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Kelp (*Saccharina latissima*) Mitigates Coastal Ocean Acidification and Increases the Growth of North Atlantic Bivalves in Lab Experiments and on an Oyster Farm

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Coastal zones can be focal points of acidification where the influx of atmospheric CO_2 can be compounded by additional sources of acidity that may collectively impair calcifying organisms. While the photosynthetic action of macrophytes may buffer against coastal ocean acidification, such activity has not been well-studied, particularly among aquacultured seaweeds. Here, we report on field and laboratory experiments performed with North Atlantic populations of juvenile hard clams (*Mercenaria mercenaria*), eastern oysters (*Crassostrea virginica*), and blue mussels (*Mytilus edulis*) grown with and without increased CO_2 and with and without North Atlantic kelp (*Saccharina latissima*) over a range of aquaculture densities (0.3 – 2 g L^{-1}). In all laboratory experiments, exposure to elevated pCO_2 (>1,800 µatm) resulted in significantly reduced shell- and/or tissue-based growth rates of bivalves relative to control conditions. This impairment was fully mitigated when bivalves were exposed to the same acidification source but also co-cultured with kelp. Saturation states of aragonite were transformed from undersaturated to saturated in the acidification treatments with kelp present, while the acidification treatments remained undersaturated. In a field experiment, oysters grown near aquacultured kelp were exposed to higher pH waters and experienced significantly faster shell and tissue based growth rates compared to individuals grown at sites away from kelp. Collectively, these results suggest that photosynthesis by *S. latissima* grown at densities associated with aquaculture increased pH and decreased pCO_2, fostering a carbonate chemistry regime that maximized the growth of juvenile bivalves. As *S. latissima* has been shown to benefit from increased CO_2, growing bivalves and kelp together under current or future acidification scenarios may be a synergistically beneficial integrated, multi-trophic aquaculture approach.

Keywords: ocean acidification, macroalgae, bivalves, aquaculture, chemical refuge

INTRODUCTION

The continued delivery of CO_2 into surface oceans is expected to alter pools of inorganic carbon (increased pCO_2 and HCO_3^-, decreased CO_3^{2-} and saturation states (Ω) of calcite and aragonite), and coastal zones are particularly prone to enhanced acidification due to processes such as upwelling, riverine discharge, and eutrophication (Meehl et al., 2007; Feely et al., 2009; Cai et al., 2011; Melzner et al., 2013). Specifically, eutrophication-enhanced microbial respiration is a strong regional source of CO_2 in coastal zones on diel and seasonal timescales that can result in pCO_2 levels that far exceed end of the century projections for the open ocean (>1,000 μatm; Cai et al., 2011; Melzner et al., 2013; Wallace et al., 2014). Present and future acidification is expected to have varying effects on marine flora and fauna, with the reduced saturation states negatively affecting the growth and survival of calcifying organisms (Gazeau et al., 2007; Talmage and Gobler, 2010; Doney et al., 2020) and the higher CO_2 levels benefitting some, but not all, photosynthetic organisms (Palacios and Zimmerman, 2007; Koch et al., 2013; Hattenrath-Lehmann et al., 2015b; Young and Gobler, 2016).

Ocean acidification is a significant environmental threat to early life stage bivalves. Acidification-induced reductions in $\Omega_{aragonite}$ and $\Omega_{calcite}$ can lower the survivorship and growth of larval- and juvenile-stage bivalves (Green et al., 2009; Talmage and Gobler, 2011; Gobler et al., 2014; Waldbusser G. et al., 2015). The shells of early life-stage bivalves are composed partly or completely of aragonite (Stenzel, 1964; Carriker, 1996; Talmage and Gobler, 2009), making them vulnerable to reductions in specifically $\Omega_{aragonite}$ (Gazeau et al., 2007; Gazeau et al., 2013). While Ω values that exceed 1.0 favor the mineral precipitation of calcium carbonate, successful larval bivalve growth and survival may require $\Omega_{aragonite} \geq 1.6$, owing to the energetics of biocalcification (Barton et al., 2012; Waldbusser et al., 2013).

In contrast to bivalves, elevated pCO_2 has been shown to enhance the growth of some species of macroalgae (Gao et al., 1993; Olischläger et al., 2013; Young et al., 2021) including species grown in aquaculture (Gao et al., 1993; Bartsch et al., 2010; Young and Gobler, 2016). Aquacultured macroalgae may provide a myriad of ecosystem services, such as carbon sequestration (Chung et al., 2011) and absorption of excessive nitrogen (Marinho-Soriano et al., 2009), with harvesting of the macroalgae representing removal of the excess carbon and nitrogen from the ecosystem. In addition, the aquaculture of seaweeds may provide a chemical refuge against acidified conditions (Anthony et al., 2013; Wahl et al., 2018; Young and Gobler, 2018), sometimes to the benefit of bivalves (Anthony et al., 2013; Wahl et al., 2018; Young and Gobler, 2018; Xiao et al., 2021).

Saccharina latissima (sugar kelp) is a bladed, cold-water brown macroalgae that can be found across the North Atlantic, Pacific, and Arctic Oceans (Brinkhuis et al., 1983; Sivertsen and Bjørge, 2014). Beyond the numerous ecosystems services (e.g., nursery habitat, predation refuge, coastal defense, carbon and nitrogen sequestration, food source) provided by kelp species such as *S. latissima* (Norderhaug et al., 2005; Chung et al., 2013; Smale et al., 2013), the commercial and aquacultural importance of kelp has expanded in the Americas and Europe (Grebe et al., 2019), In the US, there is growing interest in kelp aquaculture (Marinho et al., 2015), primarily in colder regions such as Alaska, Maine, and the Northeast U.S. (Kim et al., 2019). When grown in an aquaculture setting, particularly in eutrophic estuaries, *S. latissima* can grow robustly and extract CO_2 and nutrients from the water (Kim et al., 2015; Jiang et al., 2020). While recent studies have demonstrated *S. latissima* benefit from elevated levels of pCO_2 through enhanced growth and reduced herbivory (Young et al., 2021), the potential for *S. latissima* or any kelp to benefit co-cultured bivalves is generally unknown.

The prime objective for this study, therefore, was to assess how elevated pCO_2 and the presence of *Saccharina latissima* influence the growth of juvenile bivalves indigenous to the North Atlantic, including eastern oysters (*Crassostrea virginica*), blue mussels (*Mytilus edulis*), and hard clams (*Mercenaria mercenaria*) using laboratory experiments. The second objective was to determine if the co-culture of bivalves with *S. latissima* in an ecosystem-based aquaculture setting influences bivalve growth and settlement. Shell- and tissue-based growth of bivalves were quantified along with carbonate chemistry within experimental vessels in the laboratory and in open waters at field sites where shellfish and *S. latissimi* were cultivated using standard aquaculture practices.

METHODS

Collection and Preparation of Bivalves and *Saccharina latissima*

Hatchery produced and wild-collected bivalves were used for experiments. *Mercenaria mercenaria* were produced by the Stony Brook University shellfish hatchery in Southampton, NY (40.89° N, 72.44° W) using broodstock collected from Shinnecock Bay, NY, USA. *Crassostrea virginica* were provided by the Aeros Cultured Oyster hatchery, NY, USA (41.05° N, 72.40° W) using broodstock from the Peconic Estuary, NY, USA. *Mytilus edulis* were collected from wild populations in Old Fort Pond, NY, USA (40.89° N, 72.44° W) and Moriches Bay, NY, USA (40.78° N, 72.78° W; **Supplementary Figure S1**). *S. latissima* used for all experiments were grown on horizontal longlines at a commercial oyster farm (Great Gun Shellfish) in Moriches Bay, NY, USA (40.78° N, 72.78° W; **Supplementary Figure S1**), a lagoon contiguous with Shinnecock Bay to the east, using kelp seedstock derived from wild populations in the Long Island Sound, CT, USA. *S. latissima* was grown throughout winter and spring 2021, and was collected from early March to late May, during which laboratory and field experiments were performed. Densities of kelp on this shallow (~2 m) farm have previously estimated to range from 0.6 g L^{-1} during high tide in the early growing season to 4.4 g L^{-1} during low tide at the end of the growing season (Sylvers and Gobler, 2021). For experiments, large, well-pigmented blades of the macroalga were chosen from samples collected by hand at low tide. *S. latissima* blades were cut from their holdfasts as close to the longlines as possible and were immediately placed in seawater-filled containers and transported

to the Stony Brook Marine Science Center within 30 minutes of collection. Upon arrival to the facility, *S. latissima* were placed in a large, round ~2000 L tank filled with flowing, 1 μm filtered seawater from Shinnecock Bay.

Laboratory Experiments With Bivalves and *Saccharina latissima*

Six laboratory experiments were performed to assess the effects of elevated pCO_2 and the presence of *S. latissima* on the growth rates of *M. mercenaria*, *C. virginica*, and *M. edulis*. Prior to the laboratory experiments with bivalves and *S. latissima*, a preliminary experiment was performed to assess the ability of *S. latissima* to alter pH in experimental containers. All experiments were performed in 1 L polycarbonate containers, which were acid-washed (10% HCl) and liberally rinsed with deionized water prior to use. Experimental containers were placed in an environmental control chamber set to a consistent temperature (18.6 ± 0.3°C), light intensity (~200 μmol photons m^{-2} s^{-1}) and photoperiod (14 h: 10 h light:dark cycle). The light intensity and photoperiod of the environmental control chamber mimicked conditions observed at the *S. latissima* collection site during the time of collection (*see above*) while temperatures were indicative of the latter half of the growing season (May). Containers were filled with filtered (0.2 μm polysulfone filter capsule, Pall©) seawater to maximum capacity and covered with plexiglass with pre-drilled holes to allow delivery of dissolved gases and minimize interaction with the environment. Dissolved gases were delivered into each experimental container by aeration *via* a 3.8 x 1.3 cm air diffuser (Pentair) connected to a 1 mL, polystyrene serological pipette inserted through the pre-drilled holes in the plexiglass covers to the bottom of each container and connected *via* Tygon tubing to an air source. The containers were then randomly assigned, in quadruplicate, to each treatment (*see below*). Containers subjected to elevated (~2,000 μatm) CO_2 levels utilized a multitube gas proportionator system (Cole Parmer® Flowmeter system, multitube frame) that mixed ambient air with 5% CO_2 gas (Talmage and Gobler, 2010). The pCO_2 levels in the elevated treatments were higher than levels present at the *S. latissima* collection site but are consistent with levels present in eutrophic US East Coast estuaries (Wallace et al., 2014; Baumann et al., 2015; Wallace and Gobler, 2015) including those near the oyster farm (Wallace and Gobler, 2021; Wallace et al., 2021). Containers subjected to ambient (~400 μatm) CO_2 levels utilized a single tube proportioner system to introduce only ambient air into containers. The gases were mixed through gang valves and were delivered at a flow rate of 1000 ± 5 mL min^{-1} to experimental containers through serological pipettes inserted through the plexiglass covers. The bubbling rates in the containers turned over the volume ~100 times d^{-1}, and bubbling was initiated at least 2 – 3 d prior to the beginning of experiments to allow CO_2 levels and carbonate chemistry to reach a state of equilibrium. Continuous and discrete measurements of pH were made using an Orion Star A321 Plus electrode (± 0.001 pH unit, NBS scale) calibrated prior to each use using National Institute of Standards and Technology (NIST) traceable standards.

