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The ability of macroalgae to mitigate the negative effects of ocean acidification on four species of North Atlantic bivalve

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Abstract. Coastal ecosystems can experience acidification via upwelling, eutrophication, riverine discharge, and climate change. While the resulting increases in $p\mathrm{CO}_2$ can have deleterious effects on calcifying animals, this change in carbonate chemistry may benefit some marine autotrophs. Here, we report on experiments performed with North Atlantic populations of hard clams (*Mercenaria mercenaria*), eastern oysters (*Crassostrea virginica*), bay scallops (*Argopecten irradians*), and blue mussels (*Mytilus edulis*) grown with and without North Atlantic populations of the green macroalgae, *Ulva*. In 6 of 7 experiments, exposure to elevated $p\mathrm{CO}_2$ levels (~1,700 µatm) resulted in depressed shell- and/or tissue-based growth rates of bivalves compared to control conditions ($p<0.05$) whereas rates were significantly higher in the presence of *Ulva* in all experiments ($p<0.05$). In many cases, the co-exposure elevated $p\mathrm{CO}_2$ levels and *Ulva* had an antagonistic effect on bivalve growth rates whereby the presence of *Ulva* under elevated $p\mathrm{CO}_2$ levels significantly improved their performance compared to the acidification only treatment ($p<0.05$). Saturation states for calcium carbonate (Ω) were significantly higher in the presence of *Ulva* under both ambient and elevated CO_2 delivery rates ($p<0.05$). Collectively, the results suggest that photosynthesis and/or nitrate assimilation by *Ulva* increased alkalinity, fostering a carbonate chemistry regime more suitable for optimal growth of calcifying bivalves. This suggests that large natural and/or aquacultured collections of macroalgae in acidified environments could serve as a refuge for calcifying animals that may otherwise be negatively impacted by elevated $p\mathrm{CO}_2$ levels and depressed Ω.

1 Introduction

The continued delivery of CO_2 into surface oceans is expected to cause significant shifts in pools of inorganic carbon by the end of this century, with projected increases in CO_2 and HCO_3^- and decreases in CO_3^{2-} and the saturation states of calcite ($\Omega_{\mathrm{calcite}}$) and aragonite ($\Omega_{\mathrm{aragonite}}$) (Feely et al., 2009; Meehl et al., 2007). Beyond the delivery of CO_2 via the combustion of fossil fuels, upwelling, riverine discharge, eutrophication-accelerated microbial respiration all represent strong sources of CO_2 into coastal zones (Cai et al., 2011; Feely et al., 2008; Melzner et al., 2013; Salisbury et al., 2008; Wallace et al., 2014). Eutrophication-enhanced respiration in coastal zones can lead to the accumulation of respiratory CO_2 that can exceed concentrations projected for the end of the century (>2,000 µatm), as well as result in the undersaturation of aragonite ($\Omega_{aragonite} < 1$; Cai et al., 2017; Wallace et al., 2014).

Calcifying organisms are highly vulnerable to the projected shifts in the various pools of total dissolved inorganic carbon (DIC), with the deleterious effects of ocean acidification being well-documented for corals (Hoegh-Guldberg et al., 2007; Kleypas et al., 1999), coralline algae (Gao and Zheng, 2010; Martin and Gattuso, 2009), and bivalves (Barton et al., 2012; Gazeau et al., 2007; Talmage and Gobler, 2011). Acidification-induced reductions in $\Omega_{calcite}$ and $\Omega_{aragonite}$ can result in lowered survivorship and inhibited growth for larvae and juvenile stage bivalves (Gobler et al., 2014; Green et al., 2009; Talmage and Gobler, 2011; Waldbusser et al., 2015a). Since bivalves provide numerous ecosystem and economic services (Newell, 2004), and elevated $p\mathrm{CO}_2$ is a common occurrence in many coastal ecosystems (Feely et al., 2008; Salisbury et al., 2008; Wallace et al., 2014), it is important to understand how other co-occurring estuarine life will respond to high $p\mathrm{CO}_2$ conditions and may, in turn, effect acidification-vulnerable organisms such as bivalves.

Contrary to the negative effects of increased CO_2 on calcifying organisms, previous studies have shown that some photosynthetic organisms, such as seagrasses (Koch et al., 2013; Palacios and Zimmerman, 2007), phytoplankton (Fu et al., 2012; Hattenrath-Lehmann et al., 2015), and macroalgae (Olischläger et al., 2013; Young and Gobler, 2016) may benefit from a high CO_2 environment. Such photosynthetic autotrophs may also have the capacity to buffer carbonate chemistry, potentially alleviating the harmful effects of excessive CO_2 on calcifying organisms. For example, prior studies have observed that primary productivity within seagrass meadows can increase pH and $\Omega_{aragonite}$ which, under future acidified conditions, may provide refuge for calcifying animals (Garrard et al., 2014; Hendriks et al., 2014; Unsworth et al., 2012). Given the significant global declines in seagrass (Orth et al., 2006; Short et al., 2011; Waycott et al., 2009), as well as the overgrowth of seagrass beds by macroalgae (McGlathery, 2001; Valiela et al., 1997), it is plausible macroalgae may more commonly provide similar ecosystem services. While future increases in CO_2 may promote the growth of fast-growing, macroalgae such as *Ulva* (Björk et al., 1993; Olischläger et al., 2013; Young and Gobler, 2016, 2017) and could, in turn, could provide chemical resilience for calcifying organisms in acidified environments (Anthony et al., 2013; Wahl et al., 2017), such interactions have yet to be fully explored.

Recent studies have demonstrated that populations of *Ulva rigida* from Northwest Atlantic coastal waters experience enhanced growth under elevated CO_2 concentrations (Young and Gobler, 2016, 2017). While past studies have suggested that macroalgae may buffer carbonate chemistry to the benefit of bivalves (Anthony et al., 2013; Wahl et al., 2017), no study has assessed how *Ulva*, a common macroalga known to undergo enhanced growth under acidified and eutrophic conditions, may affect bivalves under CO_2-enhanced conditions. The objective of this study, therefore, was to assess how elevated $p\mathrm{CO}_2$ and the presence of *Ulva* influences the growth and survival of seven cohorts of small- and large-sized of juvenile bivalves indigenous to North Atlantic, including hard clams (= northern quahogs; *Mercenaria mercenaria*), eastern oysters (*Crassostrea virginica*), bay scallops (*Argopecten irradians*), and blue mussels (*Mytilus edulis*). Each bivalve cohort was grown with and without elevated CO_2 levels as well as with and without *Ulva*. Growth and survival of the bivalves were quantified along with carbonate chemistry within experimental vessels.

2 Methods

2.1 Experimental design

Seven experiments were performed to assess the effects of elevated $p\mathrm{CO}_2$ and the presence of *Ulva* on the growth and survival of *M. mercenaria*, *C. virginica*, *A. irradians*, and *M. edulis*. Experiments using smaller bivalves (1 – 5 mm) were performed in 1 L polycarbonate vessels, while experiments with larger bivalves (20 – 21 mm) were performed in larger, 8 L polycarbonate vessels. All containers were acid washed (10% HCl) and liberally rinsed with deionized water prior to use. The experimental vessels were placed in an environmental control chamber set to a consistent temperature (~21°C), light intensity (~200 µmol photons m^{-2} s^{-1}) and duration (14 h: 10 h light:dark cycle). Containers were filled with filtered (0.2µm polysulfone filter capsule, Pall©) seawater and were randomly assigned, in quadruplicate, to one of four treatments: a control with ambient CO_2 concentrations (~400 µatm) without *Ulva*, a treatment with ambient CO_2 levels that received *Ulva*, a treatment with elevated CO_2 concentrations (~1700 µatm) without *Ulva*, and a treatment with elevated CO_2 and *Ulva*, resulting in 16 experimental containers. Two additional containers were filled with filtered seawater and bubbled in a manner identical to the ambient or elevated CO_2 treatments (described below) and were used to obtain initial dissolved inorganic carbon measurements. Continuous dissolved oxygen (DO) measurements were made using HOBO optical DO sensors (Onset©) in additional parallel vessels with and without *Ulva* added at the same levels used in experimental vessels and bubbled identically to experimental vessels. All experimental containers for each experiment received nutrient additions (50µM nitrate, 3 µM phosphate) at the beginning of the experiment, as well as after each twice weekly water changes (details below) to ensure nutrient replete growth of *Ulva*. The nutrient and CO_2 concentrations used during experiments were within the range of concentrations present in US East Coast estuaries (Baumann and Smith, 2017; Baumann et al., 2015; Wallace et al., 2014; Wallace and Gobler, 2015), and were used during prior experiments that involved *Ulva* from Shinnecock Bay, NY, USA (Young and Gobler, 2016, 2017). Across all experiments, bivalves were fed a mixture of *Isochyrsis galbana* and *Chaetoceros muelleri* at rate known to be *ad libitum* (4 x 10^4 cells mL^{-1} d^{-1}) (Gobler et al., 2014). Microalgal cultures were maintained in exponential phase growth in f/2 media using standard culturing conditions (Helm et al., 2004).

