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## Research

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### Author for correspondence:

Eric Sanford

e-mail: [edsanford@ucdavis.edu](mailto:edsanford@ucdavis.edu)

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# Ocean acidification increases the vulnerability of native oysters to predation by invasive snails

Eric Sanford<sup>1</sup>, Brian Gaylord<sup>1</sup>, Annaliese Hettinger<sup>1</sup>, Elizabeth A. Lenz<sup>1</sup>, Kirstin Meyer<sup>2</sup> and Tessa M. Hill<sup>3</sup>

<sup>1</sup>Department of Evolution and Ecology and Bodega Marine Laboratory, University of California Davis, Bodega Bay, CA 94923, USA

<sup>2</sup>Department of Biology, Northern Michigan University, Marquette, MI 49855, USA

<sup>3</sup>Department of Earth and Planetary Sciences and Bodega Marine Laboratory, University of California, Davis, CA 95616, USA

There is growing concern that global environmental change might exacerbate the ecological impacts of invasive species by increasing their *per capita* effects on native species. However, the mechanisms underlying such shifts in interaction strength are poorly understood. Here, we test whether ocean acidification, driven by elevated seawater  $p\text{CO}_2$ , increases the susceptibility of native *Olympia* oysters to predation by invasive snails. Oysters raised under elevated  $p\text{CO}_2$  experienced a 20% increase in drilling predation. When presented alongside control oysters in a choice experiment, 48% more high- $\text{CO}_2$  oysters were consumed. The invasive snails were tolerant of elevated  $\text{CO}_2$  with no change in feeding behaviour. Oysters raised under acidified conditions did not have thinner shells, but were 29–40% smaller than control oysters, and these smaller individuals were consumed at disproportionately greater rates. Reduction in prey size is a common response to environmental stress that may drive increasing *per capita* effects of stress-tolerant invasive predators.

## 1. Introduction

Ecosystems are subjected to a growing number of anthropogenic impacts, creating a pressing need for studies that consider the interactive effects of these stressors [1]. In particular, there is growing concern that global environmental change might exacerbate the ecological influence of invasive species by increasing their competitive or predatory effects on native species [2–4]. Such effects could take at least two forms. Climate change could drive density-mediated effects, whereby the abundance of invasive competitors or predators increase, with detrimental consequences for native communities [2,5,6]. Alternatively, functional changes might arise (i.e. interaction modification effects; *sensu* [7]), where the *per capita* effect of an invasive competitor or predator is increased by changes in the physical environment. For example, small increases in river temperatures are predicted to increase the *per capita* effects of invasive piscivores on salmon and other native fishes in North America [3,8]. A recent meta-analysis found that increasing temperature and carbon dioxide ( $\text{CO}_2$ ) generally have negative impacts on the performance of native species in aquatic systems, with less impact on non-native species [6]. These differential responses might increase the susceptibility of native species to stress-tolerant, invasive consumers. Although interactive effects between global environmental change and invasive species are plausible, these effects have received relatively little empirical attention, and thus mechanisms underlying potential shifts in interaction strength remain poorly understood [9].

Oysters provide key ecological services in estuaries (e.g. ecosystem engineering, nutrient cycling, reduction of anthropogenic eutrophication [10]), but have been devastated in many regions of the world [11]. Such declines have

been attributed to a combination of stressors, including over-fishing, disease, habitat loss, pollution and hypoxia [10,11]. In estuaries along the west coast of North America, invasive predatory snails also threaten native oysters by drilling through oyster shells, often with strong impacts on local oyster populations [12–14].

Ocean acidification has recently been identified as an additional, growing threat to oysters and other bivalves [15–18]. As human activities have increased the atmospheric concentrations of CO<sub>2</sub>, roughly one-third of this anthropogenic CO<sub>2</sub> has been absorbed by the oceans, driving reductions in pH and carbonate ion concentrations [19]. These changes make it more difficult for many marine calcifiers, including various bivalve species, to build calcium carbonate shells [20]. As a result, ocean acidification may reduce bivalve growth and survival, and can lead to individuals with smaller and/or thinner shells [15–18]. Although the direct effects of changing carbonate chemistry have received considerable attention [20], relatively little is known about how ocean acidification might alter species interactions [21–24].

Given potential interactions between abiotic and biotic stressors, it is possible that ocean acidification could increase the vulnerability of native oysters to invasive predators. Starting in the 1800s, human exploitation reduced remarkably the abundance of native *Olympia* oysters (*Ostrea lurida*) in estuaries along the west coast of North America [25], and populations may be further threatened by invasive predators, including an invasive snail, the Atlantic oyster drill *Urosalpinx cinerea* [12–14]. *Olympia* oysters rarely co-occur with native predatory snails, and therefore drilling predation represents a relatively novel stressor for this species [12–14]. Recent studies also indicate that ocean acidification can negatively affect the early life stages of *Olympia* oysters, with exposure to elevated CO<sub>2</sub> resulting in substantially reduced juvenile growth [18,26].