Dissolved inorganic carbon (DIC) within experimental containers was measured directly from water samples collected at the beginning and end of experiments, which were preserved using a saturated mercuric chloride ($HgCl_2$) solution and stored at ~4°C until they were analyzed on a VINDTA 3D (Versatile Instrument for the Determination of Total inorganic carbon) delivery system coupled within a UIC Inc. coulometer (model CM5017O) as per Young and Gobler (2018). Total DIC, total alkalinity, pCO_2, HCO_3^-, $\Omega_{aragonite}$, and $\Omega_{calcite}$ (**Table 1**) were calculated from measured DIC levels, 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.ess-dive.lbl.gov/ftp/co2sys/). For quality assurance, DIC levels and pH within certified reference material (provided by Andrew Dickson of the University of California, San Diego, Scripps Institution of Oceanography; batches 180 = 2021.87 μmol $kgSW^{-1}$) were measured during analyses of each sample set. Analyses of samples only continued when complete recovery (>99.9%) of certified reference material was attained.

For all experiments, individual *S. latissima* blades were prepared by cutting the stipe 2.5 cm below the blade-stipe interface. Cuts were made above the blade-stipe interface in order to obtain the desired fresh weight, depending on the experiment being performed (*see below*). This was done to standardize initial *S. latissima* blade tissue type and size (Boderskov et al., 2016). All samples were extensively rinsed with filtered (0.2 μm) seawater, spun in a salad spinner to remove debris and epiphytes and excess seawater, rinsed and spun again, and weighed on a Scientech ZSA 120 digital microbalance (± 0.0001 g) to obtain initial fresh weight in grams.

An initial experiment was performed to assess the ability of *S. latissima* to alter pH in experimental conditions similar to the later laboratory experiments with bivalves and *S. latissima*. For this experiment, there were two treatments: a control with increased CO_2 without *S. latissima* and a treatment with increased delivery of CO_2 and *S. latissima*.

Four experiments (Experiments 1 – 4; **Table 2**) were performed to assess the effects of elevated pCO_2 and the presence of *S. latissima* on the growth of *C. virginica*, *M. edulis*, and *M. mercenaria*. For the first experiment, *C. virginica* (~2.6 mm) were placed, in quadruplicate, in one of two treatments: a control with elevated pCO_2 (~1700 – 1800 μatm) without *S. latissima* and a treatment with elevated pCO_2 and *S. latissima* added at a level within the range of densities found on the kelp farm (1.0 g L^{-1}; Sylvers and Gobler, 2021). The second, third, and fourth experiments placed *C. virginica* (~2.8 mm), *M. edulis* (~2.3 mm), and *M. mercenaria* (~1.1 m), respectively, in quadruplicate, in one of four treatments: a control with ambient pCO_2 (~360 – 500 μatm) without *S. latissima*, a treatment with ambient pCO_2 and *S. latissima* (1.0 *g* L^{-1}) added, a treatment with elevated pCO_2 (~2,000 μatm) without *S. latissima*, and a treatment with elevated pCO_2 and *S. latissima* (1.0 *g* L^{-1}) added. Two experiments (Experiments 5 and 6; **Table 2**) were performed to assess the

TABLE 1 | Values of *S. latissima* density (g L^{-1}), mean pH (NBS scale), temperature (°C), salinity (g kg^{-1}), pCO_2 (µatm), total alkalinity (TA; µmol $kgSW^{-1}$), total DIC (µmol $kgSW^{-1}$), HCO_3^- (µmol $kgSW^{-1}$), $\Omega_{aragonite}$, and $\Omega_{calcite}$ for all experiments in the study (n=4 for all treatments).

Expt.	Initial pCO_2	Kelp density	pH	Temp.	Salinity	TA	Total DIC	pCO_2	HCO_3^-	Ωcalc	Ωarag
1	Elevated	0.0	7.3 ± 0.2	16.8 ± 1.3	29.9 ± 0.6	1843 ± 47	1883 ± 52	2296 ± 183	1778 ± 48	0.6 ± 0.1	0.4 ± 0.1
	Elevated	1.0	8.0 ± 0.4	16.8 ± 1.3	30.0 ± 0.7	1901 ± 120	1734 ± 106	390 ± 77	1602 ± 98	2.9 ± 0.5	1.9 ± 0.3
2	Ambient	0.0	8.2 ± 0.1	18.4 ± 0.1	30.0 ± 0.0	2088 ± 34	1919 ± 9	469 ± 62	1777 ± 5	3.1 ± 0.4	2.0 ± 0.3
	Ambient	1.0	8.7 ± 0.2	18.4 ± 0.1	30.5 ± 0.0	2085 ± 45	1591 ± 17	89 ± 6	1256 ± 4	8.2 ± 0.5	5.3 ± 0.3
	Elevated	0.0	7.3 ± 0.3	18.5 ± 0.1	29.5 ± 0.0	2074 ± 21	2107 ± 2	2327 ± 330	1994 ± 9	0.8 ± 0.1	0.5 ± 0.1
	Elevated	1.0	8.2 ± 0.4	18.5 ± 0.1	30.3 ± 0.4	2193 ± 227	1922 ± 169	288 ± 30	1719 ± 124	4.8 ± 1.2	3.1 ± 0.7
3	Ambient	0.0	8.2 ± 0.1	19.1 ± 0.2	31.5 ± 0.2	1875 ± 59	1692 ± 65	375 ± 35	1554 ± 65	3.1 ± 0.1	2.0 ± 0.1
	Ambient	1.0	8.9 ± 0.2	19.2 ± 0.2	32.3 ± 0.1	2190 ± 121	1556 ± 86	59 ± 3	1127 ± 56	10.4 ± 0.7	6.7 ± 0.4
	Elevated	0.0	7.4 ± 0.1	19.2 ± 0.2	30.0 ± 1.2	2004 ± 27	2022 ± 20	2101 ± 111	1917 ± 21	0.8 ± 0.1	0.5 ± 0.1
	Elevated	1.0	8.1 ± 0.3	19.2 ± 0.2	30.9 ± 0.5	1996 ± 37	1719 ± 34	239 ± 8	1523 ± 31	4.6 ± 0.1	3.0 ± 0.1
4	Ambient	0.0	8.3 ± 0.1	18.5 ± 0.1	30.5 ± 0.7	1951 ± 69	1722 ± 42	329 ± 20	1536 ± 22	5.0 ± 0.6	3.1 ± 0.4
	Ambient	1.0	8.8 ± 0.4	18.5 ± 0.1	31.5 ± 1.4	1950 ± 88	1518 ± 33	114 ± 10	1193 ± 9	9.2 ± 1.3	5.7 ± 0.8
	Elevated	0.0	7.6 ± 0.1	18.5 ± 0.1	29.8 ± 0.4	2115 ± 29	2142 ± 21	2242 ± 96	2030 ± 22	0.8 ± 0.1	0.5 ± 0.1
	Elevated	1.0	8.2 ± 0.4	18.5 ± 0.1	30.5 ± 0.7	2053 ± 19	1778 ± 66	285 ± 71	1556 ± 97	6.1 ± 1.0	3.8 ± 0.6
5	Elevated	0.0	7.2 ± 0.1	19.1 ± 0.2	31.6 ± 0.0	2031 ± 22	2055 ± 18	2159 ± 50	1947 ± 19	0.8 ± 0.1	0.5 ± 0.1
	Elevated	0.3	7.6 ± 0.2	19.3 ± 0.2	31.3 ± 0.1	1954 ± 72	1866 ± 62	956 ± 32	1757 ± 55	2.4 ± 0.2	1.5 ± 0.1
	Elevated	0.7	7.9 ± 0.4	19.3 ± 0.3	31.1 ± 0.1	1892 ± 135	1768 ± 143	667 ± 122	1645 ± 140	2.9 ± 0.0	1.9 ± 0
	Elevated	1.0	8.1 ± 0.4	19.2 ± 0.3	31.1 ± 0.1	1918 ± 32	1571 ± 21	170 ± 4	1308 ± 12	7.3 ± 0.3	4.6 ± 0.2
6	Elevated	0.0	7.4 ± 0.1	18.6 ± 0.1	29.5 ± 0.7	1882 ± 27	1915 ± 33	2191 ± 118	1812 ± 30	0.7 ± 0.1	0.4 ± 0.1
	Elevated	0.5	7.9 ± 0.6	18.6 ± 0.1	30.5 ± 0.7	1637 ± 75	1533 ± 84	598 ± 79	1432 ± 85	2.4 ± 0.1	1.5 ± 0.1
	Elevated	1.0	8.2 ± 0.5	18.5 ± 0.1	30.0 ± 1.4	1629 ± 52	1200 ± 2	66 ± 11	898 ± 40	8.4 ± 1.2	5.3 ± 0.7
	Elevated	2.0	8.5 ± 0.6	18.6 ± 0.1	29.5 ± 0.7	1560 ± 29	1058 ± 7	36 ± 1	715 ± 8	9.6 ± 0.5	6 ± 0.3
7	Outside-kelp	N/A	8.2 ± 0.1	12.5 ± 3.5	29.8 ± 1.8	1953 ± 174	1953 ± 174	349 ± 58	1806 ± 182	3.3 ± 0.3	2.1 ± 0.2
	In-kelp		8.3 ± 0.1	12.5 ± 3.5	29.7 ± 1.6	1892 ± 92	1892 ± 92	294 ± 45	1734 ± 76	3.6 ± 0.4	2.3 ± 0.2

