Marine Biology Research, 2015
Vol. 11, No. 4, 337–348, http://dx.doi.org/10.1080/17451000.2014.932914

ORIGINAL ARTICLE

Interactive effects of ocean acidification and warming on subtidal mussels and sea stars from Atlantic Canada

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Abstract
Anthropogenic CO_2 is decreasing oceanic pH and contributing to seawater warming. We tested the effects of low pH and high temperature at levels predicted for 2100 on an ecologically important predator–prey system (sea stars, *Asterias rubens*, and mussels, *Mytilus edulis*) from the NW Atlantic coast. Mussels are dominant competitors for space and important ecosystem engineers, while sea stars control mussel populations and thus local community structure. We found sea stars to be negatively affected in growth rate by low pH, with growth further reduced by a high temperature. In contrast, mussel growth rate was positively affected by low pH, with no response to temperature within the tested range. Predation of sea stars on mussels, measured as per-capita consumption rate, decreased in acidified conditions by 50%. Our study suggests that mussels may not be negatively affected by pH at the levels predicted for the end of this century and that mussels may be subjected to a reduced predation from sea stars under future conditions.

Key words: Asterias, *mussel*, Mytilus, *Nova Scotia, ocean acidification, ocean warming, sea star*

Introduction

Unprecedented changes in the sea are being driven by anthropogenic climate change. Rising carbon dioxide (CO_2) emissions are leading to increases in the concentration of atmospheric CO_2, approximately half of which has dissolved into surface ocean waters since 1800 (Sabine et al. 2004). While oceanic uptake of CO_2 moderates rising global temperatures, it also reduces ocean pH, leading to ocean acidification (OA; Doney et al. 2009). Since the Industrial Revolution, atmospheric CO_2 has increased from approximately 280 to 395 ppm, leading to a reduction of 0.1 pH units in surface ocean waters (Raven et al. 2005). OA has already been shown experimentally to affect a variety of marine taxa at pH values predicted within this century (Pörtner et al. 2004). Atmospheric CO_2 predictions for 2100 by the Intergovernmental Panel on Climate Change (IPCC) at the time when the present study was conducted ranged from 760 ppm to more than 1000 ppm (Meehl et al. 2007), which were predicted to result in a decrease of 0.3–0.4 pH units in surface ocean pH (Caldeira & Wickett 2003, 2005; Orr et al. 2005). On the NW Atlantic coast, where this study was done, pH is predicted to drop from approximately 8.10 to 7.90 by the end of this century (Orr et al. 2005), with nearshore ocean surface temperatures predicted to rise by 3.5–4°C (Meehl et al. 2007). Atmospheric CO_2 concentration projections in the fifth IPCC report (Collins et al. 2013) have been updated to range between 800 and 1150 ppm, but ocean pH predictions for 2100 fall in the same range as reported by Meehl et al. (2007).

Much of the early research on biological effects of OA has focused on marine calcifiers that build calcium carbonate shells or other mineralized structures (Orr et al. 2005). Calcifiers were believed to be at a greater risk than other species due to the greater energetic cost of deposition or higher rate of dissolution of calcium carbonate in lower-pH, less

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Published in collaboration with the Institute of Marine Research, Norway

(Accepted 27 May 2014; first published online 8 October 2014)

carbonate-saturated waters (Fabry et al. 2008). For example, in a study on calcification of 18 marine species in reduced pH, Ries et al. (2009) found that some species respond to OA with decreased calcification rates, while others showed no change or even increased calcification. Although there was no universal trend among taxa reported, Ries et al. (2009) suggested there may be some protection from reduced-pH seawater provided by organic portions of calcareous structures, such as the chitonous shell of crustaceans and periostracum of molluscs, which prevent direct contact with seawater and reduce dissolution. Alternately, responses in calcification may be influenced by a species-specific capacity for pH regulation. Organisms with more efficient internal pH regulation, such as highly mobile organisms, may be better adapted to tolerate low-pH conditions (Dupont et al. 2008; Fabry et al. 2008). In addition, different responses have also been shown among life-history stages of the same species. Early life stages are often more sensitive to OA, particularly those that begin calcification in larval stages (Kurihara & Shirayama 2004; Kurihara 2008). OA research has since broadened to investigate a wider diversity of taxa, including primary producers (which either increase or decrease growth in low-pH seawater; Kerrison et al. 2012) and fish (which show altered olfactory-mediated predation, predator avoidance, or settlement; Dixson et al. 2010; Cripps et al. 2011; Munday et al. 2012, 2013a).

OA can also affect other physiological processes. For example, brittle stars continue calcification in reduced-pH seawater, but at the cost of reduced somatic and reproductive growth (Wood et al. 2010) or reduced arm regeneration (Wood et al. 2008). Other responses have been tested for calcifiers and non-calcifiers under predicted levels of seawater pH, including effects on overall organism growth, reproduction, or behaviour. While many species exhibit a negative response to OA (Fabry et al. 2008; Hendriks et al. 2010; Kroeker et al. 2010), some species respond with no change in growth or even higher growth rates in acidified seawater, as seen for a sea star (Gooding et al. 2009). There are species-specific differences in response to acidification between even closely-related species. For example, American lobster (*Homarus americanus* H. Milne Edwards, 1837) larvae have reduced growth rates in low pH (Keppel et al. 2012), while European lobster, *H. gammarus* (Linnaeus, 1758), larvae show no change in growth (Arnold et al. 2009). Other processes such as reproduction (Kurihara 2008) and development (Dupont et al. 2008; Kurihara 2008) also show differing trends among species.