To deliver dissolved gases, each experimental vessel was aerated via a 3.8 x 1.3 cm air diffuser (Pentair) connected to a 1 mL, polystyrene serological pipette inserted to the bottom of each vessel and connected via Tygon tubing to an air source. Containers were subjected to ambient (~400 µatm) and elevated (~1700 µatm) CO_2 concentrations via a gas proportionator system (Cole Parmer® Flowmeter system, multitube frame) that mixed ambient air with 5% CO_2 gas (Talmage and Gobler, 2010). Gases were mixed and delivered at a flow rate of 2500 ± 5 mL min^{-1} through gang valves into the serological pipettes that fit through an opening in the plexiglass used to cover the experimental containers, turning over the volume of the experimental containers >1000 times daily. Bubbling began two-to-three days prior to the start of each experiment to allow CO_2 concentrations and carbonate chemistry to reach a state of equilibrium. Experiments persisted for ~two weeks. Measurements of pH within containers were made daily with a Honeywell DuraFET III ion-sensitive field-effect transistor-based (ISFET) solid-state pH sensor (± 0.01 pH unit, total scale). Discrete water samples were collected at the beginning and conclusion of experiments to directly measure DIC within each experimental vessel. The DIC samples were preserved using a saturated mercuric chloride ($HgCl_2$) solution and stored at ~4°C until analysis. Samples were analyzed by a VINDTA 3D (Versatile INstrument for the Determination of Total inorganic carbon) delivery system coupled with a UIC Inc. coulometer (model CM5017O). During the coulometric analysis, all carbonate species were converted to CO_2 gas by the addition of excess hydrogen to the sample and the evolved CO_2 gas was subsequently carried into the titration cell of the coulometer. The gas then reacted quantitatively with an ethanolamine-based reagent to generate hydrogen ions, which were titrated with coulometrically-generated OH^-, and CO_2 was measured by integrating the total change required to titrate the hydrogen ions (Johnson et al., 1993). Total alkalinity, $\Omega_{aragonite}$, $\Omega_{calcite}$, $p\mathrm{CO}_2$, and concentrations of HCO_3^-, CO_3^{2-} and OH^- (Tables 1 and S1) were calculated from measured levels of DIC, pH, temperature, and salinity, as well as the first and second dissociation constants of carbonic acid in seawater (Millero, 2010) using the program CO2SYS (http://cdiac.ornl.gov/ftop/co2sys/). For quality assurance, levels of DIC and pH within certified reference material (provided by Dr. Andrew Dickson of the University of California, San Diego, Scripps Institution of Oceanography; batches 158, 159 = 2044, 2027 µmol DIC kg seawater^{-1}, respectively) were measured during analyses of every set of samples. The analysis of samples continued only after complete recovery (99.8 ± 0.2 %) of certified reference material was attained. Actual mean $p\mathrm{CO}_2$ and pH values were 350 µatm and 8.00, respectively for ambient conditions, and 1750 µatm and 7.38, respectively, for elevated CO_2 conditions, values within the range found seasonally in some estuarine environments (Baumann and Smith, 2017; Baumann et al., 2015; Wallace et al., 2014; Wallace and Gobler, 2015). Two-way ANOVAs and post-hoc tests were used to assess significant differences in carbonate chemistry among experimental vessels with the main treatment effects being $p\mathrm{CO}_2$ (ambient or elevated) and the presence of *Ulva* within SigmaPlot 11.0.

2.2 Assessing the effects of elevated $p\mathrm{CO}_2$ and *Ulva* on juvenile bivalves

The macroalgae used for this study were collected from Shinnecock Bay, NY, USA, (40.85° N, 72.50° W) during low tide. Permission to access this area and collect macroalgae and *M. edulis* was received from the Southampton Town Trustees, Southampton, NY, USA, who hold jurisdiction over Shinnecock Bay. Large, well-pigmented, robust fronds of *Ulva* were collected and transported to the Stony Brook Marine Science Center in seawater-filled containers within 15 minutes of collection. Previously, ITS sequencing and microscopy was used to determined that the species of *Ulva* that dominated Shinnecock Bay in summer and fall was *Ulva rigida* (Young and Gobler, 2016, 2017) and microscopic examinations during this study indicated this was the species used in all experiments presented here. We refer to the algae simply as *Ulva* throughout the study due to the plastic nature of the macroalgal taxonomic nomenclature, as well as the high similarity of ITS sequences among species of *Ulva* (Hofmann et al., 2010; Kirkendale et al., 2013).

Well-pigmented, circular sections of *Ulva* (~3.5 cm and ~7 cm for experiments in small containers and large vessels, respectively) were cut from the larger thalli with care taken to avoid the outer, potentially reproductive region of the algae (Wallace and Gobler, 2015). The weights of *Ulva* used in experiments relative to the vessels was consistent with the benthic coverage of *Ulva* in Shinnecock Bay (~8 g m^{-2}; Gobler and Young, unpublished benthic trawl data) and other estuarine regions (Liu et al., 2015; Sfriso et al., 2001). Experimental disks of *Ulva* were extensively rinsed with filtered (0.2 µm) seawater and spun in a salad spinner to remove debris and epiphytes with this step being repeated multiple times. *Ulva* samples were weighed on a Scientech ZSA 120 digital microbalance (± 0.0001 g) to obtain initial wet weight in grams. All samples were kept in 100 mL 0.2 µm filtered seawater-filled containers after spinning and weighing to prevent desiccation prior to use in experiments.

Small and large cohorts of *Mercenaria mercenaria* (~1 mm and ~5 mm, respectively) and *Argopecten irradians* (~5 mm and ~20 mm, respectively) used during experiments were spawned at the Stony Brook Marine Science Center of Stony Brook University hatchery (40.89° N, 72.44° W) using Shinnecock Bay-derived broodstock collected 1 – 2 months prior to spawning. Small and large cohorts of *Crassostrea virginica* (~2 mm and ~20 mm, respectively) used during experiments were produced by hatcheries within the Cornell Cooperative Extension of Southold, NY, USA (40.04° N, 72.39° W) using broodstock from the Peconic Estuary, NY, USA. Cohorts of small juvenile *Mytilus edulis* (~5 mm) used during experiments were collected from Shinnecock Bay, NY, USA during low tide (40.84° N, 72.50° W). Experiments using smaller bivalves (1 – 5 mm) were performed in 1 L polycarbonate vessels with 20 individuals per vessel, while experiments with larger bivalves (20 – 21 mm) were performed in larger, 8 L polycarbonate vessels with five individuals per vessel.

Experiments began with the introduction of bivalves, *Ulva*, and nutrients into experimental vessels, with discrete and continuous measurements of pH, dissolved oxygen, and temperature made as described above throughout experiments. At the beginning of each experiment, 20 individuals from each bivalve cohort were set aside to obtain initial measurements of shell length (defined here as distance from umbo to furthest ventral margin), tissue weight, and shell weight. Bivalve dimensions were determined via digital calipers and digital images with the two approaches producing nearly identical and not statistically different measurements. Captured images of bivalves were analyzed using ImageJ, with the scale of each image individually calibrated. Every three days, a complete water change was performed for all containers. Once weekly, *Ulva* disks from each container were removed, rinsed, spun in the salad spinner, weighed, and returned to the vessels. Additionally, every week, bivalves were collected on a 500 µm sieve, transferred to a petri dish, and measured for length with any mortality noted. Mortality rates were very low (always <10%) and did not differ among treatments. At the conclusion of experiments, final pH, temperature, and salinity measurements were made and final water samples for DIC analysis were collected and analyzed as described above.