Initial pCO_2 represents the pCO_2 level (ambient or elevated) that the treatments were bubbled with at the beginning of experiments. Values represent means ± standard deviation. N/A, not applicable.

minimum *S. latissima* biomass required to alter the growth of *M. edulis* and *C. virginica* when grown under elevated pCO_2. For the fifth experiment (Experiment 5; **Table 2**), *M. edulis* (~5.7 mm) were placed, in quadruplicate, in one of four treatments: a control with elevated pCO_2 (~2,700 µatm) without *S. latissima*, a treatment with elevated pCO_2 and 0.3 g L^{-1} *S. latissima*, a treatment with elevated pCO_2 and 0.7 g L^{-1} *S. latissima*, and a treatment with elevated pCO_2 and 1.0 g L^{-1} *S. latissima*. For the sixth experiment (Experiment 6; **Table 2**), *M. edulis* (~6.5 mm) and *C. virginica* (~5.1 mm) were placed, in quadruplicate, in one of four treatments: a control with elevated pCO_2 (~3,500 µatm) without *S. latissima*, a treatment with elevated pCO_2 and 0.5 g L^{-1} *S. latissima*, a treatment with elevated pCO_2 and 1.0 g L^{-1} *S. latissima*, and a treatment with elevated pCO_2 and 2.0 g L^{-1} *S. latissima*. Across all experiments, bivalves were fed a mixture of *Isochrysis galbana* and *Chaetoceros muelleri ad libitum* (4×10^4 cells mL^{-1} d^{-1}; Helm et al., 2004). In the preliminary experiment, the same microalgal mixtures were added to treatments with and without *S. latissima* and demonstrated that microalgae did not have a discernable impact on pH levels in the experimental containers. Microalgal cultures were maintained in exponential phase growth in f/2 media using standard culturing conditions (Helm et al. (2004).

Experiments began with the introduction of bivalves and *S. latissima* into polycarbonate containers fitted with continuous pH electrodes prepared as described above. Initial DIC samples were collected and discrete measurements of pH and temperature were taken and were made daily for the duration of experiments. Each experiment persisted for ~two weeks, with the exception of the preliminary experiment and Experiment 1, which persisted for ~one week and ~three weeks, respectively. At the beginning of each experiment, 15 – 20 individuals from each bivalve cohort were placed in each experimental container, in quadruplicate, with a set of 15 – 20 individuals from the same

TABLE 2 | List of experiments with their respective bivalve species and size (as shell height for *C. virginica* and *M. edulis* or shell length for *M. mercenaria*), *S. latissima* density, and conditions.

Experiment #	Bivalvespecies	Size	*S. latissima* density	Experimental conditions
1	*C. virginica*	2.6 mm	1.0 g L^{-1}	Bivalves exposed to elevated pCO_2, with and without *S. latissima*
2	*C. virginica*	2.8 mm	1.0 g L^{-1}	Bivalves exposed to ambient or elevated pCO_2, with and without *S. latissima*
3	*M. edulis*	2.3 mm	1.0 g L^{-1}	Bivalves exposed to ambient or elevated pCO_2, with and without *S. latissima*
4	*M. mercenaria*	1.1 mm	1.0 g L^{-1}	Bivalves exposed to ambient or elevated pCO_2, with and without *S. latissima*
5	*M. edulis*	5.7 mm	0.3, 0.7, 1.0 g L^{-1}	Bivalves exposed to elevated pCO_2, without or with increasing densities of *S. latissima*
6	*C. virginica*	5.1 mm	0.5, 1.0, 2.0 g L^{-1}	Bivalves exposed to elevated pCO_2, without or with increasing densities of *S. latissima*
	M. edulis	6.5 mm		
7	*C. virginica*	3.0 mm	N/A	Bivalves grown at control, near-kelp, and in-kelp sites in Moriches Bay, NY, USA.

N/A, not applicable.

cohort put aside to obtain initial measurements of shell height (for *C. virginica* and *M. edulis*) or length (for *M. mercenaria*) and tissue weight. Bivalve dimensions were determined by analysis of digital images using the software ImageJ (Young and Gobler, 2018). At the end of each week, a complete water change was performed for all containers using water bubbled in 20-L polycarbonate containers with the same gas mixtures for ambient and elevated pCO_2 treatments as described above to ensure that bivalves were exposed to the target pCO_2 levels for the duration of the experiment. At the end of experiments, final pH, temperature, and salinity measurements were made and final DIC samples were collected and analyzed and bivalves were collected on a 500 μm sieve, transferred to a graduated laminated grid sheet, and digitally imaged for shell measurements.

Field Experiment

Two field experiments (Experiment 7; **Table 2**) were conducted to assess the impacts of *S. latissima* on bivalves. For Experiment 7, the growth of *C. virginica* was monitored at the Great Gun Shellfish farm in Moriches Bay, NY, USA (40.78° N, 72.78° W), where *S. latissima* was collected for the laboratory experiments (Experiments 1 – 6). *S. latissima* was cultivated along four 30m horizontal longlines that were staked ~0.4 m above the bay bottom and spaced ~2 m apart (**Supplementary Figure S2**). The spacing of the lines in shallow water depths (~0.6 m MLW; ~2.0 m MHW) has been employed in other seaweed farms (Mongin et al., 2016).

Experimental oysters were placed at one of three locations that differed in proximity to the lines of *S. latissima*: in-kelp, near-kelp, and outside-kelp sites (**Supplementary Figure S2**). The in-kelp location was positioned in the center of the four-line kelp array, the near kelp location was positioned ~3 m away from the end of the kelp lines, and the outside kelp location was positioned ~50 m away from the kelp lines. At each location triplicate cages were each stocked with 100 experimental oysters (~3.0 mm). For each replicate, oysters were placed in a spat bag (1.0 mm mesh) housed in a floating oyster cage composed of a standard oyster 'grow-out' bag (36" x 18" x 3") made of semi-rigid polyethylene mesh (4 mm mesh size), with plastic, air-filled, cylindrical floats (3" diameter) attached to each long side. The bags were secured directly to the kelp lines in the 'in-kelp' treatment with a bridle-clip system and were attached to lines without kelp in the 'near-kelp' and 'outside-kelp' treatments. Prior to deployment, a subset (n = 100) of oysters were digitally photographed for measurement of shell height and width using ImageJ (*see above*), and then frozen for later analysis of tissue weight (*see below*).

YSI EXO3 multi-parameter sondes were deployed to continuously monitor pH (NBS scale), which internally logged data every 10 min. Calibration of the pH sensors was performed by use of three NIST pH buffers with known pH levels of 4, 7, and 10. While not shown here, temperature (°C) and conductivity (used to measure salinity) were also continuously monitored by the EXO3. Temperature was measured with a highly stable and aged thermistor that requires no prior calibration, while conductivity was calibrated using a conductivity standard with a recommended standard of 1 mS cm^{-1} (1000 μS cm^{-1}) for the highest stability. Sondes were deployed at the outside-kelp and in-kelp sites. At both sites, triplicate DIC samples were collected at the beginning, middle, and end of the field experiment. The collection, preservation, and analysis of DIC samples for the field experiment followed the same procedure as for the laboratory experiments, described above.

Post-Experimental Analyses

At the conclusion of experiments, the initial and final shell height and shell width of experimental bivalves was measured and averaged to obtain the mean shell height and width for each experimental container of the lab experiments (n = 4) or cage of the field experiment (n = 3). Shell-based growth (mm d^{-1}) was determined from the changes in shell dimensions during the experiment. Tissue weights were obtained by weighing bivalves after drying at 60°C for 72 h, combusting them at 450°C for 4 h, weighing them again, and subtracting the combusted weight from the dry weight. All individuals from each experimental container or cage were combined for drying and combustion to obtain collective weights for each replicate. Tissue-based growth (mg $bivalve^{-1}$ d^{-1}) was determined by subtracting the initial tissue weight (from the initially-collected subset of bivalves) from the final tissue weight and dividing by the duration of the experiment in days, for each individual from each replicate container, whereby tissue weight was determined by subtracting the combusted weight from the dry weight. One-way ANOVAs were performed with SigmaPlot 11.0 to assess significant differences in growth rates (Experiments 1, and 5 – 7) and *M. edulis* abundances (Experiment 7) between treatments. Two-way ANOVAs were performed to assess significant differences in growth rates (Experiments 2 – 4) where the main treatment effects were pCO_2 level (ambient or elevated) and *S. latissima* (with and without the macroalga). Normality and equal variance were tested *via* the use of Shapiro-Wilk and Levene tests within SigmaPlot 11.0; assumptions of equal variance and normality were met for all data. If significant differences were detected, a Tukey's Honest Significant Difference (HSD) test using R v.3.4.0 within RStudio v.1.0.143 was performed.

RESULTS

Experiments With and Without *Saccharina latissima*

An initial experiment was conducted to assess how *Saccharina latissima* would alter pH levels within experimental vessels that had been bubbled with CO_2 and began with a pH of ~7.2 (**Figure 1**). In the treatment with *S. latissima*, pH levels increased during the light portion of the photoperiod by ~0.4 units for the first two days, ~0.3 units the next two days, and more slowly thereafter reaching a maximum of ~8.8 on day 7 (**Figure 1**). In contrast, pH levels in the treatment without *S. latissima* increased more slowly and steadily, peaking at only 7.5 on the seventh day (**Figure 1**).