Temperature also affects the physiology of marine species by influencing metabolism (Pörtner 2001) and growth (Harley et al. 2006). Because ocean pH and temperature are changing simultaneously, combined biological effects may occur (Pörtner et al. 2005; Pörtner 2008; Wernberg et al. 2012; Koch et al. 2013; Kroeker et al. 2013). Ocean temperature increases and pH decreases predicted for 2100 individually produce a positive effect on growth and per-capita feeding rate on *Mytilus californianus* Conrad, 1837 in the Pacific sea star *Pisaster ochraceus* (Brandt, 1835) (Gooding et al. 2009). When these factors were combined, an additive effect on growth and feeding rates was observable. In the crab *Cancer pagurus* Linnaeus, 1758 and spider crab *Hyas araneus* (Linnaeus, 1758), OA reduces thermal tolerance (Metzger et al. 2007; Walther et al. 2009). Anti-synergistic effects have also been shown. In the development of larvae of the sea urchin *Tripneustes gratilla* (Linnaeus, 1758), OA leads to reduced growth while development in warmer seawater results in larger larvae, with warming reducing effects of OA (Sheppard Brennand et al. 2010). Similarly, biogenic dimethyl sulfide production in the coccolithophore *Emiliania huxleyi* (Lohmann) W. W. Hay & H. P. Mohler, 1967 is reduced by OA, but this reduction is negated by increased production due to warmer temperatures (Arnold et al. 2013). In a review of how climate change experiments are done, 82% of studies found an interactive effect of factors (Wernberg et al. 2012), which would go unnoticed in single-factor studies. Global environmental changes are occurring simultaneously, necessitating simultaneous testing of multiple stressors (Hale et al. 2011; Wernberg et al. 2012), which is becoming more prevalent in the literature (Gao et al. 2012; Harvey et al. 2013; Ban et al. 2014).

Beyond effects on individual species, climate change will influence communities through interspecific interactions (Harley et al. 2006; Kroeker et al. 2013) because different species have different tolerance ranges for environmental factors. Species that are not directly affected may be indirectly affected if other species in their community with which they interact exhibit a response. In a study on an intertidal plant–herbivore system, different responses to temperature were found. Lower algal biofilm growth occurred in warmer temperatures, while the limpet *Lottia scabra* (Gould, 1846) exhibited no change in growth with temperature (Morelissen & Harley 2007). Although there was no effect of temperature on the limpet, there may be an indirect effect as a result of decreased availability of its food source. This illustrates differential vulnerabilities between interacting species to environmental change, which could lead to changes in community structure (Hale et al. 2011; Harley 2011; Fabricius et al. 2014).

Indirect effects may be significant for interactions involving keystone species, which play a large role in controlling community structure through, for example, predation (Sanford 1999). The sea star *Asterias rubens* Linnaeus, 1758 is a major predator of the economically and ecologically important mussel *Mytilus edulis* Linnaeus, 1758 on NW Atlantic rocky shores (Pollock 1998; Tam & Scrosati 2011, 2014). Both species are central in structuring nearshore subtidal communities. *Mytilus edulis* is a competitively dominant organism from mid-intertidal to shallow subtidal communities, as it eliminates sessile species in areas without predators (Lubchenco & Menge 1978; Hunt & Scheibling 2001). *Asterias rubens* preys heavily on *M. edulis* (Lubchenco & Menge 1978; Gaymer et al. 2001), thus influencing intertidal and subtidal community structure by opening the substrate for less-competitive species. Also, as mussels are ecosystem engineers, providing habitat for many small secondary species, biodiversity is altered with changes in mussel abundance (Arribas et al. 2014). Changes in growth rates of these species, or in the consumption of mussels by sea stars, could therefore alter benthic community structure and diversity.

Here, we test the interactive effects of increased temperature and decreased pH at levels predicted for 2100 on *A. rubens* and *M. edulis*. Effects of climate change should have a greater biological impact at the extremes of a species' tolerance range (Denny et al. 2009). For example, 4°C higher temperatures in summer would be expected to be farther from optimum and stress organisms more than 4°C higher temperatures in spring or autumn. For this reason, temperatures in the warmest summer months (averaged over July–August) were used as controls in this study and raised by 4°C based on predictions for 2100 by the IPCC. Seawater pH levels were determined as pH resulting from equilibration with air at current ambient CO_2 concentration and at 2100-predicted atmospheric CO_2 concentration following the European Guide to Ocean Acidification Research (Riebesell et al. 2010) and corresponding to 2100-predicted pH decreases (Caldeira & Wickett 2005). Response variables included growth rate, final dry mass, calcified mass, and soft tissue mass of *A. rubens* and *M. edulis*, and were hypothesized to differ between present and predicted conditions. The feeding rate of *A. rubens* on *M. edulis* was measured to test for changes in predation rate, hypothesized to decrease under future conditions.