At the conclusion of experiments, measurements of shell length for bivalves within the experimental containers as well as individuals set aside for initial measurements were made, and growth (expressed as mm d^{-1}) was determined from the changes in shell dimensions during the experiment. Tissue and shell weight were obtained by weighing bivalves after drying at 60°C for 72 hr, combusting them at 450°C for 4 hr, and weighing them again. Growth (expressed as mg d^{-1}) was determined by comparing the initial and final dry and combusted weights of individuals from each replicated vessel. Specifically, tissue weight was determined by subtracting the combusted weight from the dry weight, while shell weight was determined by subtracting the tissue weight from the dry weight. Two-way ANOVAs were performed using within

SigmaPlot 11.0 to assess significant differences in growth rates based on shell length, tissue weight, shell weight, and survival during experiments, where the main treatment effects were $p\mathrm{CO_2}$ (ambient or elevated), and the presence of *Ulva*. If significant differences were detected, a Tukey Honest Significant Difference (Tukey HSD) test using R 3.4.0 within RStudio 1.0.143 was performed to identify differences among treatments.

3 Results

3.1 *Mercenaria mercenaria*

For the cohort of smaller juvenile *M. mercenaria* (1.34 ± 0.24 mm), $\Omega_{calcite}$ and $\Omega_{aragonite}$ were significantly lower in treatments with elevated CO_2 and significantly higher in treatments containing *Ulva* (Two-way ANOVA; $p<0.05$ for both; Fig. 1; Tables S2-S3). Growth of the small *M. mercenaria* based upon shell length, tissue weight, and shell weight was highly sensitive to increases in $p\mathrm{CO_2}$ as well as the presence of *Ulva*. When exposed to elevated CO_2 conditions, shell length-, tissue weight-, and shell weight-based growth rates were 49%, 41%, and 66% lower, respectively, when compared to their counterparts in ambient CO_2 treatments (Two-way ANOVA; $p<0.05$ for all; Fig. 1; Tables S4-S6). In contrast, all growth rates were significantly higher in the presence of *Ulva* (Two-way ANOVA; $p<0.05$; Fig. 1; Tables S4-S6) with growth based on shell length, tissue weight, and shell weight being 15%, 29%, and 32% higher, respectively (Fig. 1). Multiple comparison tests revealed that *Ulva* often mitigated the negative effects of elevated CO_2 on hard clams. For example, length-based growth in elevated CO_2 treatments with *Ulva* was significantly higher than elevated CO_2 treatments without *Ulva* (Tukey HSD; $p<0.05$; Table S7).

For the larger-sized cohort of *M. mercenaria* (5.00 ± 0.41 mm), $\Omega_{calcite}$ and $\Omega_{aragonite}$ were significantly higher in treatments containing *Ulva* and significantly lower in high CO_2 treatments (Two-way ANOVA; $p<0.05$ for both; Fig. 2; Tables S2-S3). Larger *M. mercenaria* responded to elevated CO_2 conditions and the presence of *Ulva* in a manner similar to that of the smaller clams. Under elevated CO_2 concentrations, length-, tissue-, and shell-based growth rates were significantly lower (by 45%, 22%, and 30%, respectively) relative than the ambient CO_2 treatments (Two-way ANOVA; $p<0.05$; Fig. 2; Tables S4-S6). In the presence of *Ulva*, however, length-, tissue-, and shell-based growth rates were significantly higher (by 26%, 16%, and 33%, respectively) relative to treatments that did not receive *Ulva* (Two-way ANOVA; $p<0.05$; Fig. 2; Tables S4-S6).

3.2 *Crassostrea virginica*

During the experiment with the cohort of small *C. virginica* (2.45 ± 0.41 mm), $\Omega_{calcite}$ and $\Omega_{aragonite}$ were significantly higher in treatments containing *Ulva* and significantly lower in treatments receiving elevated CO_2 (Two-way ANOVA; $p<0.05$ for both; Fig. 3; Tables S2-S3). Growth rates of small *C. virginica* were sensitive to elevated CO_2 concentrations and the presence of *Ulva*. Length-, tissue-, and shell weight-based growth rates were 63%, 78%, and 145% lower, respectively, when exposed to elevated CO_2 concentrations compared to control treatments (Two-way ANOVA; $p<0.05$; Fig. 3; Tables S4-S6). When in the presence of *Ulva*, shell length-based growth was significantly increased by 42% (Two-way ANOVA;

$p<0.05$; Fig. 3; Table S4), but tissue and shell weight-based growth were not significantly different than the control (Two-way ANOVA; $p>0.05$).

For the larger juvenile *C. virginica* (24.92 ± 0.89 mm), $\Omega_{calcite}$ and $\Omega_{aragonite}$ were significantly higher in treatments containing *Ulva* and significantly lower in treatments receiving elevated CO_2 (Two-way ANOVA; $p<0.05$ for both; Fig. 4; Tables S2-S3). Growth responses for the larger *C. virginica* differed from the smaller-sized juveniles. Shell length-based growth was 167% and significantly lower under elevated CO_2 concentrations relative to the control and significantly higher (by 72%) in the presence of *Ulva* relative to the control (Two-way ANOVA; $p<0.05$; Fig. 4; Table S4). While shell weight-based and tissue weight-based growth were not significantly altered by elevated CO_2 or the presence of *Ulva*, there was an antagonistic, interactive effect between both variables whereby the co-exposure to elevated CO_2 and *Ulva* yielded growth rates higher than would have been predicted by growth rates within the individual treatments (Two-way ANOVA; $p<0.05$; Fig. 4; Tables S5-S6). Consistent with this finding, shell length-based growth in elevated CO_2 treatments with *Ulva* was significantly higher than in elevated CO_2 treatments without *Ulva* (Tukey HSD; $p<0.05$; Table S7).

3.3 *Argopecten irradians*

For the cohort of small *A. irradians* (4.73 ± 0.59 mm), $\Omega_{calcite}$ and $\Omega_{aragonite}$ were significantly higher in treatments containing *Ulva* and significantly lower in treatments with elevated CO_2 (Two-way ANOVA; $p<0.05$ for both; Fig. 5; Tables S2-S3). The growth of small juvenile *A. irradians* was altered by pCO_2 and, to a lesser extent, the presence of *Ulva*. All measurements of growth were significantly reduced by exposure to elevated CO_2 concentrations (Two-way ANOVA; $p<0.05$; Fig. 5; Tables S4-S6). Specifically, growth rates based on shell length, tissue weight, and shell weight were 26%, 40%, and 43% lower, respectively, when exposed to elevated CO_2 compared to ambient CO_2 treatments (Fig. 5). Shell length-based growth was significantly higher (by 15%) in the presence of *Ulva* relative to treatments that did not receive *Ulva* (Fig. 5). In contrast, tissue and shell weight-based growth were not significantly affected by the presence of *Ulva* (Two-way ANOVA; $p>0.05$; Fig. 5; Tables S2-S3). Shell length-based growth within elevated CO_2 treatments with *Ulva* was significantly higher than in the elevated CO_2 treatments without *Ulva* (Tukey HSD; $p<0.05$; Table S7). There were no significant differences in shell or tissue weight-based growth among any treatments (Tukey HSD; $p>0.05$; Tables S8-S9).

For the larger cohorts of juvenile *A. irradians* (21.08 ± 1.06 mm), $\Omega_{calcite}$ and $\Omega_{aragonite}$ were significantly lower in treatments exposed to high CO_2 and significantly higher in treatments containing *Ulva* (Two-way ANOVA; $p<0.05$ for both; Fig. 6; Tables S2-S3). The growth rates of larger *A. irradians* based on shell length and tissue weight were significantly reduced under elevated CO_2 concentrations by 32% and 105%, respectively (Two-way ANOVA; $p<0.05$; Fig. 6; Tables S4 and S6) while shell weight-based growth was not (Two-way ANOVA; $p>0.05$; Table S5). Growth rates based on shell length and tissue weight were significantly increased in the presence of *Ulva* by 16% and 149%, respectively (Two-way ANOVA; $p<0.05$; Fig. 6; Tables S4 and S6) while shell weight-based growth was not (Two-way ANOVA; $p>0.05$; Table S5). Comparisons within individual treatments showed that shell length-based growth within elevated CO_2 treatments without *Ulva* was significantly lower than the elevated CO_2 treatments with *Ulva* (Tukey HSD; $p<0.01$; Table S7).