During the first experiment with bivalves using *C. virginica* (**Table 2** and **Figure 2**), pH values in the treatments with and without *S. latissima* ranged 7.44 – 8.48 and 7.02 – 7.69,

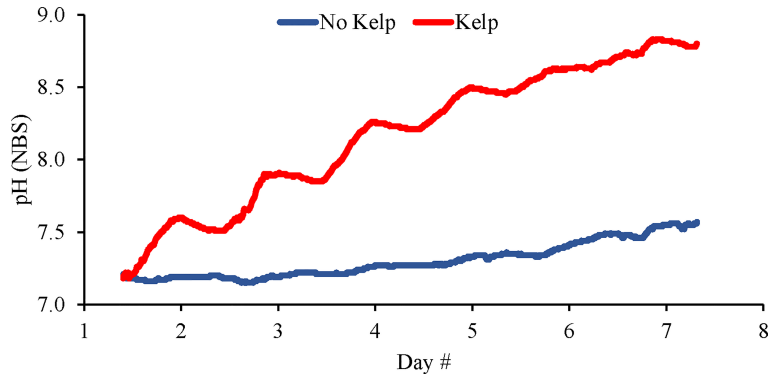

FIGURE 1 | Continuous pH (NBS scale) measurements made in elevated pCO_2 treatments with and without kelp (*S. latissima*; 1 g L^{-1}).

respectively, and pH was, on average, 7.94 ± 0.17 and 7.27 ± 0.19, respectively (**Table 1** and **Figure 2A**) and $\Omega_{aragonite}$ was 1.9 ± 0.3 and 0.4 ± 0.1 (**Table 1** and **Figure 2B**). Shell-based growth rates of *C. virginica* were significantly and 40% higher in the presence of *S. latissima* than the treatment without *S. latissima* (One-way ANOVA; $p < 0.05$; **Figure 2C** and **Supplementary Table S1**). Tissue-based *C. virginica* growth rates were significantly higher by 50% in the treatment with *S. latissima* compared to the treatment without *S. latissima* (One-way ANOVA; $p < 0.05$; **Figure 2D** and **Supplementary Table S1**).

In the second bivalve experiment with *C. virginica* (**Table 2** and **Figure 3**), pH levels in the elevated pCO_2 treatments were 8.25 ± 0.15 and 7.34 ± 0.32, respectively (**Figure 3A**) while $\Omega_{aragonite}$ in the ambient pCO_2 treatments with and without *S. latissima* were 5.2 ± 0.3 and 2.0 ± 0.3, respectively, and were 3.1 ± 0.7 and 0.5 ± 0.1 in the elevated pCO_2 treatments with and without *S. latissima*, respectively (**Table 1**; **Figure 3B**). There was a significant interaction in this experiment as the effects of pCO_2 on *C. virginica* (~2.8 mm) shell-based growth rates were dependent upon the presence of *S. latissima* (Two-way ANOVA; $p < 0.05$; **Figure 3C**). Comparing specific treatments, shell-based growth rates were significantly lower in the elevated pCO_2 treatment without *S. latissima* compared to the elevated pCO_2 treatment with *S. latissima* and the ambient pCO_2 treatments with and without *S. latissima* by 64, 60, and 58%, respectively (Tukey HSD; $p < 0.05$ for all; **Figure 3C** and **Supplementary Table S3**). There were no significant differences in tissue-based growth rates in this experiment (**Figure 3D** and **Supplementary Table S2**).

During the experiment with *Mytilus edulis* (**Table 2** and **Figure 4**), average pH levels in the ambient pCO_2 treatments with and without *S. latissima* and the elevated pCO_2 treatments with and without *S. latissima* were 8.88 ± 0.16, 8.31 ± 0.12, 8.14 ± 0.28, and 7.36 ± 0.10, respectively (**Figure 4A**). Average $\Omega_{aragonite}$ in the ambient pCO_2 treatments with and without *S. latissima* was 6.7 ± 0.4 and 2.0 ± 0.1, respectively, and was 3.0 ± 0.1 and 0.5 ± 0.1 in the elevated pCO_2 treatments with and without *S. latissima*, respectively (**Figure 4B**). There was a significant interaction between *S. latissima* and pCO_2 on shell growth for *M. edulis* (Two-way ANOVA; $p < 0.05$). Comparing specific treatments, shell-based growth rates were significantly lower in the elevated pCO_2 treatment without *S. latissima* than the elevated pCO_2 treatment with *S. latissima* and the ambient pCO_2 treatments with and without *S. latissima* by 36, 29, and 31%, respectively (Tukey HSD; $p < 0.05$ for all; **Figure 4C** and **Supplementary Table S5**). Shell-based growth rates were not different between the elevated pCO_2 treatment with *S. latissima* and ambient pCO_2 treatments with and without kelp (Tukey HSD; $p > 0.05$ for all; **Figure 4C** and **Supplementary Table S5**). Tissue-based growth was significantly higher in the presence of *S. latissima* by ~47% (Two-way ANOVA; $p < 0.05$; **Figure 4D** and **Supplementary Table S4**), and there was no significant effect of pCO_2 on tissue-based growth and no interaction detected (Tukey HSD; $p > 0.05$; **Figure 4D** and **Supplementary Table S5**).

During the experiment with *Mercenaria mercenaria* (**Table 2** and **Figure 5**), average pH levels in the ambient pCO_2 treatments without and with *S. latissima* and the elevated pCO_2 treatments without and with *S. latissima* were 8.45 ± 0.19, 8.79 ± 0.35, 7.55 ± 0.07, and 8.18 ± 0.40, respectively (**Figure 5A**). $\Omega_{aragonite}$ in the ambient pCO_2 treatments with and without *S. latissima* was 5.7 ± 0.8 and 2.1 ± 0.2, respectively, and was 3.8 ± 0.6 and 0.5 ± 0.1 in the elevated pCO_2 treatments with and without *S. latissima*, respectively (**Table 1** and **Figure 5B**). There was a significant interaction between pCO_2 and *S. latissima* for shell- and tissue-based growth rates of hard clams (Two-way ANOVA; $p < 0.05$). Shell-based growth rates of *M. mercenaria* (~1.1 mm) were significantly faster in the elevated pCO_2 treatment with *S. latissima*, and the ambient pCO_2 treatments with and without *S. latissima* than in the elevated pCO_2 treatment without *S. latissima* by ~100, ~110, and ~90%, respectively (Two-way ANOVA and Tukey HSD; $p < 0.05$ for all; **Figure 5C** and **Supplementary Tables S6, S7**); no other significant differences were detected. between treatments for shell growth. Tissue-based growth rates were significantly (two-fold) higher in the elevated pCO_2 treatment with *S. latissima* than the elevated pCO_2 treatment without *S. latissima* (Two-way ANOVA and Tukey HSD; $p < 0.05$; **Figure 5D** and **Supplementary Tables S6, S7**). In the ambient pCO_2 treatments with and without *S. latissima*,

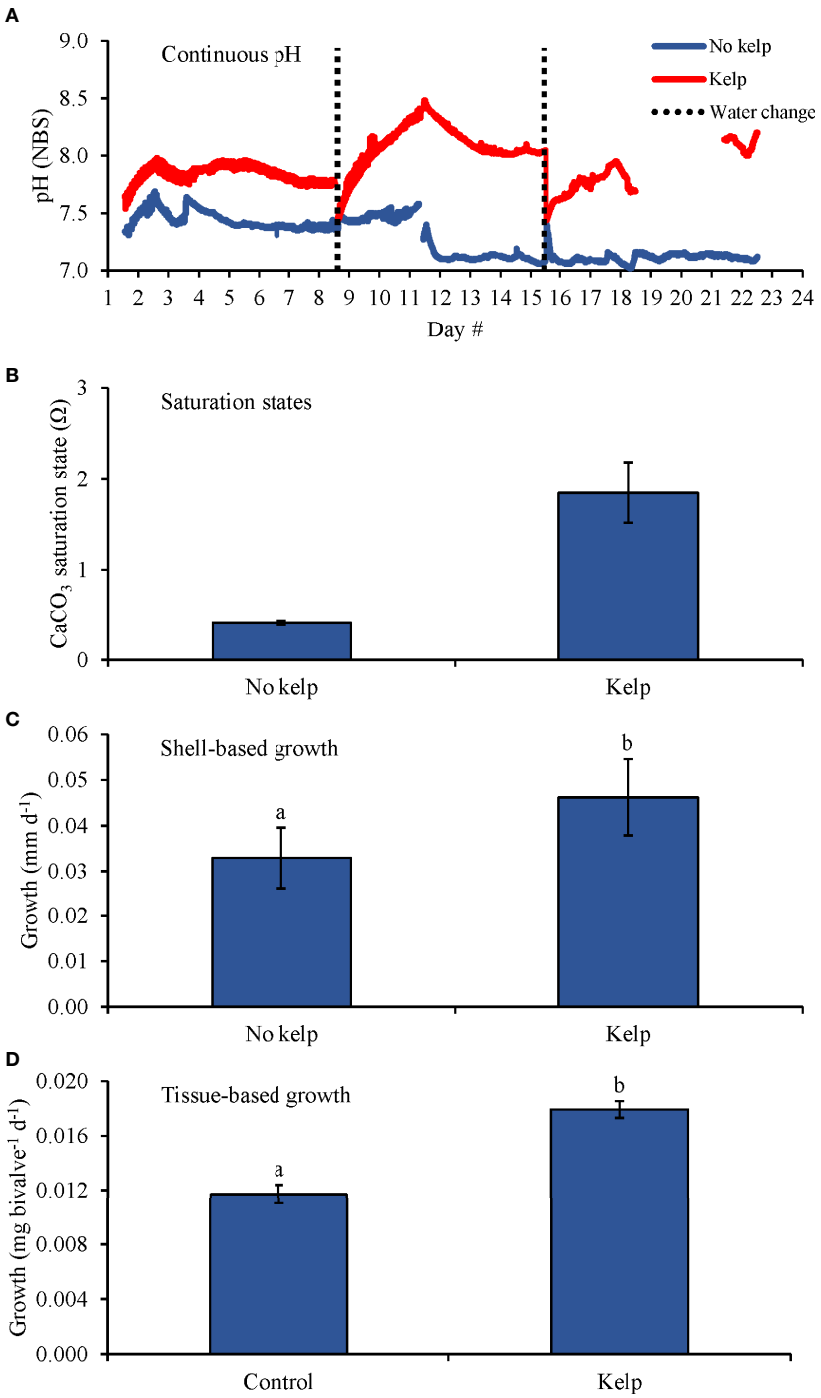

FIGURE 2 | **(A)** Continuous pH measurements, **(B)** Saturation states, **(C)** Shell-based growth, and **(D)** Tissue-based growth rates of *C. virginica* grown in elevated pCO_2, with and without kelp (*S. latissima*; 1 g L^{-1}). Letters above columns represent Tukey HSD results.

tissue-based growth was significantly higher by 100 and 150%, respectively, than in the elevated pCO_2 treatment without *S. latissima* (Two-way ANOVA and Tukey HSD; $p < 0.05$ for both; **Figure 5D** and **Supplementary Tables S6, S7**). There were no significant differences in tissue-based growth between the ambient pCO_2 treatments and the elevated pCO_2 treatment with *S. latissima* (Two-way ANOVA and Tukey HSD; $p > 0.05$ for all; **Figure 5D** and **Supplementary Tables S6, S7**).