Materials and methods

Animal collection and maintenance

We tested the effects of seawater pH and temperature on a suite of variables in *Asterias rubens* and *Mytilus edulis* over a 10 week experiment. Both species were collected from Antigonish Harbour, Nova Scotia, Canada (sea stars: 45.648°N, 61.834°W, mussels: 45.681°N, 61.869°W) at 1.0 m below chart datum in September 2010 (16°C, salinity 31). Sea star arm length was 3.3 ± 1.3 cm (mean ± SE, $n = 48$) and mussel shell length was 1.0 ± 0.2 cm ($n = 48$). Only normal-looking sea stars (not regenerating any arms) were collected. Animals were transferred to the laboratory and held in 400 litre seawater aquaria with recirculating seawater at collection temperature and salinity. They were held in the laboratory for one (mussels) or two (sea stars) weeks before the experiment, during which sea stars were fed unlimited mussels (1.5–2.5 cm long) and mussels were fed with a mix of 1/3 fish food flakes, 1/3 food-grade kelp powder, 1/3 *Spirulina* flakes, and freshly hatched brine shrimp (*Artemia franciscana* Kellog, 1906) to excess. After initial length and wet mass were measured, three sea stars or mussels were randomly assigned to 1 litre containers with assigned temperature and pH. Temperature was warmed to the experimental level at a rate of 1°C per day, after which the experimental pH levels were applied. The pH reached experimental levels within 6 h after increase of CO_2 in air supplied to containers. Animals were then acclimated to experimental conditions for two weeks. Sea stars were not fed during the week before the experiment in preparation for testing effects on consumption rate. The containers were supplied with filtered, UV-sterilized, recirculating seawater from the Northumberland Strait (salinity 31). Temperature and pH were recorded weekly in the containers, and salinity and ammonia levels of water were checked daily and water exchanged as needed. The photoperiod was 14:10 h (light:dark), consistent with average summer conditions for the region.

Temperature and pH

Individual 1 litre containers were partially submersed in one of two 200 litre water baths with thermostatically controlled heaters and chillers to maintain constant temperatures. Two treatments were used: control temperature (20°C), representing the average temperature in July–August near the collection site, and high temperature (24°C), representing control temperature plus 4°C, the average global increase predicted for 2100 by the IPCC. Control temperature was based on data collected every 15 min at a station near the collection site (45.681°N, 61.890°W) for July–August 2008–2009.

Experimental pH levels were achieved by bubbling containers with either ambient air (for control pH) or ambient air + added CO_2 (for low pH). Two

levels were tested: 8.1 (control pH) and 7.9 (low pH), which resulted from equilibrating seawater with air at current and 2100-predicted atmospheric CO_2 concentration (400 and 760 ppm, respectively). Consistent gas flow rates were kept with mass flow controllers (Sierra Instruments Smart Trak model 100). Concentration of CO_2 in air and in CO_2-enriched air was verified daily with a Qubit S151 CO_2 analyser. Resulting pH levels were recorded weekly for each container (Table SI, supplementary material). Control pH was 8.10 ± 0.002 (mean ± SE) and low pH was 7.94 ± 0.006. Total alkalinity (TA) was tested at the beginning, middle, and end of the experiment (n = 3 per pH treatment) by potentiometric closed cell titration (Dickson et al. 2007). TA was 2135 ± 26 μmol $kgSW^{-1}$ in the control pH treatment and 2172 ± 16 μmol $kgSW^{-1}$ in low pH. Control pH was similar to measurements from collection sites (8.10) and from shallow waters (0–10 m depth) in the study region: 8.05–8.16 in Halifax (May 2009–2010) and Shediac (May 2009 to December 2012). Low pH was similar to predictions for 2100 at the latitude where we conducted the study (Caldeira & Wickett 2005; Orr et al. 2005).

Four containers were randomly assigned to each of the four treatment combinations for each species, giving a total of 16 containers per species (2 temperature levels × 2 pH levels × 4 containers per temperature–pH treatment). Each container held either three sea stars or three mussels, for a total of 48 individuals of each species.

Response variables

Sea star arm length, mussel shell length, and sea star and mussel wet mass were measured at the beginning and end of the experiment. Sea star arm length was measured to the nearest mm from the madreporite to the tip of the arm immediately clockwise to it. Mussel shell length was measured as the length from the umbo to the farthest point on the posterior end to the nearest 0.1 mm. To obtain wet mass, animals were gently blotted with paper towel and placed on a digital scale, and their mass was recorded to the nearest mg. Animals were returned to containers immediately after measurements. Weekly growth rates were calculated as '(final length – initial length)/10 weeks' and as '(final wet mass – initial wet mass)/10 weeks'. Animals were ranked in size within each container to make the initial and final measurements.

After final length and wet mass measurements, animals were dried to constant mass in an oven at 70°C and dry mass was recorded. Soft tissue was removed by placing animals in a 6% bleach solution for 72 h. The solution was refreshed every 24 h. Calcified material was removed from the solution by vacuum filtration, then dried, and its mass was recorded. Relative calcification was calculated as the ratio of calcified mass to soft tissue dry mass.

Throughout the experiment, sea stars were fed an unlimited supply of mussels 1.5–2.5 cm in length. Empty mussel shells were removed, replaced, and recorded as consumed every 2 days per container.

Statistical analyses

Data were analysed through nested ANOVAs with two fixed factors (temperature and pH) and one random factor (container) nested within the temperature × pH interaction (Underwood 1997). Initial sea star arm length, mussel shell length, and sea star and mussel wet mass at the beginning of the experiment were not significantly different between any treatment combinations ($p > 0.1$). Because wet mass was significantly affected by variable water retention by temperature treatment, dry mass was used to compare final mass. Data were tested for normality with the Shapiro–Wilk test and for homoscedasticity with Cochran's C-test. Data were either log- or square-root-transformed to meet the assumptions as needed. When the interaction between temperature and pH was significant, the four treatment means were compared with Tukey HSD tests. Statistics were done with SYSTAT 13 software.