Here, we investigate whether ocean acidification and invasive oyster drills have synergistic, negative impacts on oysters native to California estuaries. Specifically, we tested two hypotheses. First, we explored whether elevated CO<sub>2</sub> would lead to oysters that had thinner shells, which could be drilled at higher rates by invasive snails. Second, because some snails that prey on bivalves are known to selectively attack thin-shelled individuals [27], we examined whether snails provided with a choice of prey raised under ambient versus elevated CO<sub>2</sub> might selectively drill oysters that had been raised under acidified conditions.

## 2. Material and methods

### (a) Study system

Both *Olympia* oysters (*Ostrea lurida*) and Atlantic oyster drills (*U. cinerea*) are reproductive during the summer months in California estuaries. Female *Olympia* oysters brood developing larvae for approximately two weeks before releasing larvae that complete development and settle on the shore after 10–20 days in the plankton [25]. Atlantic oyster drills produce benthic egg capsules, and crawl-away juveniles emerge within 8–10 weeks. In Tomales Bay, CA, USA, where animals for this study were collected, Atlantic oyster drills emerge from capsules in large numbers during the season of peak oyster settlement (August–October). Hatchling snails prey heavily on newly settled oysters and barnacles by means of acid secretions and a file-like radula with which

they drill through the shells of prey. Given that the early phase of benthic life can be a critical population bottleneck for *Olympia* oysters [25], in this study, we focused on the interaction between juvenile oysters and recently hatched invasive drills.

### (b) Larval and juvenile prey culturing

*Olympia* oysters were collected in early October 2010 from an intertidal site on the eastern shore of Tomales Bay (38°06'58" N, 122°51'16" W), and were transported to Bodega Marine Laboratory. Oysters released brooded larvae in the laboratory and replicate cultures were established, each containing approximately 1000 larvae in a 4.5 l glass jar filled with 2 l of filtered seawater (FSW). Oysters were raised through the larval phase and into early juvenile life at either an ambient partial pressure of carbon dioxide (*p*CO<sub>2</sub>; targeted at 500 µatm) or at an elevated level (targeted at 1000 µatm; *n* = 18 jars per level). The ambient level approximated a typical *p*CO<sub>2</sub> concentration that occurs presently during the summer months in Tomales Bay [18], whereas the elevated treatment was based on an increase of 500 µatm, within the range of shifts predicted to occur by the end of this century [28]. The *p*CO<sub>2</sub> levels were established by filling the culture jars with FSW that had been held in 20 l carboys bubbled for 2–3 days with gas mixtures containing fixed CO<sub>2</sub> concentrations (traceable to the US National Institute of Standards and Technology). To minimize off-gassing and maintain the desired *p*CO<sub>2</sub> within the culture jars, the same mixed gases were added continuously to the sealed air spaces over the jars (for additional description of the culturing system see [18]). Every other day, 90% of the seawater in each jar was removed via reverse-filtration through 125 µm mesh, and jars were refilled with carboy water pre-equilibrated to the appropriate *p*CO<sub>2</sub> level. Immediately after each water change, cultured microalgae (*Isochrysis galbana*) were added to each jar to create a food concentration of approximately 100 000 cells ml<sup>-1</sup>. Larval cultures were maintained at a constant 20°C (±0.02°C).

In preparation for larval settlement, larvae were transferred on day 9 to new jars that had been prepared by removing and replacing the bases with roughened PVC sheets (5 mm thick). Most larvae settled on the PVC bases on days 13 and 14. Metamorphosed juveniles were maintained under the same *p*CO<sub>2</sub> levels, with water changes and feeding continuing on the same schedule as during the larval phase. On day 20, approximately one week after larval settlement, the PVC bases were gently removed from the jars. The bases had been previously scored on the underside, so that each base could be easily separated into four wedge-shaped tiles with juvenile oysters attached. The predation experiments required only half of the available tiles, so the two tiles from each jar that had the most oysters present were selected (mean ± s.e. = 128.0 ± 5.7 oysters per tile, *n* = 72 tiles).

### (c) Predator rearing

In preparation for the predation experiments, four sets of egg capsules of *U. cinerea* were collected in early October 2010 from an intertidal cobble beach in Tomales Bay, just north of Chicken Ranch Beach (38°06'42" N, 122°52'00" W). Each set was placed in a separate mesh-sided container and maintained in ambient flow-through seawater at Bodega Marine Laboratory. Juvenile snails hatched within 10 days and were fed small barnacles (*Chthamalus dalli*) attached to pieces of mussel shell. All snails were acclimated to the *p*CO<sub>2</sub> level that they subsequently experienced during the predation experiments. Immediately prior to the start of the predation trials, snails from each set of egg capsules were divided into two groups that were held for 13 days in carboys continuously bubbled at a *p*CO<sub>2</sub> level of either 500 or 1000 µatm. Snails were starved for the final 7 days of this period.

### (d) Predation experiments

The wedge-shaped tiles with oysters were distributed into new 4.5 l glass jars for two concurrent predation experiments (see the electronic supplementary material, figure S1). The first was a non-choice experiment, in which two tiles were placed side-by-side on the bottom of each jar. Oysters on both tiles had been raised continuously in the same culturing jar at either 500 or 1000  $\mu\text{atm}$  ( $n = 9$  jars per  $p\text{CO}_2$  level). Snails were added to each jar, and predation was quantified at the same  $p\text{CO}_2$  level under which the oysters and snails had been held. This design tested whether oysters raised and maintained under different  $\text{CO}_2$  levels experienced different predation rates.