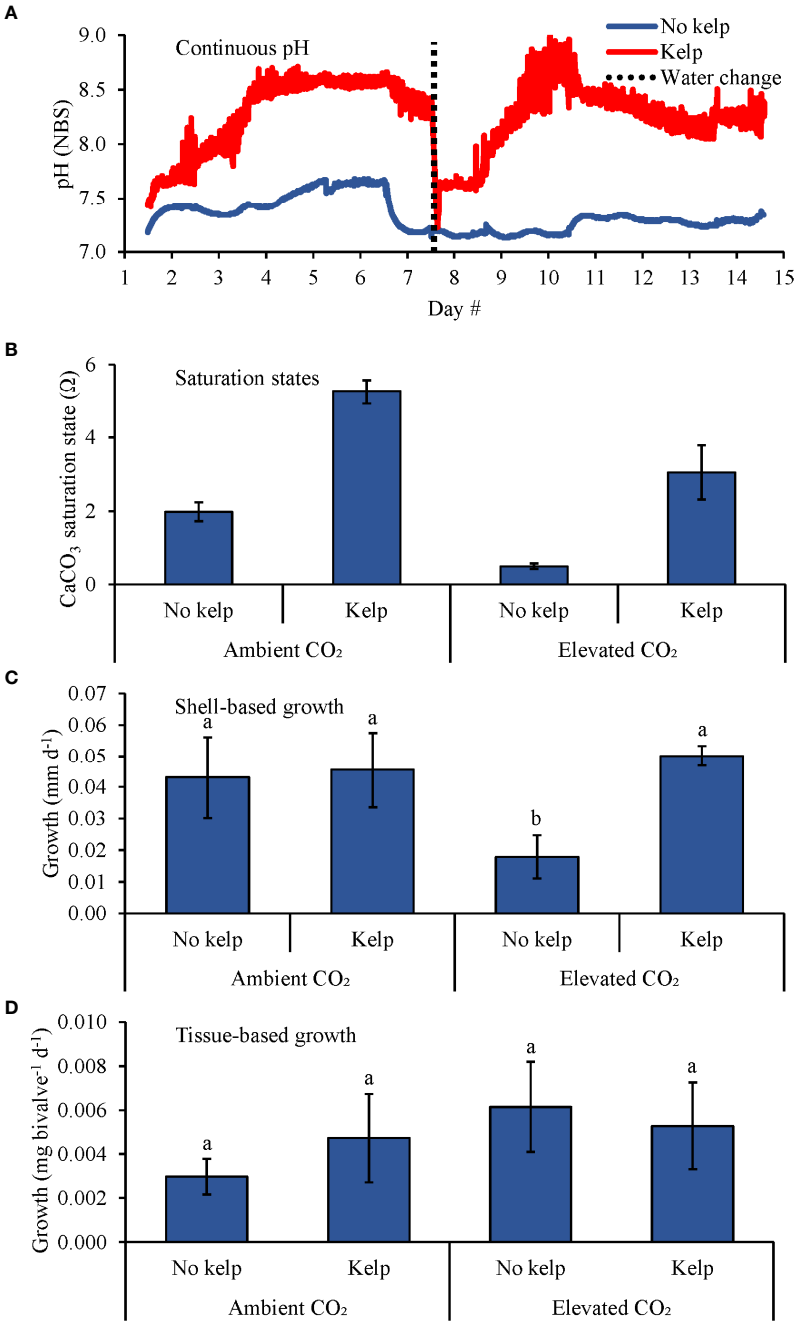

FIGURE 3 | **(A)** Continuous pH measurements, **(B)** Saturation states, **(C)** Shell-based growth, and **(D)** Tissue-based growth rates of *C. virginica* grown in ambient and elevated pCO_2, with and without kelp (*S. latissima*; 1 g L^{-1}). Letters above columns represent Tukey HSD results.

Experiments With Multiple Levels of *Saccharina latissima*

During the fifth experiment growing *M. edulis* with four levels of kelp (**Table 2** and **Figure 6**), pH levels in the 0.0 (control), 0.3, 0.7, and 1.0 g L^{-1} were, on average, 7.44 ± 0.10, 7.74 ± 0.15, 8.01 ± 0.24, and 8.42 ± 0.33, respectively (**Figure 6A**), while $\Omega_{aragonite}$ values were 0.5 ± 0.1, 1.5 ± 0.1, 1.9 ± 0.1, and 4.6 ± 0.2, respectively (**Table 1** and **Figure 6B**). Shell-based growth rates were significantly higher in the 0.3, 0.7, and 1.0 g L^{-1} treatments than in the control by ~50, ~55, and ~70%, respectively, but there were no differences in shell-based growth between the 0.3, 0.7, and 1.0 g L^{-1} treatments (One-way ANOVA and Tukey HSD; $p < 0.05$ for all

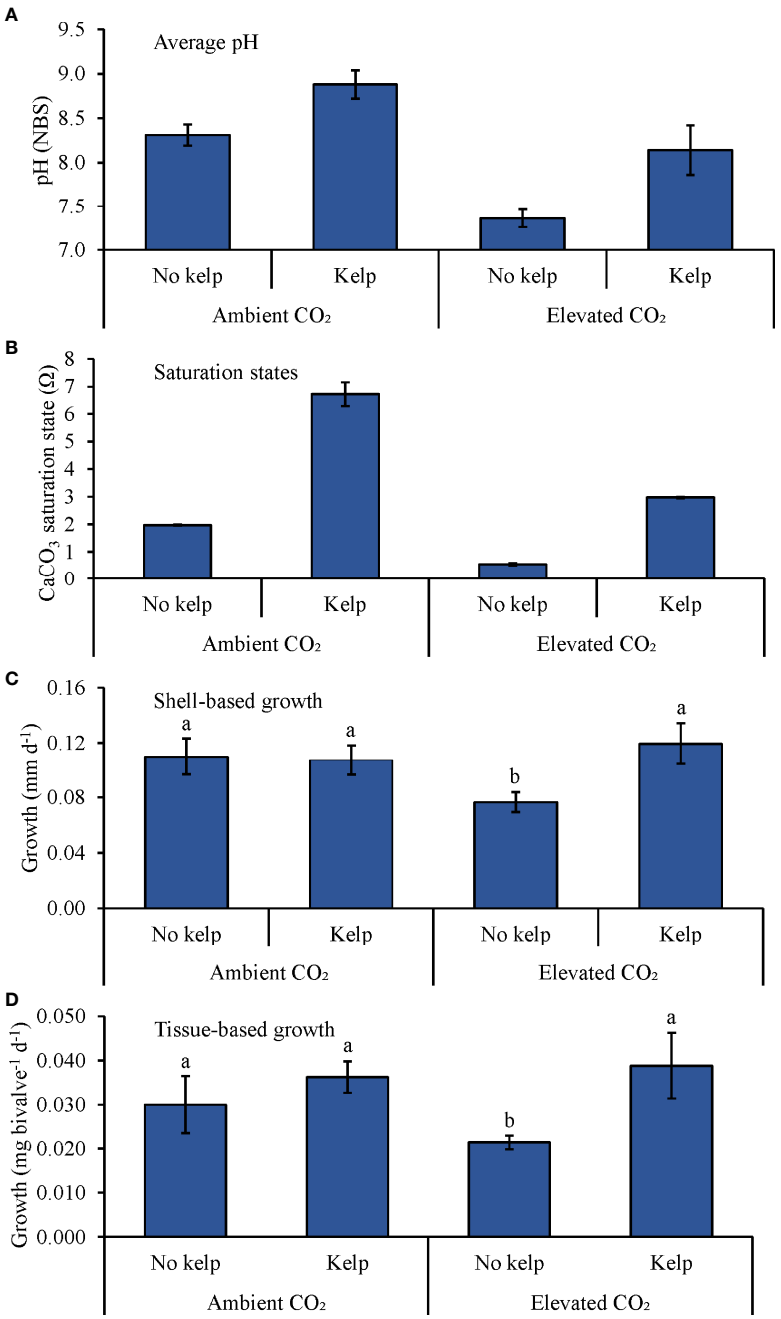

FIGURE 4 | **(A)** Average pH measurements, **(B)** Saturation states, **(C)** Shell-based growth, and **(D)** Tissue-based growth rates of *M. edulis* grown in ambient and elevated pCO^2, with and with kelp (*S. latissima*; 1 g L^{-1}). Letters above columns represent Tukey HSD results.

significant differences; **Figure 6C**; **Supplementary Tables and S8 and S9**). Tissue-based growth rates were significantly higher in the 1.0 g L^{-1} treatment than in the control, 0.3, and 0.7 g L^{-1} treatments by ~45, ~40, and ~40%, respectively; there were no other significant differences among tissue-based growth rates (One-way ANOVA and Tukey HSD; $p < 0.05$ for all significant differences; **Figure 6D**; **Supplementary Tables and S8 and S9**).