3.4 *Mytilus edulis*

During the experiments with *M. edulis* (4.87 ± 0.92 mm), $\Omega_{calcite}$ and $\Omega_{aragonite}$ were significantly higher in treatments containing *Ulva* and significantly lower in treatments exposed to high CO_2 (Two-way ANOVA; $p<0.05$ for both; Fig. 7; Tables S2-S3). Growth rates of *M. edulis* based on shell length, tissue weight, and shell weight were all not significantly changed by exposure to elevated CO_2 concentrations (Two-way ANOVA; $p>0.05$; Fig. 7; Tables S4-S6). In contrast, all growth measurements were significantly higher in the presence of *Ulva* (Two-way ANOVA; $p<0.05$; Fig. 7; Tables S4-S6). Specifically, in the presence of *Ulva*, growth based on shell length, tissue weight, and shell weight was 21%, 25%, and 41% higher, respectively, relative to treatments that did not receive *Ulva*, regardless of CO_2 concentration (Fig. 7).

4 Discussion

During this study, elevated CO_2 concentrations significantly reduced at least one or more growth measurements of small- and large-sized cohorts of juvenile *Mercenaria mercenaria*, *Crassostrea virginica*, and *Argopecten irradians*, but not *Mytilus edulis*. The presence of *Ulva* significantly increased the growth of all cohorts of all bivalve species. Comparisons of individual treatments indicated that under elevated CO_2 concentrations, the addition of *Ulva* often significantly increased growth rates for cohorts of clams, scallops, and oysters. Both $\Omega_{aragonite}$ and $\Omega_{calcite}$ were significantly higher in the presence of *Ulva* in all experiments under both high and low CO_2 regimes, despite the rapid turnover of dissolved gas pools in experiments (>1000 time per day). Collectively, these findings provide insight regarding the ability of macroalgae such as *Ulva* to mitigate the deleterious effects of ocean acidification on bivalves, and, potentially, other calcifying organisms.

The negative effects of ocean acidification on the growth and survival of bivalves and other calcifying organisms have been well-documented. Consistent with prior studies that have gauged the response of juvenile bivalves to elevated CO_2 (Gazeau et al., 2007; Green et al., 2009; Talmage and Gobler, 2011), the results of the current study show decreased tissue growth as well as calcification in the form of shell length- and weight-based growth, a finding consistent with significantly lower $\Omega_{aragonite}$ and $\Omega_{calcite}$ in elevated CO_2 treatments. Early life-stage bivalve shells are composed partly or completely of aragonite, making them vulnerable to undersaturation of aragonite (Carriker, 1996; Stenzel, 1964; Talmage and Gobler, 2009). While the formation of calcium carbonate is thermodynamically favored when Ω exceeds 1.0, biotic aragonite is less crystalline than nonbiogenic aragonite (Weiss et al., 2002) and studies of early life stage Pacific oysters have suggested that a $\Omega_{aragonite}$ exceeding 1.6 may be required to yield successful growth and survival (Barton et al., 2012). Similarly, Talmage and Gobler (2010) found that increases in $\Omega_{aragonite}$ within the saturated range ($\Omega_{aragonite}$ increases from 2.9 to 3.3) significantly increased the growth of early life stage *M. mercenaria* and *A. irradians*, a finding suggesting that acidification since pre-industrial time depresses the performance of these individuals. In the current study, growth rates of bivalves exposed to *Ulva* under ambient pCO_2 frequently exceeded those of individuals grown under the same CO_2 delivery rate without *Ulva* as $\Omega_{aragonite}$ was significantly increased, on average from 1.91 to 2.16 (Table 1), with both levels being saturated but also being below the threshold that yielded maximal growth rates in early life stage bivalves for Talmage and Gobler (2010). Hence, the potential benefits of macroalgae to calcifying bivalves may be realized in both acidified and 'normal' conditions.

Acidification can have cascading negative physiological consequences for bivalves. In larval bivalves, high CO_2 depresses calcification, lipid content, RNA:DNA ratios, metamorphosis, and growth rates (Gobler and Talmage, 2013). The reduction in tissue weight-based growth under elevated CO_2 concentrations found during the present study is consistent with Beniash et al. (2010), who found significant declines in soft body mass of juvenile *C. virginica* maintained in hypercapnia (pH 7.5). Additionally, the same study and others (Gazeau et al., 2007; Matoo et al., 2013) have reported increased metabolic rates in bivalves exposed to elevated CO_2 levels. As suggested by Waldbusser et al. (2015b), decreasing $\Omega_{aragonite}$ increases the amount of energy spent by bivalves on shell formation which diverts energy away from maintaining homeostasis and other metabolic processes including those that contribute toward growth (Beniash et al., 2010; Waldbusser et al., 2015b).

Macroalgae can control carbonate chemistry in shallow ecosystems and, in turn, can affect the performance of carbonaceous organisms. A study by Anthony et al. (2013) found that within mixed assemblages of turf and fleshy macroalgae, the saturation state of aragonite increased during the daytime. Krause-Jensen et al. (2015) reported that macroalgae may provide a refuge for calcifying organisms. Specifically, within a subarctic fjord, macroalgae drove strong diel variability in pH and $\Omega_{aragonite}$, with *M. edulis* being found to grow in close association with macroalgae, even in tidal pools that became supersaturated and undersaturated between day and night cycles, respectively (Krause-Jensen et al., 2015). Additionally, Wahl et al. (2017) demonstrated that daytime increases in pH associated with the macroalgae *Fucus vesciculosus* provided a refuge against acidified conditions for *M. edulis*, with calcification rates of *M. edulis* increasing with increases in pH wrought by the algae. In the current study, *Ulva* yielded significantly increased $\Omega_{aragonite}$, $\Omega_{calcite}$, and bivalve growth in all seven experiments performed. Furthermore, dissolved oxygen levels were high (> 7 mg L^{-1}) in all treatments and the growth rates of bivalves were often significantly higher in high CO_2 treatments with *Ulva* compared to those without. Hence, it seems likely that the macroalgae buffered carbonate chemistry to the benefit of bivalves.

Beyond photosynthesis, macroalgae may also alter carbonate chemistry via the uptake of nitrogenous nutrients. Specifically, the uptake of nitrate or ammonium by marine autotrophs results in an equimolar increase or decrease in total alkalinity, respectively (Brewer and Goldman, 1976; Goldman and Brewer, 1980; Talmage and Gobler, 2012), which occurs due to the production of OH^- and H^+ to balance the uptake of nitrate and ammonium, respectively (Brewer and Goldman, 1976; Goldman and Brewer, 1980; Redfield et al., 1963). Given that 50µM nitrate was added to all experimental vessels with *Ulva* to promote its growth during each experimental water change, it is possible that the assimilation of this nitrate by *Ulva* contributed to the average 10 – 20 µM increase in total alkalinity observed within treatments with *Ulva* (Two-way ANOVA; $p<0.05$; Table 1; Tables S10-S11). Higher alkalinity seawater requires higher concentrations of CO_2 to reduce pH, thus resulting in smaller changes in $\Omega_{aragonite}$ and $\Omega_{calcite}$. Given the rapid turnover of dissolved gasses in experimental vessels, it is possible the nitrogen assimilation effects on alkalinity outweighed the effects of photosynthetic consumption of DIC.

Prior studies have found that *Ulva* can experience enhanced growth (Björk et al., 1993; Olischläger et al., 2013; Young and Gobler, 2016) and outcompete other autotrophs (Young and Gobler, 2017) under elevated CO_2 concentrations.