We also conducted a choice experiment to test whether snails differentially selected oysters raised under one of the  $p\text{CO}_2$  levels. Two tiles were again placed side-by-side in each jar. However, in this case, oysters on one tile had been raised at 500  $\mu\text{atm}$ , and oysters on the other tile had been raised at 1000  $\mu\text{atm}$ . The mean number of oysters present did not differ between tiles from the two  $p\text{CO}_2$  levels ( $t$ -test,  $t_{34} = 0.214$ ,  $p = 0.832$ ; mean  $\pm$  s.e. =  $118.0 \pm 6.5$  versus  $116.28 \pm 4.8$  oysters, for 500 versus 1000  $\mu\text{atm}$  tiles, respectively). The choice experiment was conducted with half of the sets of oysters and snails immersed in ambient  $p\text{CO}_2$  seawater, and the other half immersed in elevated  $p\text{CO}_2$  ( $n = 9$  jars per level).

After the tiles were distributed, four pre-acclimated juvenile snails (one from each set of egg capsules) were added to each jar, and the jars were assigned randomly to spaces in the culturing system where they were maintained at the appropriate  $p\text{CO}_2$  level. All snails had a shell length of 1.6–2.5 mm, and the lengths of snails did not differ between  $\text{CO}_2$  levels in either experiment ( $t$ -tests; non-choice:  $t_{12} = 1.149$ ,  $p = 0.273$ ; choice:  $t_9 = 1.696$ ,  $p = 0.124$ ). Snails were placed at the junction between the two adjacent tiles in the jar so that they had equal access to both tiles and could crawl freely between them during the experiment. The duration of the trial was set to 48 h to ensure that depletion of oysters did not influence prey choice. On average, only  $20.6 \pm 0.82\%$  (mean  $\pm$  s.e.) of the oysters in each jar was consumed (range = 10–30%).

### (e) Water chemistry

During water changes conducted every other day, samples of jar water (drained from the jars) and carboy water (refilling the jars) were collected for *in situ* and laboratory analyses. Seawater pH (US National Bureau of Standards scale) and temperature were quantified using a pH/temperature meter (Accumet Excel XL60) equipped with glass double-junction electrodes calibrated in low-ionic strength certified buffers. Salinity was determined using a YSI 6600V2 multi-parameter probe. Total alkalinity ( $A_T$ ) was measured using automated Gran titration (Metrohm 809), and standardized using certified reference material (A. Dickson, Scripps Institution of Oceanography). Accepted methods for sampling and standardization were used throughout the study [29]. Additional carbonate system parameters were then calculated using the software program, CO2SYS [30], using  $\text{pH}_{\text{NBS}}$  and  $A_T$  as the primary input variables, equilibrium constants  $K_1$  and  $K_2$ , and  $\text{KSO}_4$  (as described in [18,26]).

### (f) Predation rates and prey size

At the conclusion of the 48 h experiments, predation in each replicate jar was assessed under a dissecting microscope by counting the number of drilled oysters on each tile (see the electronic supplementary material, figure S2a). No mortality was observed in oysters without drill holes. For both predation experiments, we also tested whether the size of drilled oysters differed between the two  $\text{CO}_2$  levels. We photographed the top valve of all drilled oysters and used image analysis software (IMAGEJ

v. 1.37, National Institutes of Health) to determine the projected area of the valve. To assess whether snails selectively consumed oysters of a particular size, we photographed and measured 25 non-drilled oysters from each tile as an indicator of prey sizes available. Snails preyed on oysters in localized sections of the tiles, and so we were able to sample randomly from those areas of the tile that contained no drilled oysters (i.e. where size frequencies had not been influenced by predation).

### (g) Shell thickness of drilled oysters

We used scanning electron microscopy (SEM) to quantify the thickness of drilled shells in the ambient ( $n = 22$ ) and elevated  $p\text{CO}_2$  treatments ( $n = 20$ ) of the non-choice experiment. For each group, we haphazardly selected drilled oysters from seven to nine tiles to represent the full range of oyster sizes (shell areas) present. For each oyster, the drilled top valve was cross-sectioned through the centre of the drill hole, perpendicular to the anterior–posterior axis of the shell (see the electronic supplementary material, figure S2a). SEM images were collected using a Philips XL30 Turbo-Molecular Pump scanning microscope (FEI Company, Hillsboro, OR, USA), and shell thickness in the region that had been drilled was estimated using image analysis software (see the electronic supplementary material, figure S2b).

### (h) Statistical analyses

For all analyses, assumptions of normality and homogeneity of variance were assessed using Shapiro–Wilk and Levene's tests, respectively. For the cases where these assumptions were not satisfied by the raw data, data were log-transformed prior to analysis as specified below. Water chemistry was analysed separately for two periods: the culturing phase (days 1–20) and the subsequent 48 h predation experiments. Photosynthesis of the algal food and organism respiration probably contributed to the relatively minor changes observed in water chemistry within the culture jars during the 2 days separating water changes (see the electronic supplementary material, table S1). To compare typical conditions under the two  $p\text{CO}_2$  levels, seawater parameters within each jar were first estimated by averaging all measurements of water entering and exiting that jar during that phase. These jar averages were then compared using Student's  $t$ -tests to evaluate whether seawater parameters differed between the two  $p\text{CO}_2$  levels.