During the sixth and final experiment that grew *C. virginica* and *M. edulis* with four levels of kelp (**Table 2** and **Figure 7**), pH levels in the 0.0 (control), 0.5, 1.0, and 2.0 g L^{-1} treatments were, on average, 7.37 ± 0.10, 7.66 ± 0.40, 8.19 ± 0.51, and 8.53 ± 0.39, respectively (**Figure 7A**), while $\Omega_{aragonite}$ values were 0.4 ± 0.1, 1.5 ± 0.1, 5.3 ± 0.7, and 6.0 ± 0.3, respectively (**Table 1** and **Figure 7B**). Shell-based growth rates of *C. virginica* (~5.1 mm)

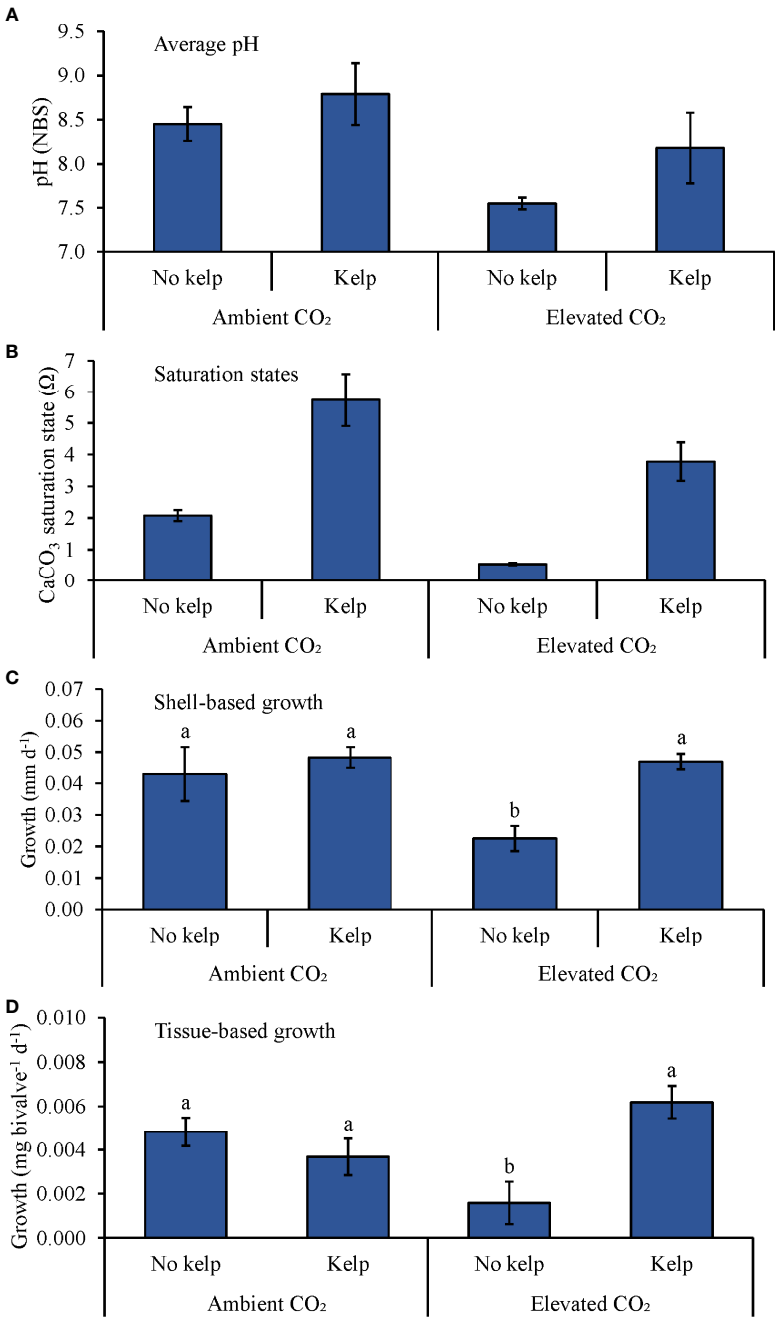

FIGURE 5 | **(A)** Continuous pH measurements, **(B)** Saturation states, **(C)** Shell-based growth, and **(D)** Tissue-based growth rates of *M. mercenaria* grown in ambient and elevated pCO_2, with and without kelp (*S. latissima;* 1 *g* L^{-1}). Letters above columns represent Tukey HSD results.

were significantly higher in the 0.5, 1.0, and 2.0 g L^{-1} treatments compared to the 0.0 g L^{-1} treatment by ~140, ~280, and ~290%, respectively (One-way ANOVA and Tukey HSD; $p < 0.05$ for all; **Figure 7C** and **Supplementary Tables S10, S11**). Additionally, *C. virginica* shell-based growth rates were significantly higher in the 1.0 and 2.0 g L^{-1} treatments than in the 0.5 g L^{-1} treatment by ~60% but did not differ between the former two treatments (One-way ANOVA and Tukey HSD; $p < 0.05$ for all significant differences; **Figure 7C** and **Supplementary Tables S10, S11**). Tissue-based growth rates for *C. virginica* were significantly higher in the 1.0 and 2.0 g L^{-1} treatments than in the control by ~160 and ~150%, respectively, but there were no differences detected between other treatment combinations (One-way ANOVA and Tukey HSD; $p < 0.05$ for all significant

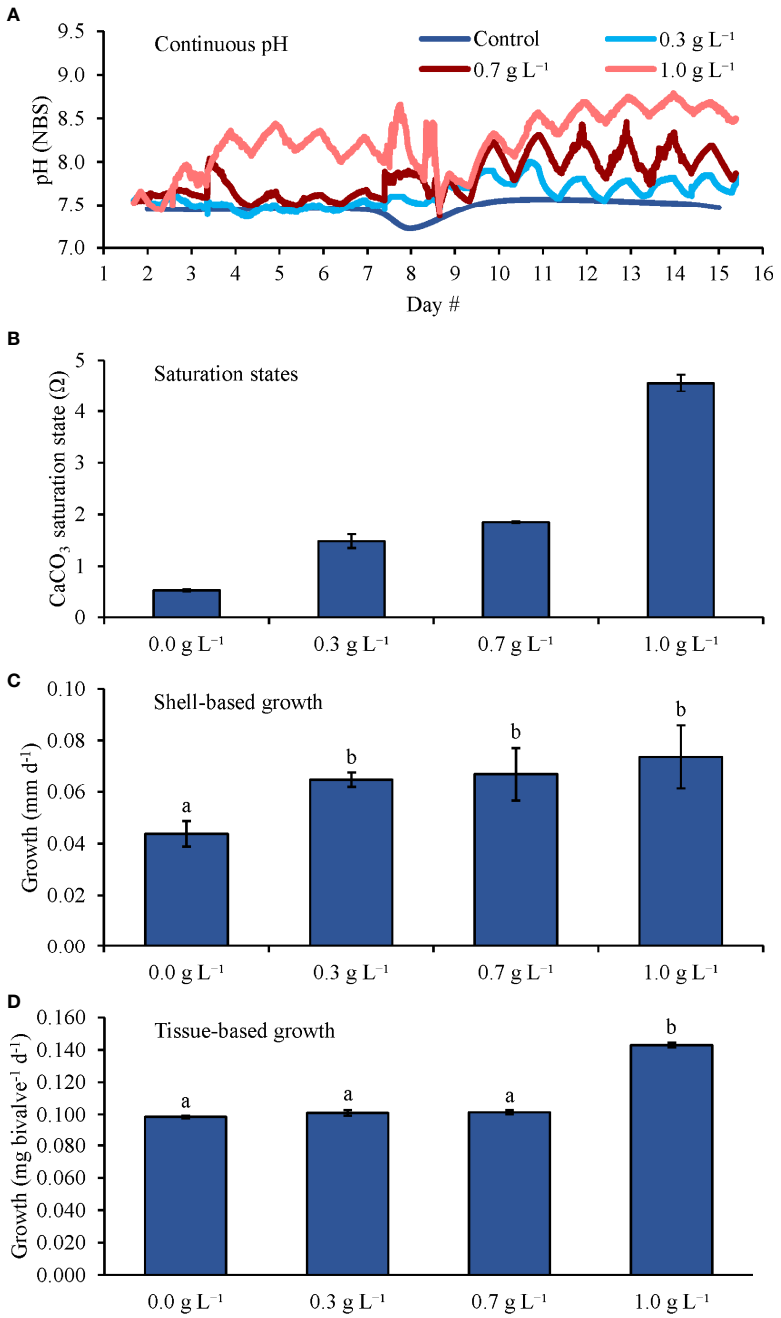

FIGURE 6 | **(A)** Continuous pH measurements, **(B)** Saturation states, **(C)** Shell-based growth, and **(D)** Tissue-based growth rates of *M. edulis* grown in elevated pCO_2, with increasing densities of kelp (*S. latissima*). Letters above columns represent Tukey HSD results.

differences; **Figure 7D** and **Supplementary Tables S10, S11**). For *M. edulis* (~6.5 mm), shell-based growth rates were significantly higher in the 0.5, 1.0, and 2.0 g L^{-1} treatments than in the control by ~90, 100, and ~130%, respectively (One-way ANOVA and Tukey HSD; $p < 0.05$ for all; **Figure 7C** and **Supplementary Tables S12, S13**). There were no differences in *M. edulis* shell-based growth between the 0.5, 1.0, and 2.0 g L^{-1} treatments (One-way ANOVA and Tukey HSD; $p > 0.05$ for all; **Figure 7C** and **Supplementary Tables S12, S13**). Tissue-based growth rates for *M. edulis* were significantly higher in the 0.5, 1.0, and 2.0 g L^{-1} treatments than in the control by ~135, ~110, and ~150%, respectively, but there were no significant differences in *M. edulis* tissue-based growth rates between the 0.5, 1.0, and 2.0 g L^{-1} treatments (One-way ANOVA and Tukey HSD; $p < 0.05$ for all significant differences; **Figure 7D** and **Supplementary Tables S12, S13**).