Results

Sea stars

Three sea stars died during the experiment, although each one was in a different temperature–pH treatment combination (excepting the 20°C and 760 ppm CO_2 treatment). Those cases were accounted for during data analyses using the mixed means model for missing data cells. The ANOVA revealed a significant interaction between pH and temperature for sea star growth in length, which decreased from present to future conditions by a factor of 3 (Figure 1A, Table I). Low pH alone resulted in a significantly lower growth rate in wet mass, with further reduction with high temperature by a factor of 5 (Figure 1B, Table I). Sea star dry mass under low-pH conditions was significantly lower at the end of the experiment than under control pH by nearly a half, while temperature had no significant effect (Figure 1C, Table I). There was a significant interaction between pH and temperature for calcified mass, which decreased from current conditions (low temperature and high pH) to predicted conditions (high temperature and low pH). Mass of dry soft tissue was significantly reduced in low pH by a factor of 2, while temperature had no significant effect (Figure 1E,

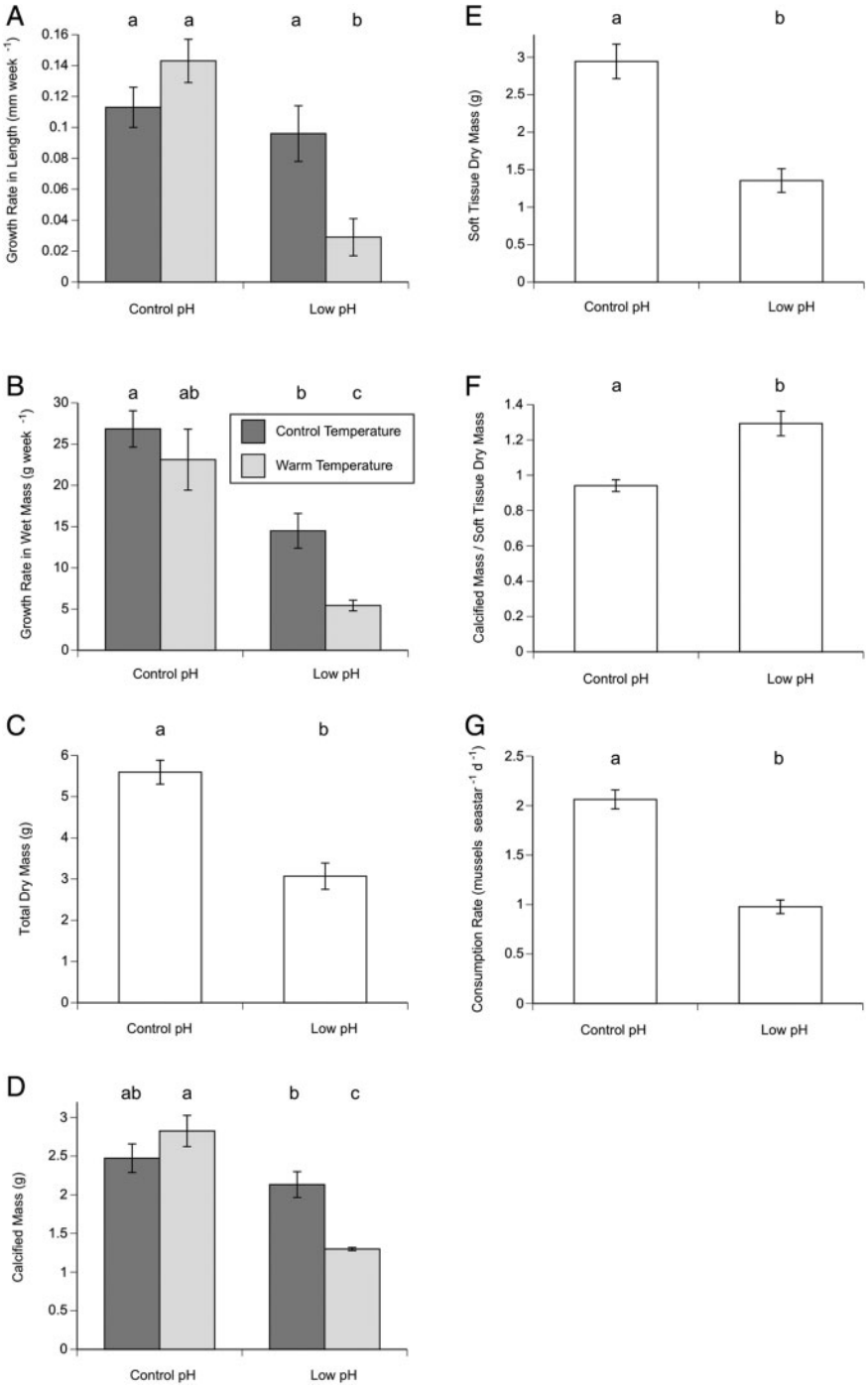

Figure 1. Response of *Asterias rubens* (mean ± SE) to low pH (control pH = 8.10, low pH = 7.94) and increased temperature (control temperature = 20°C, high temperature = 24°C) in (A) growth rate in length, (B) growth rate in wet mass, (C) total dry mass, (D) calcified mass, (E) soft tissue dry mass, (F) calcified mass/soft tissue dry mass, and (G) consumption rate of mussels. Means for the four possible treatment combinations are shown if there was a significant temperature × pH interaction (A,B,D). If no significant interaction and temperature effects occurred, only means for the two pH treatments are shown (C,E–G). Significant differences between any two treatments ($p < 0.05$) are indicated by the occurrence of different letters above the corresponding two bars.