In the non-choice experiment, the numbers of oysters drilled per tile were analysed using a mixed-model ANOVA (proc mixed in SAS, v. 9.3). The rearing condition of the oysters, i.e. Oyster  $\text{CO}_2$  (ambient, high), was treated as a fixed effect, and Jar [Oyster  $\text{CO}_2$ ] and Tile [Oyster  $\text{CO}_2 \times$  Jar] were incorporated as random effects. The covariance structure was chosen, so that the jars were assumed to be independent of each other, but the two tiles within a jar were not assumed to be independent (because predation on the two tiles could be negatively correlated). The log-transformed sizes of oysters (shell area) were analysed using a separate mixed-model ANOVA. Oyster  $\text{CO}_2$  (ambient, high) and Oyster Status (drilled, available) were treated as fixed effects, and Jar [Oyster  $\text{CO}_2$ ] was included as a random effect.

For the non-choice predation experiment, we also tested whether the thickness of drill holes differed between the two  $\text{CO}_2$  levels using analysis of covariance (ANCOVA), with Oyster  $\text{CO}_2$  as the main effect and Oyster Size (shell area) as the covariate.

Analyses of the choice experiment paralleled those of the non-choice experiment, with the exception that, because predation was tested under two  $\text{CO}_2$  levels (ambient, high), Jar  $\text{CO}_2$  was included as an additional fixed effect in the mixed-model ANOVAs used to analyse the number of oysters drilled and the log-transformed sizes of oysters.

We also tested whether predators preferentially selected high- $\text{CO}_2$  oysters over ambient- $\text{CO}_2$  oysters when they were presented together in the choice experiment. In such a scenario,

predation on tiles with high-CO<sub>2</sub> oysters would be greater in the choice experiment than in the non-choice experiment. Conversely, predation would be lower on ambient-CO<sub>2</sub> oysters in the choice versus non-choice experiments. To test this hypothesis, we analysed numbers of oysters drilled per tile in both experiments in a single mixed-model ANOVA (proc glm in SAS, v. 9.3). Oyster CO<sub>2</sub> (ambient, high) and Experiment Type (non-choice, choice) were treated as fixed effects, and Jar[Oyster CO<sub>2</sub> × Experiment Type] was included as a random effect. A significant interaction (Oyster CO<sub>2</sub> × Experiment Type) would be expected if snails consumed high-CO<sub>2</sub> oysters in the choice experiment at a greater rate than when high-CO<sub>2</sub> oysters were offered alone in the non-choice experiment.

### 3. Results

#### (a) Water chemistry

Seawater properties remained relatively stable throughout the study with minor variation among replicate jars within the two pH levels (table 1). As expected, pH levels differed significantly between the two experimental pCO<sub>2</sub> levels during the initial rearing phase (*t*-test, *t*<sub>34</sub> = 221.5, *p* < 0.001), the non-choice predation experiment (*t*-test, *t*<sub>16</sub> = 32.6, *p* < 0.001) and the choice experiment (*t*-test, *t*<sub>16</sub> = 39.4, *p* < 0.001). During the rearing phase, total alkalinity (*A*<sub>T</sub>) was slightly higher in the elevated pCO<sub>2</sub> treatment (*t*<sub>34</sub> = -6.77, *p* < 0.001), but mean *A*<sub>T</sub> differed by only approximately 10 μmol kg<sup>-1</sup> of seawater (table 1). *A*<sub>T</sub> did not differ between pCO<sub>2</sub> levels during the two predation experiments (*t*-tests, *p* > 0.20).

#### (b) Non-choice predation experiment

Snails drilled 20.2% more oysters in the elevated-CO<sub>2</sub> jars than in the ambient-CO<sub>2</sub> jars (figure 1*a*; mixed-model ANOVA, Oyster CO<sub>2</sub>, *F*<sub>1,16</sub> = 8.22, *p* = 0.011). Oysters that had been raised under elevated CO<sub>2</sub> were smaller than those raised under ambient conditions (mixed-model ANOVA, Oyster CO<sub>2</sub>, *F*<sub>1,16</sub> = 43.02, *p* < 0.0001). Drilled oysters in the high-CO<sub>2</sub> treatment were 29.2% smaller than oysters drilled under ambient conditions (figure 1*b*). At both CO<sub>2</sub> levels, drilled oysters were on average smaller than the mean size available (Oyster Status, *F*<sub>1,1767</sub> = 53.70, *p* < 0.0001; electronic supplementary material, figures S3 and S4). This selection of smaller oysters was accentuated under high-CO<sub>2</sub> conditions (mixed-model ANOVA, Oyster Status × Oyster CO<sub>2</sub>, *F*<sub>1,1767</sub> = 9.33, *p* = 0.002).

The thickness of drill holes was positively correlated with the size of the juvenile oyster, but did not differ between CO<sub>2</sub> levels (figure 2; ANCOVA, Oyster Size, *F*<sub>1,39</sub> = 87.93, *p* < 0.0001; Oyster CO<sub>2</sub>, *F*<sub>1,39</sub> = 0.61, *p* = 0.439; Oyster Size × Oyster CO<sub>2</sub>, *F*<sub>1,38</sub> = 0.23, *p* = 0.632).