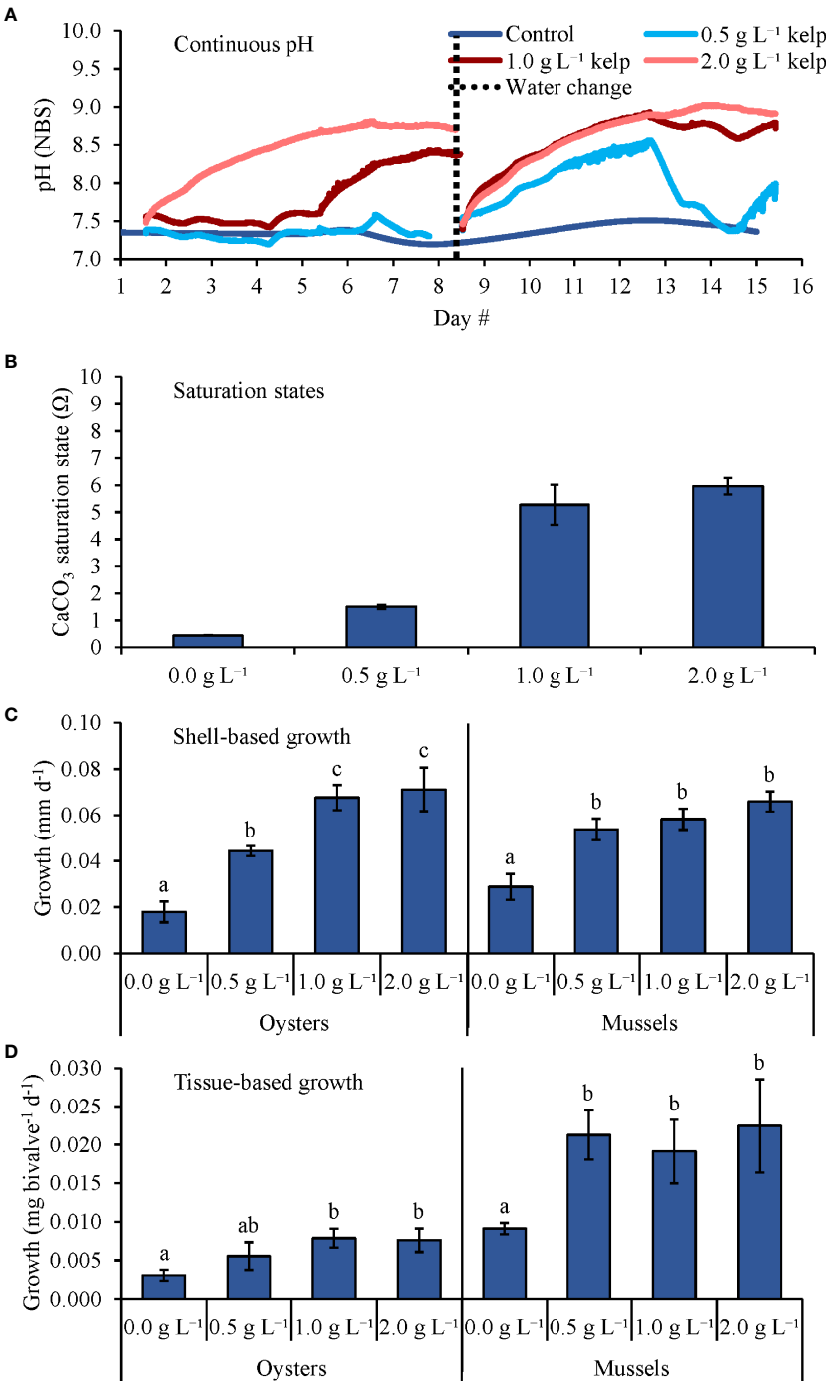

FIGURE 7 | **(A)** Continuous pH measurements, **(B)** Saturation states, **(C)** Shell-based growth, and **(D)** Tissue-based growth rates of *C. virginica* and *M. edulis* grown in elevated pCO_2, with increasing densities of kelp (*S. latissima*). Letters above columns represent Tukey HSD results. Tukey HSD tests were performed for *C. virginica* and *M. edulis* separately.

Field Experiment

For the one-month field experiment (Experiment 7; **Table 2** and **Figure 8**), pH levels at the outside-kelp and in-kelp sites were, on average, 7.71 ± 0.16 and 7.86 ± 0.18, respectively (**Figure 8A**) while average $\Omega_{aragonite}$ values were 2.1 ± 0.2 and 2.3 ± 0.2, respectively (**Table 1** and **Figure 8B**). pH differences between within and outside of the kelp were pronounced for the first two weeks of the experiment, small for the third week, and near absent for the final week (Fig, 8A). *C. virginica* (~3.0 mm) shell-based growth rates were significantly faster in the in- and near-kelp sites than at the

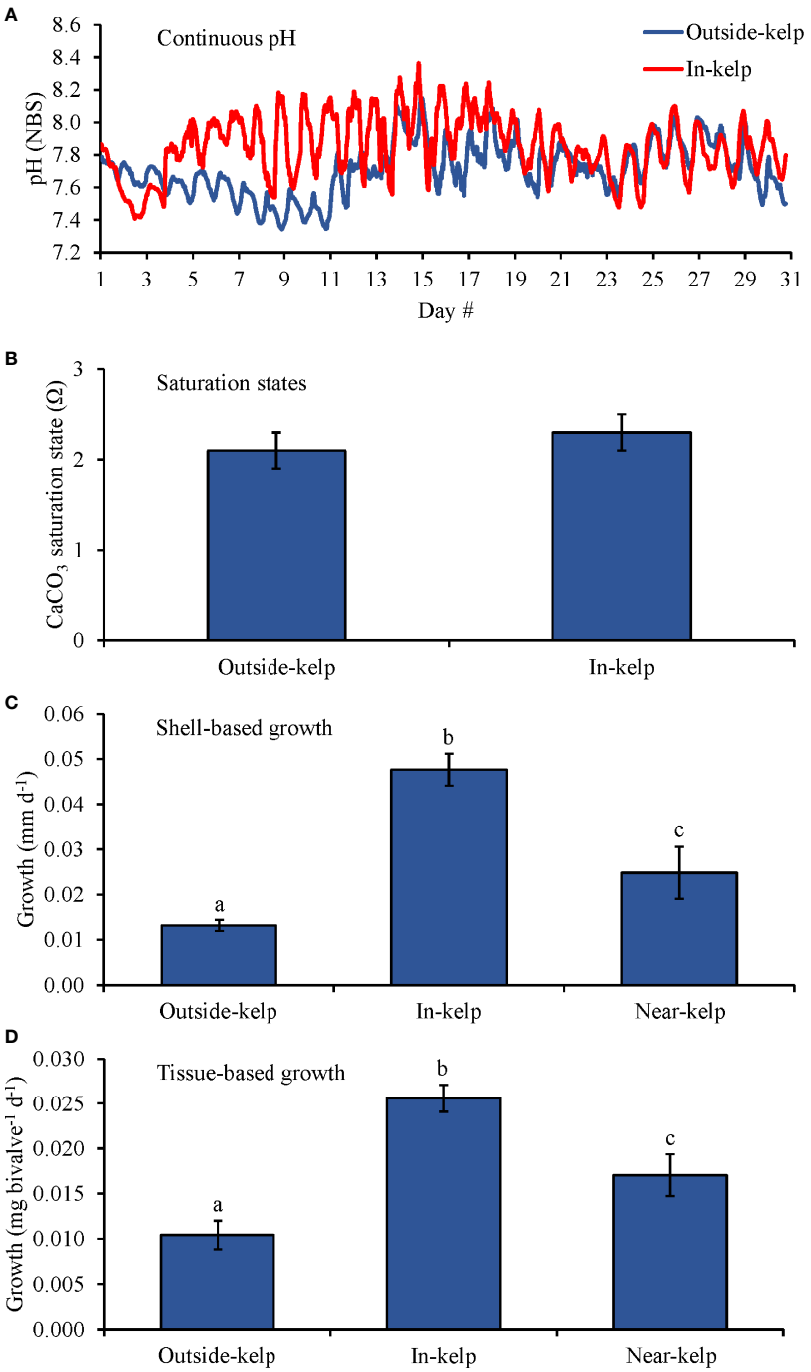

FIGURE 8 | **(A)** Continuous pH measurements, **(B)** Saturation states, **(C)** Shell-based growth, and **(D)** Tissue-based growth rates of *C. virginica* grown at outside-kelp (control), on-kelp, and off-kelp (*S. latissima*) sites at the Great Gun oyster farm in Center Moriches, NY, USA during May 2021. Letters above columns represent Tukey HSD results.

outside-kelp site by ~270 and ~90%, respectively (One-way ANOVA and Tukey HSD; $p < 0.05$ for both; **Figure 8C** and **Supplementary Tables S14, S15**). Shell-based growth rates were significantly faster at the in-kelp site than at the near-kelp site by ~90% (One-way ANOVA and Tukey HSD; $p < 0.05$; **Figure 8C** and **Supplementary Tables S14, S15**). Tissue-based growth rates were also significantly higher at the in-kelp site than at the outside-kelp and near-kelp sites by 160 and ~55%, respectively (One-way ANOVA and Tukey HSD; $p < 0.05$ for both; **Figure 8D** and **Supplementary Tables S14, S15**). Additionally, tissue-based growth

was significantly higher at the near-kelp site than at the outside-kelp site by 70% (One-way ANOVA and Tukey HSD; $p < 0.05$; **Figure 8D** and **Supplementary Tables S14, S15**).

DISCUSSION

During this study, exposure of bivalves to elevated pCO_2 (>1,800 µatm) resulted in significantly reduced shell- and tissue-based growth rates for all bivalve species (*Crassostrea virginica*, *Mytilus edulis*, and *Mercenaria mercenaria*) relative to control conditions in all experiments. The co-exposure of these bivalves to *Saccharina latissima*, however, fully ameliorated the negative effects of the same source of pCO_2, resulting in growth rates of bivalves that were no different than control conditions. Improvements in growth rates were likely a consequence of changes in carbonate chemistry as $\Omega_{aragonite}$ was transformed from undersaturated to saturated by the presence of kelp. When grown on an aquaculture farm, the growth rates of *C. virginica* increased with increasing proximity to aquacultured kelp. Collectively, these findings provide insight regarding the ability of kelps such as *S. latissima* to mitigate the deleterious effects of ocean acidification on bivalves with practical implications for aquaculture.

The negative effects of acidification on the growth and survival of bivalves have been well documented. Consistent with previous studies that have gauged the response of juvenile bivalves to increased levels of pCO_2 (Gazeau et al., 2007; Green et al., 2009; Talmage and Gobler, 2011; Young & Gobler, 2018), all species of bivalves in the present study experienced significantly slower shell- and tissue-based growth rates under elevated pCO_2 relative to their counterparts in ambient pCO_2 treatments. Elevated pCO_2 treatments without *S. latissima* contained average $\Omega_{calcite}$ and $\Omega_{aragonite}$ values that < 1.0 in all experiments. Early-life-stage bivalves are particularly vulnerable to the undersaturation of aragonite due to their shells consisting partially or completely of aragonite (Stenzel, 1964; Carriker, 1996; Talmage and Gobler, 2009). While the formation of calcium carbonate is thermodynamically favored when Ω is greater than 1.0, biotic aragonite is less crystalline than non-biogenic aragonite (Weiss et al., 2002; Ramesh et al., 2018), and $\Omega_{aragonite}$ values exceeding 1.6 may be required to yield successful growth and survival of bivalves (Barton et al., 2012) with enhanced growth under increasingly higher $\Omega_{aragonite}$ values (Talmage and Gobler, 2010). Beyond reductions in shell growth rates, tissue-based growth rates were reduced in most experiments under elevated pCO_2 levels without *S. latissima* compared to ambient pCO_2 treatments, which is consistent with Beniash et al. (2010), who found significantly lower soft body mass of juvenile *C. virginica* under hypercapnia (pH = 7.5). The proposed mechanism for reduced bivalve growth and calcification under increased pCO_2 is that decreased $\Omega_{aragonite}$ increases the amount of energy used by bivalves for shell formation, which diverts energy away from maintaining homeostasis and other metabolic processes, including those that contribute toward growth (Beniash et al., 2010; Waldbusser G. G. et al., 2015). Bivalve responses to acidification can, however, be more nuanced and complex at later life stages and across generations. For example, transgenerational acclimation to ocean acidification varies among bivalve species (Griffith and Gobler, 2017; Zhao et al., 2019; Zhao et al., 2020). Further research is required to determine if the results of the present study would translate to later life stages or across generations of the bivalve species utilized.