Table I). The ratio of the mass of calcified material to mass of dry soft tissue was significantly higher in low pH, while temperature had no significant effect (Figure 1F, Table I). Consumption rate (number of mussels consumed per sea star per day) was significantly lower under low pH, while temperature had no significant effect (Figure 1G, Table I). A decrease in consumption rate was evident by the second week of the experiment, with a significantly lower per-capita consumption rate in the low-pH treatment at that time ($p = 0.03$), confirming that the response was due to treatment effects and not lower consumption

Table I. Effects of pH and temperature on sea stars: summary results of nested ANOVAs.

	pH F (P) (df = 1)	Temperature F (P) (df = 1)	pH × Temperature F (P) (df = 1)	Container F (P) (df = 12)
Growth rate in length (mm week^{-1})	31.11 (< 0.001)	2.01 (0.166)	17.46 (< 0.001)	2.76 (0.011)
Growth rate in wet mass (g week^{-1})	70.91 (< 0.001)	24.23 (< 0.001)	7.20 (0.012)	2.16 (0.045)
Total dry mass (g)	41.03 (< 0.001)	2.92 (0.126)	4.69 (0.062)	0.29 (0.876)
Calcified mass (g)	50.43 (< 0.001)	3.37 (0.104)	20.39 (0.002)	2.46 (0.130)
Soft tissue dry mass (g)	25.62 (0.001)	1.89 (0.207)	0.68 (0.434)	0.13 (0.967)
Calcified mass/soft tissue dry mass	8.09 (0.022)	0.38 (0.553)	0.22 (0.652)	0.96 (0.480)
Consumption rate (mussels sea star^{-1} day^{-1})	85.22 (< 0.001)	5.08 (0.054)	0.22 (0.652)	0.20 (0.930)

associated with sea star size as the experiment progressed. Overall, temperature only significantly affected the variables influenced by water retention (wet mass and growth rate in length, through interactions with pH) as well as calcified mass (through interaction with pH).

Mussels

Between one and three mussels died for each treatment combination, although always at least two mussels survived in each container until the end of the experiment. To maintain a balanced design, containers in which all initial mussels survived had one mussel randomly removed for data analyses. The ANOVA indicated that there was no significant effect of temperature on mussel growth rate in shell length or wet mass, total dry mass, or calcified (shell) mass, while low pH resulted in an increase for each of these variables (Figure 2A–D, Table II). Mass of dry soft tissue did not show significant differences between pH or temperature treatments (Figure 2E, Table II). Predicted conditions (high temperature and low pH) resulted in a significantly higher ratio of shell mass to mass of dry soft tissue compared with current temperature and pH conditions (Figure 2F, Table II).

Discussion

The present study shows that OA affects growth and calcification in the sea star *Asterias rubens* and the mussel *Mytilus edulis* at pH levels predicted to occur by 2100. There were no response variables in which temperature alone caused a significant difference. The combination of warmer temperature with OA, however, did amplify some of the effects of OA (e.g. sea star growth in wet mass), as well as cause a significant difference in some variables that did not change with lower pH alone (e.g. sea star growth in length). In general, sea stars exhibited a negative response to future conditions through a reduction in growth rate, consumption rate, and calcified mass, while mussels exhibited a higher growth rate and shell mass.

Sea stars

The decrease in growth rate in *Asterias rubens* under predicted conditions was dominated by acidification effects. OA alone led to lower growth rate in wet mass and lower dry mass at the end of the experiment. Warming alone did not reduce growth rate, but in combination with low pH, further reduced growth in wet mass and length. Both growth variables where temperature had an interactive effect with pH may be influenced by water retention. As final dry mass at the end of the experiment was lower with acidification with no effect of higher temperature, it appeared that warmer temperature only interacts with pH to reduce growth due to temperature-dependent water retention effects. Thus, acidification, not warming, was the driver of reduced growth.

Table II. Effects of pH and temperature on mussels: summary results of nested ANOVAs.

	pH F (P) (df = 1)	Temperature F (P) (df = 1)	pH × Temperature F (P) (df = 1)	Container F (P) (df = 12)
Growth rate in length (mm week^{-1})	10.93 (0.013)	0.06 (0.809)	1.47 (0.265)	2.02 (0.182)
Growth rate in wet mass (g week^{-1})	13.70 (0.002)	0.01 (0.946)	0.76 (0.396)	2.04 (0.092)
Total dry mass (g)	72.56 (0.014)	14.22 (0.064)	8.98 (0.096)	8.93 (0.105)
Calcified mass (g)	61.21 (< 0.001)	4.40 (0.069)	0.92 (0.365)	11.55 (0.002)
Soft tissue dry mass (g)	3.39 (0.207)	6.09 (0.132)	15.32 (0.060)	4.54 (0.194)
Calcified mass/soft tissue dry mass	12.19 (0.008)	1.57 (0.245)	8.77 (0.018)	2.54 (0.122)