#### (c) Choice predation experiment

In a side-by-side choice, predation on oysters that had been raised under elevated CO<sub>2</sub> conditions was greater than predation on control oysters (figure 3; mixed-model ANOVA, Oyster CO<sub>2</sub>, *F*<sub>1,16</sub> = 4.86, *p* = 0.043). This effect was consistent whether the choice trials were run under high CO<sub>2</sub> or ambient conditions (figure 3; Oyster CO<sub>2</sub> × Jar CO<sub>2</sub>, *F*<sub>1,16</sub> = 0.10, *p* = 0.754). On average, snails consumed 47.7% more high-CO<sub>2</sub> oysters than control oysters.

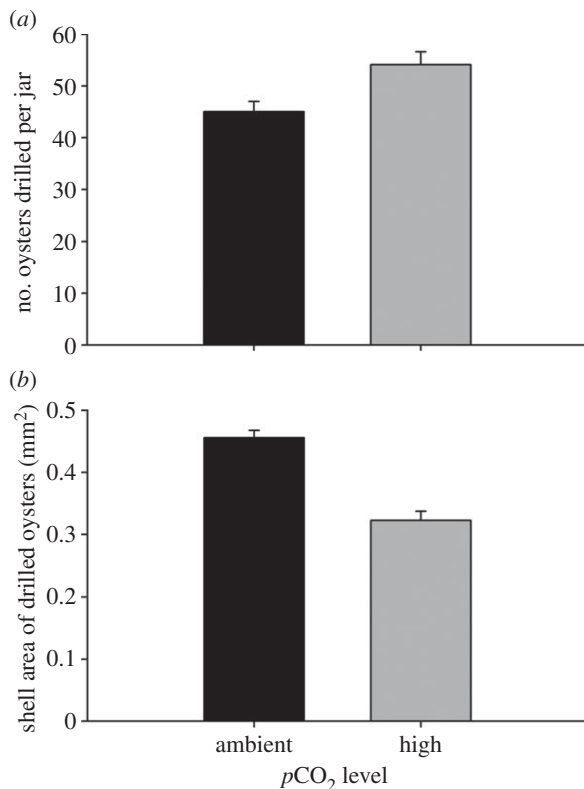
As in the non-choice experiment, oysters raised under elevated CO<sub>2</sub> were smaller than those raised under control

**Table 1.** Seawater properties during the larval and juvenile rearing phase (day 1–20, i.e. ending approx. 7 days post-settlement), and the two subsequent 48 h predation experiments. (Values are means ± s.d. computed from the jar replicates. Temperature, salinity, total alkalinity and pH<sub>NBS</sub> are measured values, and pCO<sub>2calc</sub>, Ω<sub>calcite</sub> and Ω<sub>aragonite</sub> are values calculated using the carbonate system analysis software program, CO2SYS. Asterisks indicate seawater parameters that differed significantly between the two pCO<sub>2</sub> levels (*t*-tests, *p* < 0.05).)

larval and juvenile rearing	ambient pCO <sub>2</sub>	high pCO <sub>2</sub>
temperature (°C)	19.37 ± 0.028*	19.35 ± 0.019*
salinity	34.1 ± 0.004	34.1 ± 0.003
total alkalinity (μmol kg <sub>sw</sub> <sup>-1</sup> )	2238 ± 5*	2248 ± 4*
pH <sub>NBS</sub>	8.09 ± 0.004*	7.80 ± 0.004*
pCO <sub>2calc</sub>	500 ± 6*	1047 ± 9*
Ω <sub>calcite</sub>	3.54 ± 0.024*	2.00 ± 0.017*
Ω <sub>aragonite</sub>	2.30 ± 0.016*	1.30 ± 0.011*
predation exp. (non-choice)	ambient pCO <sub>2</sub>	high pCO <sub>2</sub>
temperature (°C)	19.31 ± 0.100*	19.46 ± 0.096*
salinity	34.3 ± 0.00	34.3 ± 0.00
total alkalinity (μmol kg <sub>sw</sub> <sup>-1</sup> )	2245 ± 2	2247 ± 5
pH <sub>NBS</sub>	8.08 ± 0.020*	7.82 ± 0.013*
pCO <sub>2calc</sub>	500 ± 34*	959 ± 22*
Ω <sub>calcite</sub>	3.56 ± 0.174*	2.16 ± 0.044*
Ω <sub>aragonite</sub>	2.31 ± 0.113*	1.40 ± 0.028*
predation exp. (choice)	ambient pCO <sub>2</sub>	high pCO <sub>2</sub>
temperature (°C)	19.36 ± 0.077*	19.46 ± 0.085*
salinity	34.3 ± 0.00	34.3 ± 0.00
total alkalinity (μmol kg <sub>sw</sub> <sup>-1</sup> )	2245 ± 4	2245 ± 10
pH <sub>NBS</sub>	8.07 ± 0.016*	7.82 ± 0.009*
pCO <sub>2calc</sub>	520 ± 32*	966 ± 29*
Ω <sub>calcite</sub>	3.45 ± 0.150*	2.14 ± 0.052*
Ω <sub>aragonite</sub>	2.24 ± 0.098*	1.39 ± 0.034*