The culture of kelp was consistently capable of fully ameliorating acidified conditions and significantly increasing bivalve growth rates during this study. In experiments 2-4 that exposed bivalves to ambient or elevated pCO_2 with and without *S. latissima* (**Table 2**), the presence of *S. latissima* yielded higher pH, pCO_2 values in-line with control values, and $\Omega_{aragonite}$ values that always exceeded 2.0 with a mean value of ~4.6 (**Table 1**). In experiments where bivalves were exposed to increasing densities of *S. latissima* (Experiments 5 and 6; **Table 2**), even the lowest densities of the macroalga (0.3 – 0.5 g L^{-1}) were capable of yielding $\Omega_{aragonite}$ values of 1.5 and improving growth rates while the higher densities (1.0 – 2.0 g L^{-1}) yielded values of ≥4.6 (**Table 1**). In both sets of experiments, $\Omega_{aragonite}$ in the combined kelp-enhanced CO_2 delivery treatments frequently exceeded the thresholds for maximal growth rates in early-life-stage bivalves (Talmage and Gobler, 2010; Barton et al., 2012). Additionally, in the field experiment of the present study, bivalve growth rates significantly increased with increasing proximity to aquacultured *S. latissima*, which may be the result of minor but sustained improvements to carbonate chemistry that can significantly affect growth of juvenile bivalves (Talmage and Gobler, 2011; Waldbusser G. et al., 2015).

Aquacultured macroalgae such as kelp may buffer carbonate chemistry to the benefit of nearby aquacultured bivalves. Previous laboratory studies have demonstrated that primary productivity by macroalgae can promote the growth and survival of calcifying organisms, even under acidified conditions, by increasing pH and Ω (Wahl et al., 2018; Young and Gobler, 2018). Continuous pH measurements from the field experiment reported here demonstrated that pH values were, on average, ~0.15 units higher within kelp lines compared to the control site, presumably due to increased primary productivity at the in-kelp site. While the control site pH (7.8) during this experiment was lowered than the open ocean global average (8.1), it is consistent with levels measure in many estuaries which experience acidification due eutrophication (Wallace et al., 2014; Cai et al., 2017; Wallace and Gobler, 2021; Wallace et al., 2021). In a manner similar to the observations here, Xiao et al. (2021) reported a 0.10 pH unit increase and 58.7 ± 15.9 µatm decrease within a *Saccharina japonica* aquaculture area compared to a control site. While the mean pCO_2 levels were 20% lower at the 'in kelp site' and $\Omega_{aragonite}$ was 10% higher evidencing the photosynthetic influence of the kelp, $\Omega_{aragonite}$ was saturated (>3) suggesting this field site did not experiencing extreme acidification used in labortatory experiments. Still, unlike pH that was measured many times a day for one month, only three DIC samples were collected. Daytime primary productivity within kelp beds has been shown to significantly increase pH and reduce pCO_2 compared to outside

the bed across horizontal and vertical gradients on diel and even seasonal timescales (Delille et al., 2000; Delille et al., 2009; Hofmann et al., 2011). Conversely, respiration during the night by macrophyte assemblages release CO_2 (Hofmann et al., 2011; Cornwall et al., 2013), thereby reducing pH and potentially lowering the potential for calcification during the night (Saderne et al., 2015), a patterna reflected in the continuous pH measurements, but not captured by carbonate chemistry measurements. Given this, it is likely that $\Omega_{aragonite}$ was lower at night during this study and that the extent of acidification observed in the pH record would have been reflected in the carbonate chemistry record had nocturnal samples or if more samples had been collected. Regardless, during the present study, oysters had significantly higher growth rates at the in-kelp site than the outside-kelp site, a pattern mimicking trends in pH and, to a lesser extent, carbonate chemistry. Beyond *S. latissima* buffering carbonate chemistry, kelp detritus has been shown to be a potential food source for bivalves (Duggins et al., 1989; Duggins and Eckman, 1997; Levinton and Shumway, 2002). Hence, kelp may enhance the growth of bivalves by mitigation acidification and/or, potentially, by enhancing the nutritional status of bivalves.

Eutrophication can act as a driver of acidification and hypoxia in coastal zones (Wallace et al., 2014; Baumann et al., 2015; Wallace and Gobler, 2021), which can negatively affect the growth and survival of bivalves (Gobler et al., 2014; Stevens and Gobler, 2018). Some species of kelp, including *S. latissima*, experience enhanced growth under elevated nutrient conditions (Xu et al., 2011; Young et al., 2021) and grow robustly when aquacultured in eutrophic estuaries (Kim et al., 2015; Jiang et al., 2020). Given that harmful algal blooms (HABs) flourish in eutrophic zones, (Anderson et al., 2002; Anderson et al., 2008), the application of kelp in aquaculture to remove excess nutrients may reduce the intensity of HABs, which may indirectly benefit bivalves that are directly harmed by such events (Shumway, 1990). Kelp and other aquacultured macroalgae may also benefit nearby bivalves by directly reducing densities of HAB species. Various species of red, green, and brown macroalgae have been shown to directly reduce HAB-forming microalgae through allelopathy (Wang et al., 2007; Tang and Gobler, 2011; Tang et al., 2015; Sylvers and Gobler, 2021; Benitt et al., 2022). Sylvers and Gobler (2021) found that *S. latissima* reduced densities of the HAB-forming dinoflagellate *Alexandrium catenella* by 50 – 95% within an experimental setting and reduced the accumulation of saxitoxin in *M. edulis* below the US FDA closure limit for bivalves. Additionally, the mitigation of HABs (i.e., *A. catenella*) by kelp could also benefit shellfish industries that are damaged by toxin-producing dinoflagellates due to closures and contamination (Hoagland et al., 2002).

In present and future acidification scenarios, macroalgae such as kelp may directly benefit from increased pCO_2. In a previous study (Young et al., 2021), *S. latissima* was shown to benefit directly from elevated pCO_2 due to enhanced growth rates and indirectly due to reduced grazing pressure by gastropods. When exposed to elevated pCO_2 levels, macroalgae may be relieved of carbon limitation (assuming its inorganic carbon uptake is not substrate-saturated) and/or may downregulate carbon-concentrating mechanisms used to convert HCO_3^- to CO_2, thus allowing for additional energy to be available for vegetative growth (Mercado et al., 1998; Koch et al., 2013). While global distributions of *S. latissima* are declining due to warming oceans (Filbee-Dexter et al., 2016), eutrophication (Moy and Christie, 2012), and overfishing of predators that prey on kelp grazers (Steneck et al., 2002), increased growth rates by exposure to elevated pCO_2 may counteract these processes (Hepburn et al., 2011; Young et al., 2021) and, in turn, may provide localized benefits to calcifying organisms.

This study has additional broad implications for ecosystems where kelp and bivalves are aquacultured together. The harvest of aquacultured macroalgae, such as *S. latissima*, represents the direct removal of sequestered carbon and nitrogen (Marinho-Soriano et al., 2009; Chung et al., 2011), rather than the return of these elements back into the ecosystem through the eventual degradation of the macroalgae (Bricker et al., 2008). Beyond nutrient assimilation by kelp, aquacultured bivalves have the capacity to remove excess nutrients by harvesting of the bivalves as well as by denitrification of particulate organic nitrogen (PON) transferred to the sediment surface *via* biodeposition (Newell, 2004; Shpigel, 2005). Additionally, suspension-feeding activity by bivalves can reduce phytoplankton biomass in the water column and increase light penetration to the benthos, which benefits seagrass (Newell, 1988; Wall et al., 2008). Finally, cultivated bivalves, kelp, and associated aquaculture gear can provide forage and breeding habitats, as well as a predation refuge for marine life (Walls et al., 2016; O'Brien et al., 2018; Theuerkauf et al., 2021).

In the future, the benefits of kelp aquaculture to bivalves may become more habitat specific. While the net growth rates of kelp accelerate in reponse to high CO_2 (Young et al., 2021), rising temperarures will continue to force kelp into higher latitude environments this century (Wernberg et al., 2010; Filbee-Dexter et al., 2016). Warming and acidification represent a dual threat to coastal ecosystems, in general, (Agostini et al., 2021), and to bivalves in particular, (Talmage and Gobler, 2011; Matoo et al., 2013). Hence, the ability of kelp to serves as a biogenic buffer again ocean acidification for bivalves may be most probable to continue in coastal zones where temperatures remain optimal for both kelp and bivalves for extended periods of the year.

In conclusion, primary productivity by *S. latissima* significantly lowered pH, increased $\Omega_{aragonite}$ and enhanced shell- and tissue-based growth rates of bivalves by mitigating the deleterious effects of high CO_2. Even the lowest densities of *S. latissima* (0.3 – 0.5 g L^{-1}) were able to increase $\Omega_{aragonite}$ to ~1.5 and significantly increase bivalve growth rates. In the field, primary productivity by aquacultured *S. latissima* increased pH by ~0.15 units relative to the control site and oyster growth rates significantly increased with increasing proximity to kelp. This study, therefore, demonstrates that the purposeful deployment of kelp, such as *S. latissima*, in an aquaculture setting is a beneficial strategy for protecting bivalves against acidification and may have additional ecosystem and aquaculture benefits including the sequestration and extraction of carbon and nitrogen and the mitigation of HABs. Collectively,

the cultivation of kelp constitutes an environmentally-friendly means of protecting shellfisheries against present and future ocean acidification and other coastal stressors.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**. Further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

CG, CY, and MD conceived and designed the experiments. CY and AL performed the experiments and post-experimental analyses. CY, LS, SJT, and CS collected data for the field experiment. CY, CG, MD, LS, and SJT analysed the data. CG contributed reagents, materials, and analysis tools. CY and CG wrote the paper. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2022.881254/full#supplementary-material

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