Hence, the dominance of *Ulva* and similar macroalgae in estuaries that experience seasonal acidification (Wallace and Gobler, 2015) could ultimately benefit bivalves and other calcifying organisms. In the present experiments, *Ulva* growth was, on average, ~20% higher under elevated CO_2 conditions (One-way ANOVA; $p<0.05$; Fig. S1 and Table S12). Furthermore, the presence of the macroalgae frequently transformed $\Omega_{aragonite}$ of elevated CO_2 treatments from undersaturated to nearly saturated (Tables 1 and S1) and often yielded growth rates of bivalves significantly greater than the elevated CO_2 treatments without *Ulva*. Had the dissolved gas pools within experimental vessels not been turned over rapidly via aeration, it is possible the effects of *Ulva* on the carbonate chemistry would have been even greater.

The benefits of *Ulva* and detriments of high CO_2 to the four bivalves studied differed by species. While every cohort displayed significantly enhanced growth in the presence of *Ulva*, scallops were the only species to experience significantly higher growth in the elevated CO_2 treatment with *Ulva* compared to the elevated CO_2 treatment with *Ulva* for both the small and large juvenile cohorts. In contrast, for clams and oysters, only one of the two cohorts displayed this specific response. Early life stages of bay scallops have been consistently shown to be more vulnerable to acidification than the other bivalve species studied here (Stevens and Gobler, in revision; Talmage and Gobler, 2009, 2011). This may be due in part to its rapid growth and metabolism compared to other bivalves (Kennedy et al., 1996; Kraeuter and Castagna, 2001; Shumway and Parsons, 2006), traits that may also make it more likely to benefit from the improved carbonate chemistry wrought by the presence of *Ulva*. The resistance of *M. edulis* to elevated CO_2 concentrations contrasted with prior studies of European strains (Berge et al., 2006; Gazeau et al., 2007) but is consistent with prior cohorts of this species isolated from Shinnecock Bay, NY, USA (Stevens and Gobler, in revision). However, Thomsen et al. (2012) found that growth and calcification of juvenile *M. edulis* were dependent more on food availability than carbonate chemistry. Given that food was supplied *ad libitum* in the present study, it is possible that the negative effects of elevated CO_2 concentrations on *M. edulis* may have been mitigated by adequate food availability as well as improved carbonate chemistry facilitated by *Ulva*.

Beyond the modification of carbonate chemistry, there are additional ecosystem benefits that may be provided by macroalgae. Macroalgal beds can serve as an nursery habitat for juvenile *Callinectes sapidus* (Wilson et al., 1990), as well as other decapods (Heck et al., 2003; Sogard and Able, 1991). Macroalgae can also serve as a refuge from predation for some juvenile and adult bivalves (Carroll et al., 2010). An additional potential benefit provided to bivalves by *Ulva* and other macroalgae is their ability to inhibit the growth of phytoplankton species that cause harmful algal blooms (HABs; Tang and Gobler, 2011; Tang et al., 2015) that can directly harm the bivalve species used in the present study (Gobler and Sunda, 2012; Leverone et al., 2006; Stoecker et al., 2008; Tang and Gobler, 2009). Furthermore, given its ability to rapidly assimilate and store nitrate and ammonium (Pedersen and Borum, 1997), *Ulva* can serve as a biofilter within eutrophic ecosystems (Hernández et al., 2002; Neori et al., 2003). Given that harmful algal blooms flourish in eutrophic zones (Anderson et al., 2008; Anderson et al., 2002), the mitigation of high nutrient conditions by *Ulva* may reduce the intensity of HABs, which may indirectly benefit bivalve species that are negatively impacted by the occurrence of such events. Finally, there is great precedent for the deployment of macroalgae as a principal component of integrated multi-trophic aquaculture systems whereby seaweeds are co-cultivated with aquacultured shellfish with the macroalgae often being harvested for profit

(Neori, 2008; Nobre et al., 2010; Troell et al., 2009). Such an approach may be increasingly important for the protection of aquacultured bivalves in an increasing acidified ocean in the future.

Despite the reported positive interactions between *Ulva* and the various species of bivalves in prior studies (Carroll et al., 2010; Heck et al., 2003; Sogard and Able, 1991; Wilson et al., 1990; this study), macroalgae can negatively impact bivalves and other calcifying organisms. Secondary metabolites released by *Ulva* can elevate mortality rates in the larval stages of bivalves (Diederich, 2005; Nelson et al., 2003), barnacles (Brock et al., 2007; Magre, 1974), crabs (Johnson and Welsh, 1985), and molluscs (Wang et al., 2011). *Ulva* can form "green tides" (Smetacek and Zingone, 2013) that, upon their collapse, can create hypoxic regions (Valiela et al., 1992) that can negatively affect benthic fauna (Viaroli et al., 2001). Furthermore, extensive coverage of bivalves by *Ulva* and the subsequent decomposition of the algae can also result in the accumulation of H_2S, which, when coupled with low dissolved oxygen, can depress the growth and survival of bivalves (Tyler, 2007). However, as pointed out by Wilson et al. (1990), the accumulation of secondary metabolites and decreased dissolved oxygen associated with the overgrowth of *Ulva* is often mitigated in high-flow areas, alleviating potential harm to the nearby organisms. Furthermore, it is plausible that other macroalgae that are not known to negatively impact marine life provide similar buffering of carbonate chemistry (Anthony et al., 2013; Krause-Jensen et al., 2015; Wahl et al., 2017).

Numerous species of seagrass experience enhanced growth under elevated CO_2 concentrations (Beer and Koch, 1996; Palacios and Zimmerman, 2007; Zimmerman et al., 1997) and can buffer ocean acidification thus benefiting calcifying organisms (Garrard et al., 2014; Hendriks et al., 2014; Unsworth et al., 2012). For example, Unsworth et al. (2012) found that seagrass meadows increased pH and $\Omega_{aragonite}$ by 0.38 and 2.9 units, respectively, which resulted in calcification by corals downstream of the seagrass to be ~18% higher relative to environments without seagrass. However, this ecosystem service provided by seagrass meadows may be disrupted by eutrophication and acidification of coastal ecosystems which may favor the growth of macroalgae over seagrass (Valiela et al., 1997; Young et al., in revision). Fast-growing, opportunistic macroalgae such as *Ulva* can inhibit the growth of seagrasses through shading (Valiela et al., 1997), competition for nutrients (Duarte, 1995), changes in the biogeochemical environment (Hauxwell et al., 2001), and under high CO_2 conditions (Young et al., in revision). *Ulva* has, however, been shown to serve as a nursery habitat for epibenthic invertebrates at densities comparable to *Zostera* meadows (Heck et al., 2003; Sogard and Able, 1991) in areas where there is a lack of the seagrass. As seagrasses decline worldwide (Orth et al., 2006; Short et al., 2011), the ecosystem services provided by seagrasses, such as being nursery habitats or buffering against ocean acidification, may, in some cases, be provided by macroalgae, potentially benefiting calcifying organisms such as bivalves that had formerly depended on seagrass as a refuge habitat.

In conclusion, during this study photosynthetic activity and/or nitrate assimilation by *Ulva* increased $\Omega_{aragonite}$ and $\Omega_{calcite}$ and yielded enhanced growth of bivalves by mitigating the deleterious effects of elevated pCO$_2$. This benefit was not exclusive to acidified conditions, as evidenced by increased bivalve growth in the presence of *Ulva* within ambient CO_2 treatments. While macroalgae can have adverse effects on some larval-staged bivalves, the chemical resilience provided by the macroalgae, *Ulva*, along with other potential ecosystem benefits such as providing nursery habitat (Wilson et al., 1990), predation refuge (Carroll et al., 2010), and inhibiting the growth of harmful microalgae (Tang and Gobler, 2011; Tang et al.,

2015) may, in some case, outweigh the negative effects. Although seagrass meadows can also buffer carbonate chemistry to the benefit of bivalves and other calcifying organisms, their populations continue to display worldwide declines (Orth et al., 2006; Short et al., 2011). Given that macroalgae tend to outcompete seagrass under high CO_2 conditions (Young et al., in revision), the ability of macroalgae to provide ecosystem services similar to those of seagrass, particularly buffering carbonate chemistry, may be increasingly important for calcifying organisms in modern-day eutrophic, acidified estuaries, as well as within future, ocean acidification scenarios. Finally, the purposeful deployment of seaweeds in an aquaculture setting would seem to be a beneficial strategy for protecting bivalves against current and future acidification.