conditions (Oyster CO<sub>2</sub>, *F*<sub>1,32</sub> = 127.95, *p* < 0.0001). Drilled oysters that had been raised under high CO<sub>2</sub> were 39.9% smaller than the drilled oysters that had been raised under ambient conditions (figure 4). As in the non-choice experiment, predators in the choice experiment drilled oysters that were on average smaller than the mean size available (mixed-model ANOVA, Oyster Status, *F*<sub>1,1700</sub> = 91.92, *p* < 0.0001; electronic supplementary material, figures S5 and S6). This tendency to select smaller oysters relative to the sizes available occurred, regardless of the CO<sub>2</sub> level that the oysters were raised under (Oyster Status × Oyster CO<sub>2</sub>, *F*<sub>1,1700</sub> = 0.89, *p* = 0.347), or the CO<sub>2</sub> level during the predation trial (Oyster Status × Jar CO<sub>2</sub>, *F*<sub>1,1700</sub> = 0.04, *p* = 0.841).

We also tested whether predators preferentially selected high-CO<sub>2</sub> oysters in the choice experiment at rates that were

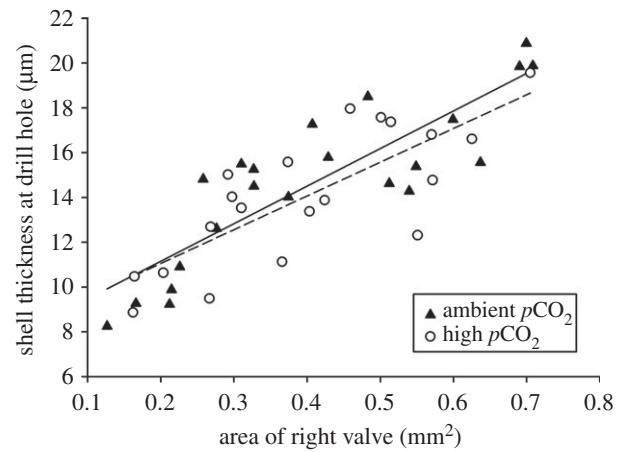


**Figure 1.** Results of non-choice experiment quantifying predation by Atlantic oyster drills upon native oysters cultured under either ambient (500  $\mu\text{atm}$ ) or high (1000  $\mu\text{atm}$ )  $p\text{CO}_2$  levels. (a) Mean predation (+s.e.) during the 48 h experiment ( $n = 9$  jars per  $p\text{CO}_2$  level). (b) Mean shell size (area + s.e.) of all drilled oysters in replicate jars ( $n = 9$  jars per  $p\text{CO}_2$  level). Drills consumed 20.2% more oysters under high  $p\text{CO}_2$  conditions, and these oysters were smaller in size ( $t$ -test,  $t_{16} = 7.01$ ,  $p < 0.0001$ ).

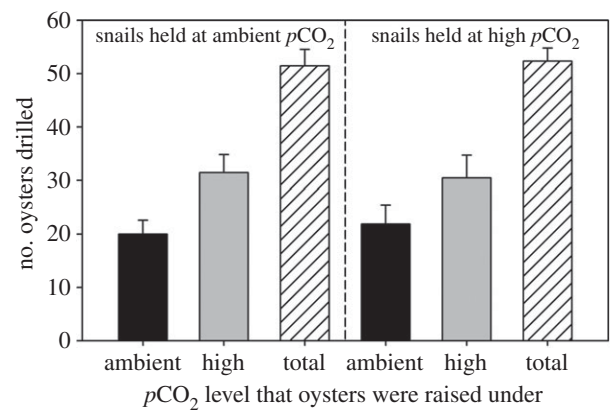
greater than predicted from the non-choice experiment. As expected, there was higher predation on high- $\text{CO}_2$  oysters than on ambient- $\text{CO}_2$  oysters in the choice experiment (mixed-model ANOVA, Oyster  $\text{CO}_2$ ,  $F_{1,10} = 19.81$ ,  $p = 0.001$ ). There was suggestive evidence that predators consumed more high- $\text{CO}_2$  oysters per tile and fewer ambient- $\text{CO}_2$  oysters per tile in the choice experiment than in the non-choice experiment, but this interaction was not significant statistically (Experiment Type  $\times$  Oyster  $\text{CO}_2$ ,  $F_{1,7} = 3.04$ ,  $p = 0.123$ ).

## 4. Discussion

There is growing concern that global environmental change might exacerbate the impacts of invasive species on native communities [2,4]. To date, most attention has focused on the potential for environmental change to alter the growth, survival and fecundity of native versus non-native species. A recent meta-analysis found that increasing temperature and  $\text{CO}_2$  generally have negative impacts on the performance of native species in aquatic systems, with less impact on non-native species [6]. The greater resilience of invasive species to environmental change might arise if the introduction process itself has selected for species with broad tolerances and high phenotypic plasticity [6,9]. Through effects on performance, increasing temperature,  $\text{CO}_2$  and anthropogenic nutrient inputs might, in turn, alter competitive interactions between native and non-native species [2], although these effects have rarely been quantified experimentally (but see [31,32]).