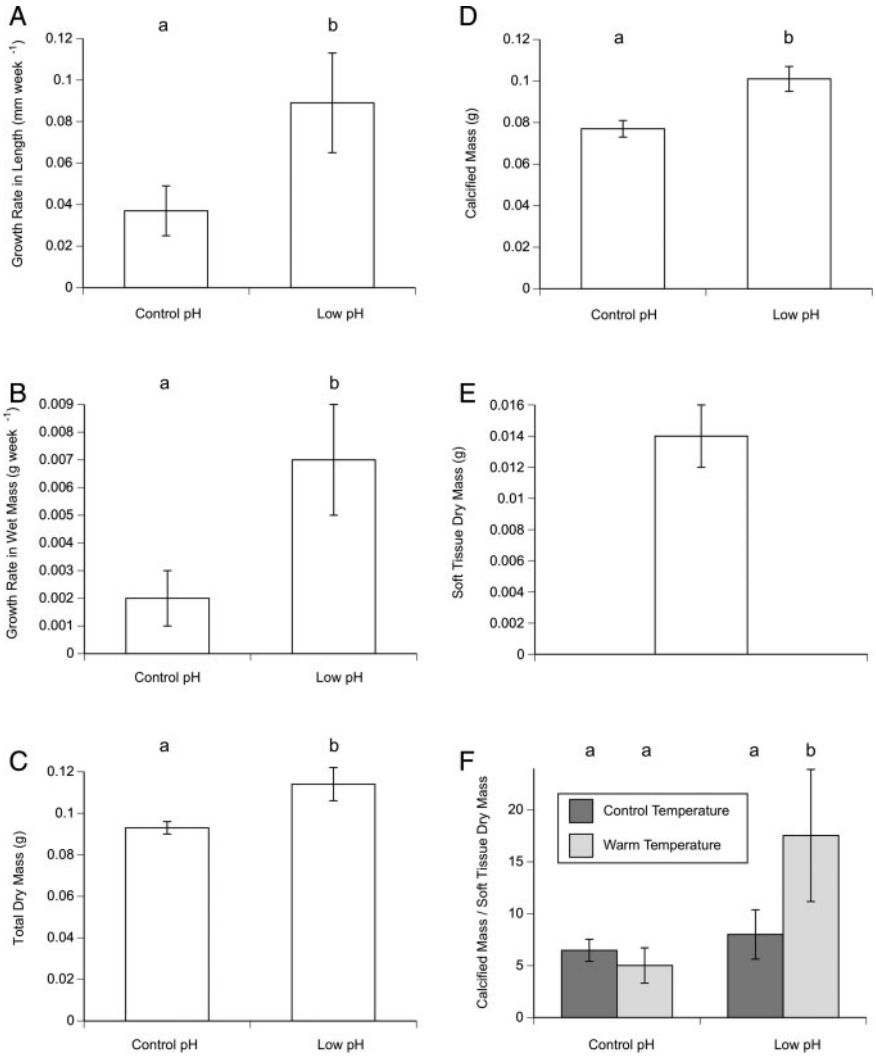

Figure 2. Response of *Mytilus edulis* (mean ± SE) to low pH (control pH = 8.10, low pH = 7.94) and increased temperature (control temperature = 20°C, high temperature = 24°C) in (A) growth rate in length, (B) growth rate in wet mass, (C) total dry mass, (D) calcified mass, (E) soft tissue dry mass, and (F) calcified mass/soft tissue dry mass. Means for the four possible treatment combinations are shown if there was a significant temperature × pH interaction (F). If no significant interaction and temperature effects occurred, only means for the two pH treatments are shown (A–D). If no significant effects occurred, only one bar summarizing the results is shown (E). Significant differences between any two treatments ($p < 0.05$) are indicated by the occurrence of different letters above the corresponding two bars.

The results on sea star growth in our study differ from those for a sea star from the northeast Pacific coast, *Pisaster ochraceus* (Gooding et al. 2009), for which acidification and warmer temperature caused a positive, additive response. Because the experimental methods and levels used here followed those used in the *P. ochraceus* study, the differing results are likely due to species differences in response to acidification. Control and warmer temperature treatments used in each study were different. In the Pacific sea star study, control temperature was 12°C and warm temperature was 15°C, which fall near the annual average temperature for that region. For the present study, we used temperatures at the upper end of the range currently experienced by *A. rubens* plus increases predicted through climate change, as this species has been found to maintain growth rates at average temperatures within its present natural range (Guillou et al. 2012) and climatic extremes are predicted to have a greater effect than average increases (Denny et al. 2009). However, Gooding et al. (2009) also conducted a temperature study (without acidification) using temperatures up to 21°C (correlating with maximum field measurements of sea star body temperature (Broitman et al. 2009)), which found *P. ochraceus* continued to respond positively in growth. This is likely due to a higher upper thermal range, since *P. ochraceus* inhabits the

intertidal zone, where it is exposed to aerial temperatures that regularly exceed seawater temperatures. Thus, the different trends between *P. ochraceus* and *A. rubens* are possibly due to species differences in response to future climate conditions, not experimental procedures. This difference may in part also be due to exposure of *P. ochraceus* to greater environmental pH variability than *A. rubens*. *Pisaster ochraceus* occurs on the Pacific coast of North America, which is subjected to wider fluctuations in pH due to seasonal coastal upwelling of more acidic water (Feely et al. 2008, 2010; Johannessen & MacDonald 2009). Upwelled water as low as pH 7.6 flows into the Salish Sea from the continental shelf between April and October, where it mixes with surface waters due to tidal currents (Crawford & Thomsen 1991; Masson 2002). Measurements near Gooding et al.'s (2009) collection site yielded pH values between 7.3 and 7.9, sometimes with even greater extremes (Marliave et al. 2011). Long-term exposure to lower-pH seawater may have led to greater tolerance of, or adaptation to, low-pH conditions in *P. ochraceus*. Species not exposed to upwelling and an associated broader range of pH may not respond in a similar way, although adaptation to a broader range of pH levels does not necessarily translate to future ocean pH conditions (Evans et al. 2013). Although a long-term pH data set is not yet available for Atlantic Canada, recent surveys found pH within 8.05–8.16 (K. Azetsu-Scott, unpublished data).