5 Author contributions

Conceived and designed the experiments: C.J.G., C.S.Y. Performed the experiments: C.S.Y. Analyzed the data: C.S.Y., C.J.G. Contributed reagents/materials/analysis tools: C.J.G. Wrote the manuscript: C.S.Y., C.J.G.

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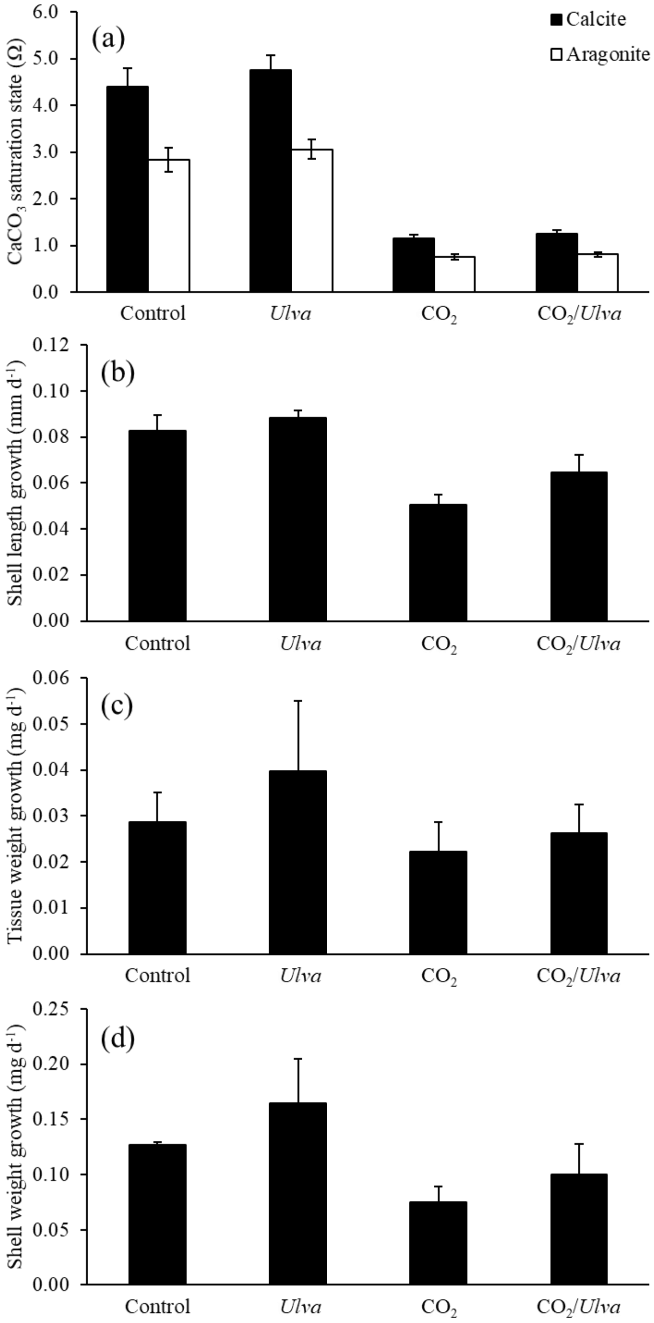

Figure 1. Experiment with small juvenile *Mercenaria mercenaria* exposed to ambient and elevated concentrations of CO$_2$ with and without the presence of *Ulva*.; (a) $\Omega_{calcite}$ and $\Omega_{aragonite}$; Growth was based on (b) shell length; (c) tissue weight; and (d) shell weight.

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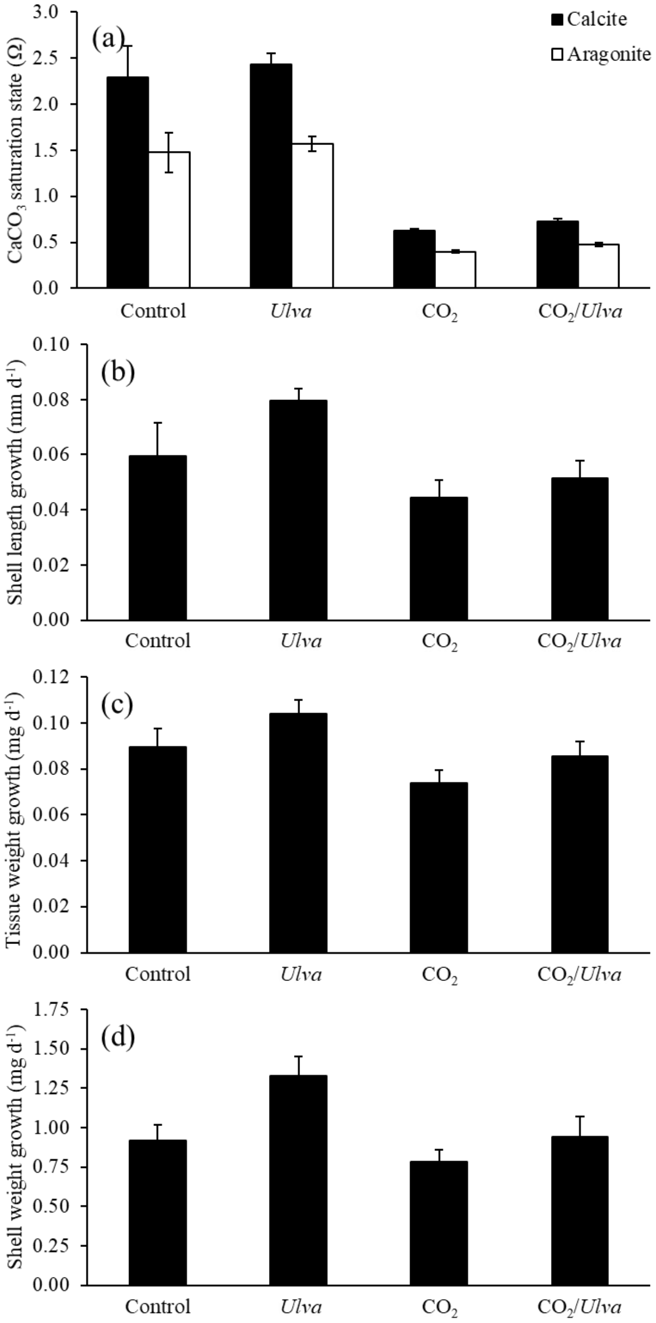

Figure 2. Experiment with large juvenile *Mercenaria mercenaria* exposed to ambient and elevated concentrations of CO_2 with and without the presence of *Ulva*. (a) $\Omega_{calcite}$ and $\Omega_{aragonite}$; Growth was based on (b) shell length; (c) tissue weight; and (d) shell weight.