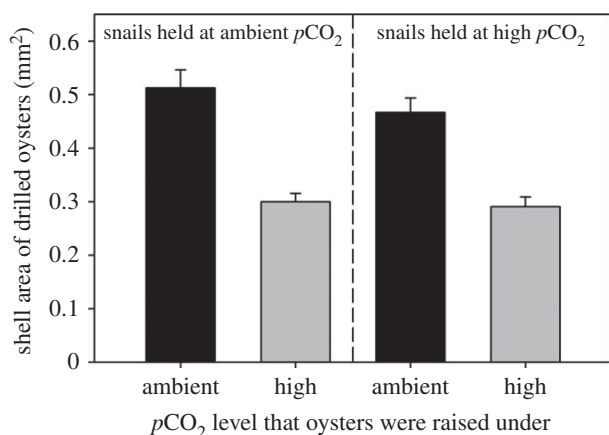
**Figure 2.** Shell thickness versus shell size (projected area) of juvenile oysters cultured under ambient (500  $\mu\text{atm}$ ) and elevated (1000  $\mu\text{atm}$ )  $p\text{CO}_2$  levels in the non-choice experiment. We selected drilled oysters from the range of sizes present within the ambient ( $n = 22$ ) and high  $p\text{CO}_2$  treatment ( $n = 20$ ). Cross-sectional shell thickness at the drill hole was quantified using scanning electron microscopy. Separate linear regressions are plotted for the ambient (solid line) and high  $p\text{CO}_2$  treatments (dashed line). Larger oysters had thicker shells, but the thickness of drill holes in shells of a given size did not differ between  $p\text{CO}_2$  levels (see Results).



**Figure 3.** Results of choice experiment quantifying predation by Atlantic oyster drills offered a side-by-side choice of oysters cultured under both ambient (500  $\mu\text{atm}$ ) and high (1000  $\mu\text{atm}$ )  $p\text{CO}_2$  levels. The experiment was conducted with drills held under both ambient and elevated  $p\text{CO}_2$  levels ( $n = 9$  jars per  $p\text{CO}_2$  level). Bars are the mean number (+s.e.) of oysters drilled during the 48 h experiment: control oysters (black bars), high- $p\text{CO}_2$  oysters (grey bars) and total (cross-hatched bars). Overall, drills consumed 48% more high- $p\text{CO}_2$  oysters than control oysters.

The potential for environmental change to increase the consumptive effects of invaders on native species has received even less attention [3]. These impacts could arise via numerical effects, where environmental change increases the abundance of invasive consumers [33]. Alternatively, environmental change might increase the *per capita* effect of an invasive predator. Such interaction modification effects [7] could occur, for example, if warmer temperatures increased the consumption rates of the predator [3,33], through effects on its activity and physiology. Although seldom considered, the *per capita* effects of an invasive predator might also be increased if environmental stress causes native prey to become more vulnerable to predation, for example as a result of weakened defences.

We found that ocean acidification led to a striking 20–48% increase in predation by invasive snails on native



**Figure 4.** Size (area + s.e.) of oysters drilled in the ambient (500  $\mu\text{atm}$ , black bars) and high (1000  $\mu\text{atm}$ , grey bars)  $p\text{CO}_2$  groups during the choice experiment. The experiment was conducted with drills held under both ambient and high- $p\text{CO}_2$  levels ( $n = 9$  jars per level). Drilled oysters from the high- $p\text{CO}_2$  group were significantly smaller than control oysters (paired  $t$ -test,  $t_{16} = 7.39$ ,  $p < 0.0001$ ).

oysters. Increased *per capita* effects under elevated  $\text{CO}_2$  did not appear to arise from a thinning of oyster shells under acidified conditions or from physiological effects on predators. Rather, oysters raised under elevated  $\text{CO}_2$  appeared to be handled and consumed more quickly because of their smaller size. We discuss these findings in more detail in the following sections.

### (a) Effects of elevated $\text{CO}_2$ on prey

Relative to ambient conditions, oysters of a given size did not secrete thinner shells when raised under elevated  $\text{CO}_2$ . The lack of an effect of  $\text{CO}_2$  on shell thickness contrasts with a study of the Atlantic oyster, *Crassostrea virginica* [16]. In that study, juvenile oysters exposed for 20 weeks to extreme  $p\text{CO}_2$  levels (3500  $\mu\text{atm}$ ) had less shell mass, but similar shell area, compared with oysters reared in ambient conditions. Because shell area did not differ with  $\text{CO}_2$  level, those results indicated that oysters secreted thinner shells, at least under strongly acidified conditions. Similarly, adult mussels were found to grow thinner shells in association with low pH at hydrothermal vents [34], and the shells of larval bivalves can be thinner when raised under elevated  $\text{CO}_2$  [15,17].