Further to growth effects on *A. rubens*, analysis of dry soft tissue mass and calcified mass separately showed a reduction of both in low-pH seawater, although the relative calcified material was higher with acidification. This suggests that there was a greater reduction in growth of soft tissue than calcified tissue, with maintenance of calcified structures taking precedence over somatic growth. In contrast to *A. rubens*, *P. ochraceus* appears to allocate energy to growth in soft tissue in acidified conditions, while relative calcified material decreases (Gooding et al. 2009). Intertidal invertebrates can experience wide fluctuations in internal pH during periods of emersion at low tide. Some bivalves reduce calcification and even undergo dissolution of the shell at the internal surface to compensate for increased internal acidosis (Akberali et al. 1983). *Pisaster ochraceus* may similarly be adapted to tolerate low-pH seawater during coastal upwelling, during which they endure a reduction in calcified structures in low-pH seawater (Gooding et al. 2009) and resume deposition of calcium carbonate when upwelling subsides and pH levels return to winter levels. A similar response to *A. rubens*, however, has been shown for other echinoderms in OA experiments. The brittlestars *Amphiura filiformis* (O. F. Müller, 1776) and *Ophiura ophiura* (Linnaeus, 1758) maintain calcification of skeletal structures in low-pH seawater at the cost of muscle wastage (Wood et al. 2008) or arm regeneration (Wood et al. 2010). These echinoderms appear to allocate additional resources to maintain calcification and preserve skeletal structure, reducing energy available for tissue growth. Another echinoderm, the sea urchin *Strongylocentrotus droebachiensis* (O. F. Müller, 1776), exhibited decreased somatic tissue growth and gonad growth in low-pH seawater, but no shell dissolution (Stumpp et al. 2012).

The only clear effect of temperature on sea stars was in combination with pH on calcified mass. The mechanism for this effect is not known, but it is suspected that the high temperature approached the thermal limit for *A. rubens*, and the added thermal stress resulted in a greater reduction of calcification than with just a reduction in pH.

Mussels

OA effects on *Mytilus edulis*, and bivalves in general, have been studied more than for sea stars due to the expectation of a greater impact on highly calcified species and the economic importance of mussels. In the present study, mussels exhibited a positive growth response to lower seawater pH and no change with higher temperature in all variables except relative calcified mass, suggesting that the mussels were still within their thermal tolerance range at the experimental temperatures. Growth increases were also seen for blue mussels in high-pCO_2 (up to 1000 µatm) areas of Kiel Fjord, northeast Atlantic, with high food availability (Thomsen et al. 2013). Under those conditions, mussels appear to compensate for low-pH conditions and upregulate growth. Examined separately, shell mass was higher for mussels in low pH than in controls, compared with no difference in dry soft tissue mass. The results for growth in length were consistent with another study that found no reduction in calcification rate in *M. edulis* among pH levels of 8.15, 8.02, 7.83 and 7.45 over 60 days (Ries et al. 2009). That is also consistent with the findings that positive growth in length occurs for *M. edulis* in pH 7.4 at rates similar to pH 8.0–8.1 (Berge et al. 2006; Melzner et al. 2011). Contrasting results were reported for *M. edulis* in another study, which found a linear trend of reduced calcification rate with decreasing pH (Gazeau et al. 2007), with shell dissolution exceeding calcification below a pH of 7.5. However, that study tested calcification rates over shorter periods of two-hour incubations at low pH. There may be some acclimation of mussels to

pH reductions over time that was not demonstrable in the study by Gazeau et al. (2007). Studies of other species have shown initial effects of exposure to low pH, followed by acclimation to (and no effect of) low pH. In the sea urchin *Strongylocentrotus droebachiensis*, short-term (4 days) exposure to low pH resulted in reduced internal pH, followed by acclimation (return to control internal pH) after 10 days (Stumpp et al. 2012).

Other studies of OA effects on *M. edulis* have shown decreasing shell growth (Berge et al. 2006; Melzner et al. 2011). However, those studies tested growth at further reduced pH levels to evaluate effects at levels farther into the future, or in the event of a leak from submarine CO_2 storage (pH 7.6, 7.4, 7.1 and 6.7, and pH 7.7, 7.4 and 7.2, respectively). From the present study, *M. edulis* growth in length is higher at pH 7.94 than at pH 8.10, which appears counterintuitive, as mussel populations may be expected to experience highest growth rates at present-day ambient pH. Although the mussels used here were collected subtidally, they also inhabit the intertidal zone, where they experience low tides daily (Scrosati & Heaven 2007). During aerial exposure, bivalves remain closed to prevent desiccation and internal pH drops (Akberali et al. 1983), which may have led to an adaptation to a broader range of pH values. Furthermore, mussels inhabiting coastal zones are subjected to occasional freshwater inputs (e.g. during spring melts) with associated decreases in pH, which may force adaptation to tolerance of low pH. It therefore appears as though *M. edulis* is tolerant of predicted pH and temperature levels for this century on the NW Atlantic coast. Further coastal sampling is required to determine the minimum pH experienced on the NW Atlantic and other coasts, and associated testing for pH tolerance of *M. edulis* from its various locations.