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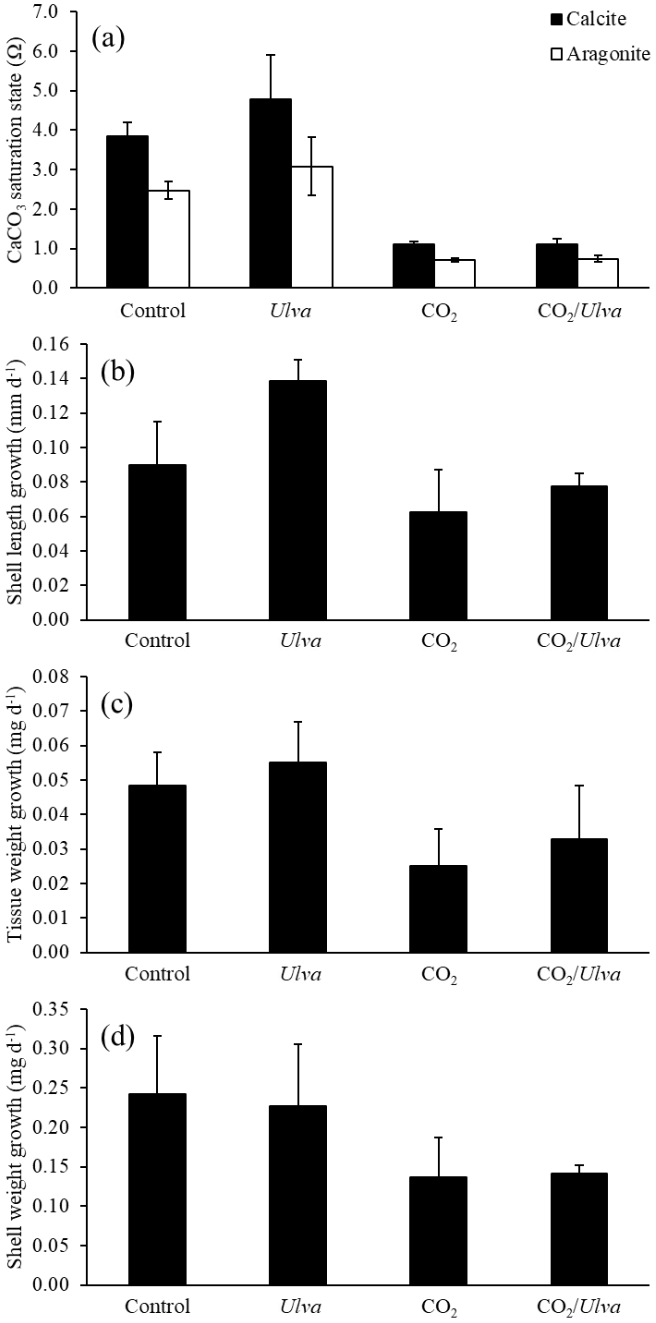

Figure 3. Experiment with small juvenile *Crassostrea virginica* exposed to ambient and elevated concentrations of CO_2 with and without the presence of *Ulva*. (a) $\Omega_{calcite}$ and $\Omega_{aragonite}$; Growth was based on (b) shell length; (c) tissue weight; and (d) shell weight.

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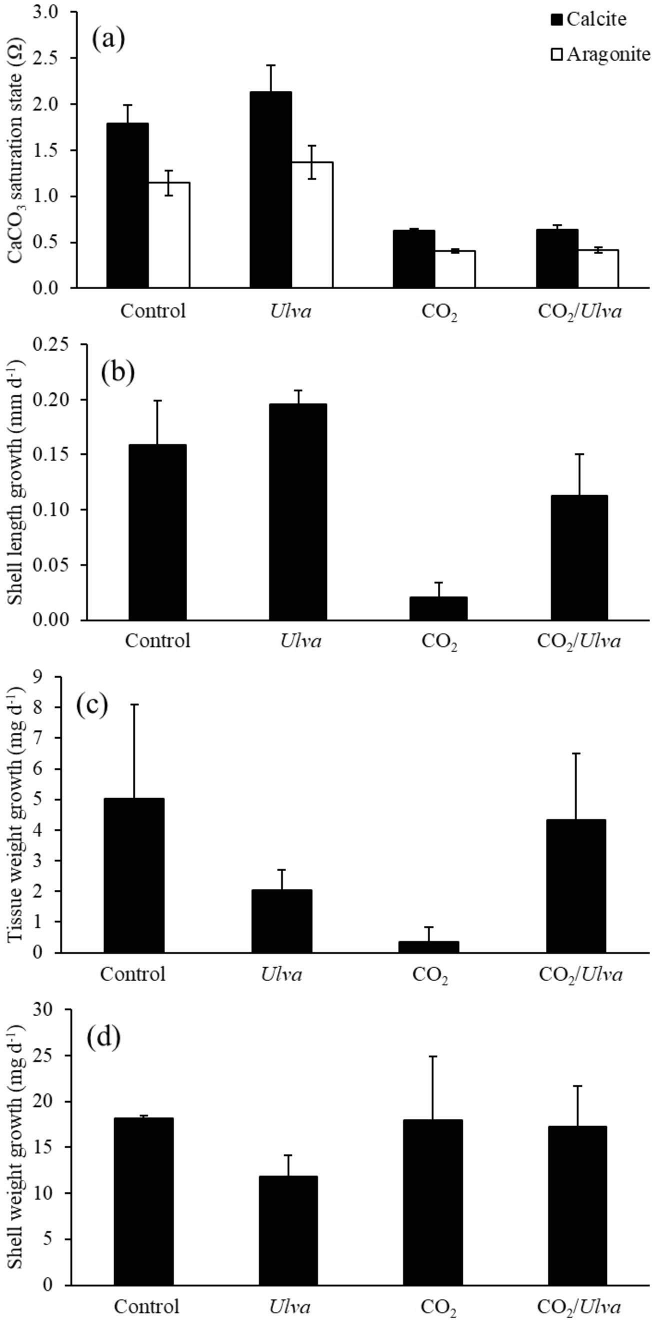

Figure 4. Experiment with large juvenile *Crassostrea virginica* exposed to ambient and elevated concentrations of CO_2 with and without the presence of *Ulva*. (a) $\Omega_{calcite}$ and $\Omega_{aragonite}$; Growth was based on (b) shell length; (c) tissue weight; and (d) shell weight.

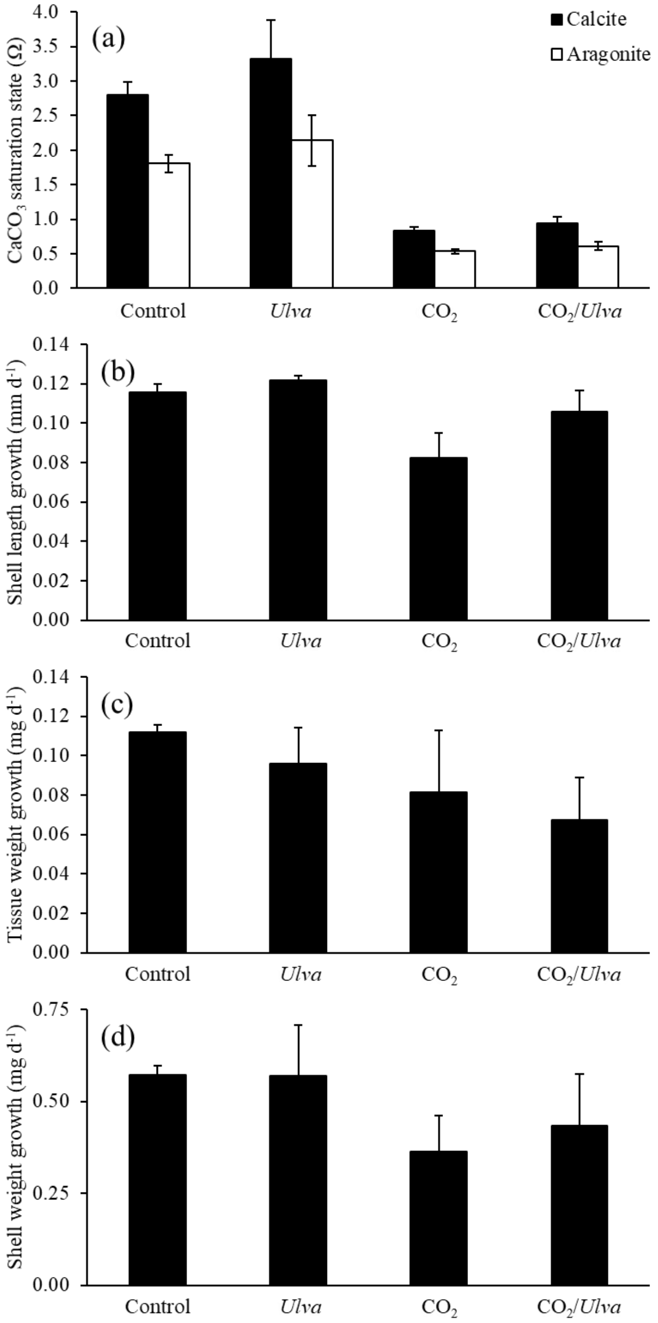

Figure 5. Experiment with small juvenile *Argopecten irradians* exposed to ambient and elevated concentrations of CO$_2$ with and without the presence of *Ulva*. (a) $\Omega_{calcite}$ and $\Omega_{aragonite}$; Growth was based on (b) shell length; (c) tissue weight; and (d) shell weight.