However, shell thickness in bivalves is not always reduced under experimentally elevated  $\text{CO}_2$ . Rather, faced with increased costs of calcification, some species appear to allocate energy towards maintaining shell thickness at the expense of reduced shell growth [35]. To the extent that shell thickness influences susceptibility to predation and physical disturbance [17,36], there may be selection to maintain shell thickness—even if it comes at a cost of reduced growth in overall shell area. Our results are consistent with such a trade-off. Although shell thickness was not reduced under elevated  $\text{CO}_2$ , the mean size of oysters drilled under these conditions was 29–40% smaller than under ambient conditions. Given the relationship between oyster size and shell thickness (figure 2), these smaller oysters had approximately 14–20% thinner shells than the average oyster drilled in the controls, and thus probably took less time to drill through, as has been shown in other predatory snails [36]. In addition, smaller oysters probably contained less tissue that was consumed more quickly and yielded smaller

caloric rewards. Prey size is known to have a strong effect on predator functional responses and predator–prey dynamics [37–39]. Smaller prey often take less time to subdue, consume and digest, and these effects all decrease handling time and thus increase *per capita* rates of predation [37].

We cannot rule out the possibility that in addition to decreasing oyster size, elevated  $\text{CO}_2$  may have led to shifts in shell composition and reduced hardness [16] that also reduced handling time. Previous work documented that Sydney rock oysters from sites with strongly acidified waters (pH < 7.0, driven by the run-off of acid sulfate soils) were consumed more quickly by predatory snails than oysters from control sites [40]. Although shell thickness and growth were not quantified in this particular study, oysters from the acidified sites had weaker shells that were crushed more easily.

### (b) Effect of elevated $\text{CO}_2$ on predators

The very similar predation rates observed in the choice experiment under the two  $\text{CO}_2$  levels (figure 3) suggests that any physiological effects of elevated  $\text{CO}_2$  on the snails did not influence their feeding behaviour, in contrast to effects seen in some coral reef fishes [24]. Predatory snails drill through the shell of their prey using their radula to slowly rasp away shell material that is softened by acidic secretions produced by a specialized boring organ. Radular teeth are chitinous, rather than calcareous, and thus the drilling apparatus itself may not be influenced by decreased pH [40]. Although snails in our study were acclimated to the two  $\text{CO}_2$  levels for two weeks, they were not raised for extended periods under these conditions. We selected snails that were all within a narrow size range for these experiments and did not test whether long-term exposure to elevated  $\text{CO}_2$  might impact the growth or performance of these calcifying predators [41,42]. Many predator–prey interactions are size-structured, and reductions in the growth rate of predators might have important consequences for prey population dynamics [36,39,43].

Our results provided some support for the hypothesis that snails preferentially consume oysters raised under elevated  $\text{CO}_2$  when offered alongside control oysters. Relative to ambient- $\text{CO}_2$  oysters, snails consumed about 20% more high- $\text{CO}_2$  oysters in the non-choice experiment (figure 1), but 48% more high- $\text{CO}_2$  oysters in the choice experiment (figure 3). Statistical evidence for preferential consumption of high- $\text{CO}_2$  oysters in the choice experiment was equivocal, and follow-up experiments are needed. A trend towards preferential consumption of high- $\text{CO}_2$  oysters might arise if predators were attracted to oysters of smaller size, which were more common on the high- $\text{CO}_2$  tiles. Alternatively, snails might have been attracted by chemical cues released by oysters raised under elevated  $\text{CO}_2$ . Interestingly, previous work indicated that *U. cinerea* were attracted to faster growing oysters that had higher metabolic rates [44]. Juvenile Atlantic oysters exposed to elevated  $\text{CO}_2$  were found to have higher metabolic rates, perhaps reflecting higher energetic costs of homeostasis [16]. Although we did not quantify metabolic rates in this study, it is possible that oyster drills are attracted to juvenile oysters raised under elevated  $\text{CO}_2$  because they have persistently higher metabolic rates. More detailed experiments are needed to investigate this hypothesis.

### (c) Global environmental change and invasive predators

Our results suggest that ocean acidification may exacerbate the impacts of invasive predators on native *Olympia* oyster populations. Estuaries along the west coast of North America already experience periods of low pH, and ocean acidification is expected to lead to further reductions in estuarine pH [45]. The synergistic effects of ocean acidification and invasive predators may thus hinder efforts to restore native oyster populations in California estuaries, especially in combination with other anthropogenic stressors facing native oysters (e.g. habitat loss and pollution). Other climatic changes expected on the California coast during this century, including increases in air temperature [46], may generate complex interactive effects [47] that also influence intertidal oysters and their predators. Predicting the net effect of environmental changes on the dynamics of a predator–prey interaction is complex, because both species might be impacted [21,22,42]. For example, lowered pH can alter both prey detection and predator avoidance in coral reef fishes through effects on olfactory pathways [23,24,48]. However, if invasive species tend to be more tolerant of environmental change [6,9], then the *per capita* effects of invasive consumers might be increased as a consequence of stress experienced by native prey species.

A growing body of evidence suggests that increased stress associated with global environmental change is reducing body size in multiple taxa [20,49]. Reductions in prey size may result from the direct effects of environmental stress,

phenological shifts or trade-offs in allocation of limited energy (e.g. to stress responses, defence against predation and/or growth), with important consequences for predator–prey dynamics [43]. For example, thermal stress and exposure to toxins can reduce the size of zooplankton in lakes, with rippling effects on fish populations and ecosystem function [50]. These complex effects of environmental change may be more common than is generally appreciated. Predicting the interactive effects of global environmental change and invasive consumers on native assemblages will thus benefit from addressing how stress alters resource allocation to prey defences and growth, and how shifts in these traits ultimately influence predator–prey dynamics.

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