Thomsen et al. (2010) investigated a naturally low-pH area in the Kiel Fjord (between pH 7.5 and 8.2). They examined shell mass and growth in length of *M. edulis* and found no difference in growth between pH 7.7 and 8.2. Location and history of pH exposure may thus play an important role in how mussels may respond to future ocean pH. Those results show that blue mussels have adapted to regions of naturally lower pH and could, therefore, also adapt to future conditions. However, the rate at which ocean pH is dropping is faster than in the past 20 million years (Feely et al. 2004), so it is unknown the extent to which mussels will be able to adapt. Investigations on genotypic and phenotypic variation could provide some insight into the potential for species to adapt and persist in future oceanic conditions (Munday et al. 2013b; Sunday et al. 2014).

In addition to higher growth rates for *M. edulis* in acidified conditions, relative shell mass (ratio of shell mass to dry tissue mass) was higher in predicted conditions of lower pH and warmer temperature. Increases in shell growth rate with temperature are common. It seems as though the temperature difference in our experiment did not exceed the thermal limit for *M. edulis* growth and, furthermore, resulted in an additive effect of acidification and temperature for calcified mass. Feely et al. (2010) suggested that some species might increase calcification to compensate, and potentially overcompensate, for shell dissolution, obscuring effects of OA. This could be the case here, but further investigation into these two processes is required to tease apart low-pH effects. As noted above, this mussel may also be tolerant of predicted pH and temperature levels for later this century. Further testing at higher temperatures may elucidate its thermal limits, particularly its tolerance for extreme temperature events that may have a greater impact on survival than average increases (Denny et al. 2009). The observed relative increase in shell mass could mean an increase in shell thickness, which could benefit mussels through a greater resistance to predation pressure. Future experiments would benefit from examining shell thickness and strength in predicted ocean pH and temperature conditions.

Potential community effects

Biodiversity can affect community function through food production, habitat creation, and resistance to disturbances and species invasions (Hooper et al. 2005; Barry et al. 2011). Risks of biodiversity loss exist in marine communities because of climate change (Fabry et al. 2008). The link between diversity and function is evident in benthic marine habitats, where reduced diversity can alter trophic interactions, with strong effects when keystone predators or ecosystem engineers are lost (Sanford 1999; Maggi et al. 2009; Fabricius et al. 2014). *Asterias rubens* controls *Mytilus edulis* populations on subtidal and low-intertidal habitats through predation, clearing substrata for settlement of less competitive species that are otherwise absent (Lubchenco & Menge 1978). The consumption rate of *A. rubens* on *M. edulis* was 50% lower in low-pH seawater. Reduced consumption could affect benthic community structure in two ways. On the one hand, predation pressure on *M. edulis* could decrease, allowing mussels to dominate the available substrate, decreasing the diversity of primary-space holders (Lubchenco & Menge 1978). On the other hand, the increase in microhabitat complexity caused by mussel beds could increase the

diversity of small invertebrates, which normally thrive among the mussels (Arribas et al. 2014). Additionally, a higher growth rate of mussels under future conditions could lead to greater predation escape through faster attainment of a size refuge (Sommer et al. 1999).

Another effect that reduced consumption of mussels may have is a potential shift in prey species for *A. rubens*. While sea stars in low-pH conditions had a lower consumption, they were often observed hunched in the feeding position with a mussel in their grasp and stomach everted, suggesting a reduced feeding ability. Although mussels are the preferred prey for *A. rubens* (Lubchenco & Menge 1978; Gaymer et al. 2001), lower ability to consume them may force a shift to consumption of alternate prey such as economically important sea scallops, *Placopecten magellanicus* (O. F. Müller, 1776) (Wong & Barbeau 2005), or the ecologically important sea urchin, *Strongylocentrus droebachiensis* (Gaymer et al. 2004). A switch to prey species that belong to different functional groups could have a profound impact on community composition. For example, a switch to a grazer prey species could reduce grazing pressure and impose changes in seaweed composition. Effects can ripple through communities by affecting various interspecific interactions, leading to overall shifts in community structure.

In summary, we show that the sea star *A. rubens* and its preferred prey, *M. edulis*, respond in opposing ways to changes predicted in the marine environment by 2100. *Asterias rubens* shows lower growth and consumption rates under low pH, with temperature further reducing growth, while *M. edulis* growth rates are higher under low pH. Under predicted conditions, *M. edulis* may benefit from lower predation pressure due to a combination of lower consumption rate of the sea stars and faster attainment of a size refuge. OA and warming may thus lead to altered sea star and mussel populations and associated changes in community structure.

Acknowledgements

We thank Christopher Harley and Jocelyn Nelson for introducing us to acidification experiments and two anonymous reviewers for useful comments on the original manuscript.

Funding

This project was funded by grants awarded to R.A.S. by the Canada Research Chairs program (CRC), the Canada Foundation for Innovation (CFI), and the Natural Sciences and Engineering Research Council (NSERC, Discovery Grant) and by a grant awarded to S.C.C. by the Department of Fisheries and Oceans Canada (DFO).

Supplementary material

Supplementary material for this article is available via the Supplemental tab of the article's online page at http://dx.doi.org/10.1080/17451000.2014.932914

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Editorial responsibility: Geir Ottersen