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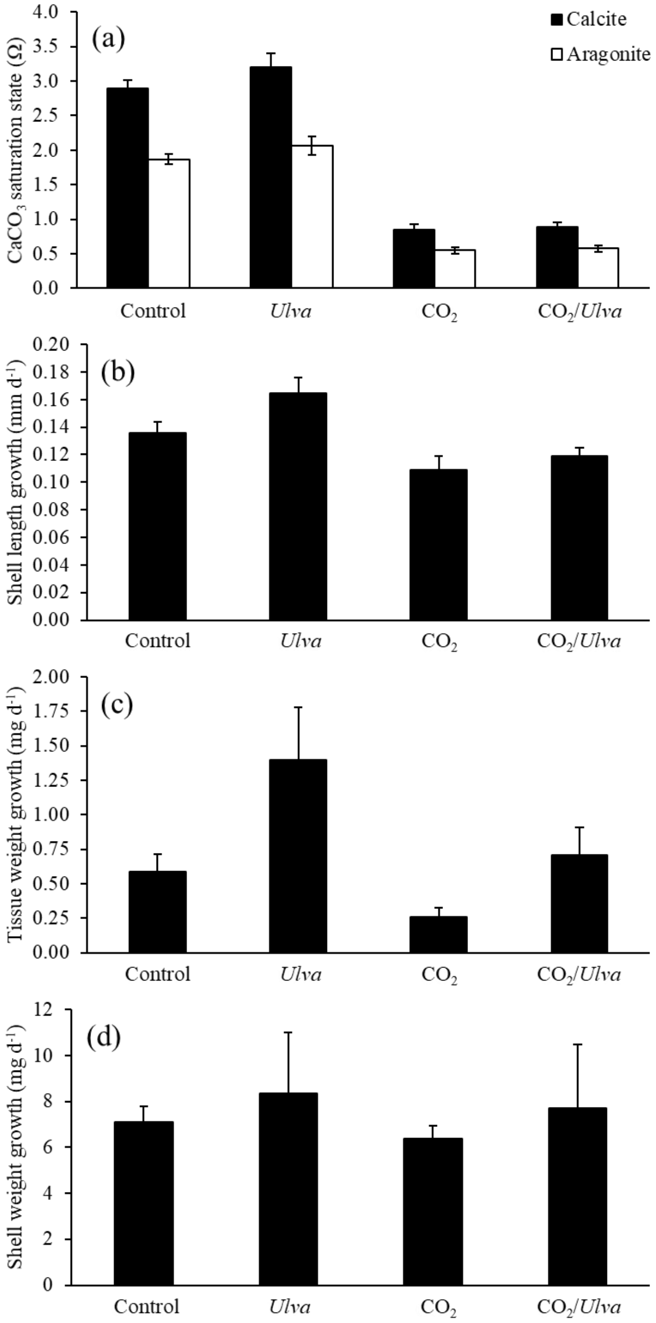

Figure 6. Experiment with large *Argopecten irradians* exposed to ambient and elevated concentrations of CO_2 with and without the presence of *Ulva*. (a) $\Omega_{calcite}$ and $\Omega_{aragonite}$; Growth was based on (b) shell length; (c) tissue weight; and (d) shell weight.

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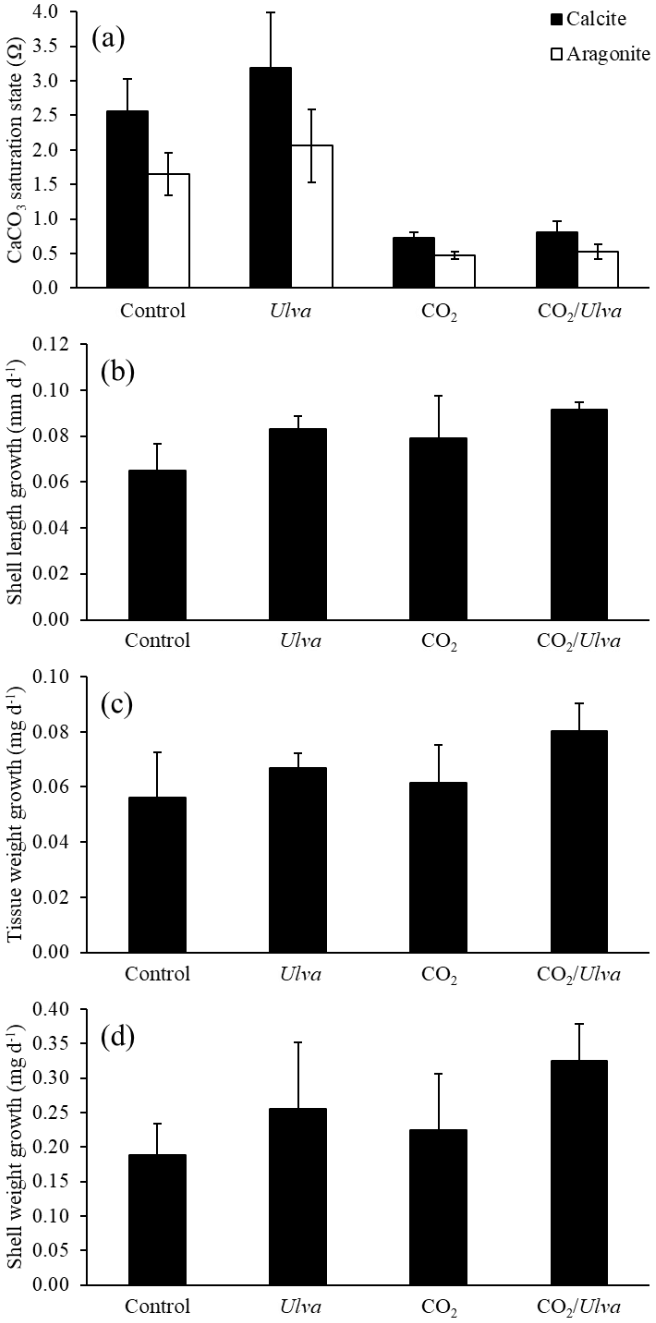

Figure 7. Experiment with *Mytilus edulis* exposed to ambient and elevated concentrations of CO_2 with and without the presence of *Ulva*. (a) $\Omega_{calcite}$ and $\Omega_{aragonite}$; Growth was based on (b) shell length; (c) tissue weight; and (d) shell weight.

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Table 1. Values of pH (total scale), temperature (°C), dissolved oxygen (DO; mg L^{-1}), salinity (g kg^{-1}), pCO_2 (µatm), total alkalinity (µmol $kgSW^{-1}$), total DIC (µmol $kgSW^{-1}$), HCO_3^- (µmol $kgSW^{-1}$), CO_3^{2-} (µmol $kgSW^{-1}$), OH^- (µmol $kgSW^{-1}$), $\Omega_{calcite}$, and $\Omega_{aragonite}$ for June through November experiments. Values represent means ± standard error. Data from individual 5 experiments appear within Tables S1.

Parameter	Control	*Ulva*	CO_2	CO_2/*Ulva*
pH	7.98±0.01	8.03±0.01	7.37±0.01	7.39±0.01
Temperature	21.3±0.1	21.2±0.1	21.3±0.1	21.3±0.1
DO	9.06±0.01	9.00±0.01	9.17±0.01	9.10±0.01
Salinity	30.0±0.1	30.1±0.1	30.0±0.1	30.0±0.1
pCO_2	373±8	335±9	1763±27	1721±27
Total alkalinity	1740±26	1759±26	1792±25	1803±21
Total DIC	1561±19	1557±21	1782±22	1797±19
HCO_3^-	1428±16	1413±18	1690±21	1706±19
CO_3^{2-}	119±4	134±5	35±1	37±1
OH^-	3.84±0.12	4.51±0.18	0.95±0.02	1.01±0.02
$\Omega_{calcite}$	2.97±0.11	3.36±0.13	0.86±0.03	0.90±0.03
$\Omega_{aragonite}$	1.91±0.07	2.16±0.09	0.56±0.02	0.59±0.02