakened *T. funebralis* become a more favoured prey item. Furthermore, *T. funebralis* shells are proportionately stronger than shells of *N. ostrina* (based on both mass and size; Tables S1 & S3). As *T. funebralis* only exhibit behavioural fleeing responses to predation cues (Jacobsen & Stabell 2004), this species appears to rely on its shell and ability to flee to deter predation. Not only are crabs much more mobile than gastropods, but *T. funebralis* also exhibit impaired antipredatory responses under decreased seawater pH (Jellison et al. 2016). Therefore, the large reductions in shell growth and strength, combined with impaired antipredatory responses, indicate that *T. funebralis* are likely to be increasingly vulnerable to predation under seawater acidification. Disproportionate effects on any one species in a food web could not only have notable consequences for populations of species, such as *T. funebralis*, but could also potentially change the ranking or favourability of prey items, increasing predation pressure on those species.

Shell composition also may contribute to the different responses to OA for the 2 gastropods. While nacre (produced by *T. funebralis*) is mechanically stronger than other shell forms, it is energetically expensive to produce and susceptible to dissolution (Currey 1988). In contrast, calcite (the outer layer of *N. ostrina* and other muricoid shells) is energetically cheaper and more resistant to dissolution (Currey 1988, Palmer 1992), possibly buffering the effects of OA (Nienhuis et al. 2010). Examining shell composition and strength provides insight into how OA affects shells, and which species may be more or less vulnerable to OA. Taxonomic groups of molluscs have predictable shell compositions (Watabe 1988), yet composition as a means of identifying susceptibility to OA has been underutilized (Leung et al. 2017b).

While it is possible that crabs may also be affected by OA (Landes & Zimmer 2012, Dodd et al. 2015, Coffey et al. 2017, Lord et al. 2017), the literature is less conclusive for crabs, other crustaceans, and arthropods in general (Amaral et al. 2012, Kroeker et al. 2013, 2014), minimally suggesting asymmetrical effects on molluscs relative to their crustacean predators. Although one study has shown mechanical weakness of crab chelae material (Coffey et al. 2017), material weakness of the chelae may not affect the muscular strength of the chelae or ability of the crab to force-pulse, as the forces exerted by crabs are still typically much less than that which is required to break the shells of their prey outright (Boulding & LaBarbera 1986, Miller & LaBarbera 1995). Another long-term study found that the length of the claw closer musculature of green crabs *Carcinus maenas* decreased with exposure to OA, yet claw strength appeared unaffected by OA and was instead significantly stronger with increased temperature (Landes & Zimmer 2012).

The cryptic reductions in shell strength, regardless of size, suggest easily overlooked consequences of OA that will increase the vulnerability of calcifying organisms to predation, and emphasize the importance of biomechanical experiments. Direct tests of shell strength are therefore critical to fully evaluate the vulnerability of calcifying organisms to OA. Impaired shell strength and growth of gastropods also suggest indirect ecological effects, potentially reducing handling times for prey and increasing the per capita consumption rates on gastropod populations. However, the dissimilar effects of OA on both species studied here also suggests that shifts in biotic interactions will be asymmetrical, further disrupting the balance of these ecosystems, and highlighting the importance of species-level assessments. We are therefore likely underesti-mating the ecological effects of OA, particularly the differential increased vulnerability of calcifiers to predation.

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