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Novel in situ CO_2 enrichment system reveals seagrass meadows are a refugium against coastal acidification for North Atlantic bivalves

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Abstract. While the accumulation of anthropogenic CO_2 in the atmosphere is causing a decline in global ocean pH, many eutrophic estuaries are already experiencing acidification due to accelerated respiration driving the consumption of dissolved oxygen (DO) and production of CO_2, decreasing available carbonate ions (CO_3^{2-}) and threatening marine calcifiers. Here, a novel in situ CO_2 enrichment system was constructed to examine the effects of coastal acidification on the growth and survival of two species of North Atlantic bivalves (*Argopecten irradians* and *Crassostrea virginica*) in two distinct estuarine habitats: a seagrass meadow and an unvegetated sandy bottom in an open water estuary. The in-situ system captured natural diel dynamics as ambient chambers displayed chemistry nearly identical to the surrounding water, while CO_2-enriched, acidified chambers maintained a consistent ~Δ 0.3 – 0.5 pH offset. At the unvegetated sandy bottom site, *A. irradians* and *C. virginica* displayed significant reductions in growth and survival in the acidified chambers (pH_T = 7.3 – 7.5; saturation state of aragonite, Ω_{Ar} = 0.6 – 0.9) relative to ambient conditions (pH_T = 7.6 – 7.9; Ω_{Ar} = 1.6 – 2). At the seagrass site, while growth of *A. irradians* and *C. virginica* in the acidified treatments (pH_T = 7.3 – 7.7; Ω_{Ar} = 0.7) receiving the same delivery of CO_2 was, again, significantly slowed compared to the control (pH_T = 7.5 – 8.1; Ω_{Ar} = 2 – 2.8), the growth reduction, mortality rates, and levels of acidification were attenuated compared to the sandy bottom experiment, evidencing the ability of seagrass to buffer seawater and serve as a potential acidification refuge for bivalves. Collectively, the novel experimental CO_2 enrichment system constructed for this project demonstrates that coastal acidification can have deleterious effects on marine bivalve populations, and that future conditions as well as the habitat refuge offered by seagrasses must be considered when developing management and restoration plans for temperate estuaries.

1 Introduction

As anthropogenic CO_2 increases within the atmosphere, it also accumulates within terrestrial biomes and the world's oceans (Bates et al. 2012). The ocean uptakes approximately 30% of atmospheric CO_2 altering seawater chemistry by reducing pH and decreasing calcium carbonate ($CaCO_3$) saturation states (Caldeira and Wickett 2003, Doney et al. 2009, Orr et al. 2005). Since the beginning of the Industrial Revolution, ocean pH has decreased by ~ 0.1 units and will likely decrease another 0.3 to 0.5 units by the year 2100 resulting in deleterious effects on marine systems (IPCC 2021).

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Modulations in open ocean carbonate chemistry may be mirrored by changes in coastal systems as anthropogenic CO_2 enrichment shifts thermodynamic equilibria to favor decreased pH and increased CO_2 (Borges and Gypens 2010). These alterations are less understood in coastal regions, especially in environments that are biologically rich or suffer from intense anthropogenic eutrophication (Cai et al. 2011, Wallace et al. 2014, Wallace and Gobler 2021). The chemical response of estuarine environments to acidification is especially difficult to quantify because biological activity may amplify predicted chemical changes resulting from increased atmospheric CO_2 (Wallace et al. 2021). Estuaries experiencing intense nutrient enrichment already experience localized increases in CO_2 concentrations (Strong et al. 2014) far exceeding predicted values in the open ocean over the next century (Wallace et al. 2014, Wallace and Gobler 2021). Understanding how coastal acidification integrates into organismal response is critical to understanding long term ecosystem stability.

Coastal waters currently experience significant decreases in pH as a product of coastal acidification resulting in significant effects for estuarine species (Borges and Gypens 2010, Doney et al. 2009, Drake et al. 2018). In the US, landings of estuarine species of finfish and shellfish comprise 68% of the commercial value and 46% of the total harvested weight (Lellis-Dibble et al. 2008). Bivalves alone comprise approximately 20% of the total U.S. commercial catch, with an estimated value of $760 million USD (Cooley and Doney 2009). Since 1985, landings of oysters and bay scallops have decreased more than any other commercial bivalve species in US estuaries (Lellis-Dibble et al. 2008). Restoration efforts have been impaired for a myriad of reasons not limited to changes in carbonate chemistry. Bivalves accrete shells made of $CaCO_3$, and acidification can decrease the concentration of carbonate ions available for shell construction (Gazeau et al. 2011, Thomsen et al. 2015). In extreme cases, acidification can promote the dissolution of $CaCO_3$; thereby inhibiting calcification (Green et al. 2009). Many studies have shown that the effects of acidification can be size-dependent (Clements and George 2022, Dupont et al. 2013, Gazeau et al. 2007). Acidification can be especially problematic for juvenile species of bivalves (Green et al. 1998, Stevens and Gobler 2018, Talmage and Gobler 2011, Weiss et al. 2002). The levels of acidification documented in some estuaries (Cai et al. 2011, Feely et al. 2010, Feely et al. 2008, Wallace and Gobler 2021) have already exceeded levels known to negatively affect calcifying bivalves (Gazeau et al. 2013, Talmage and Gobler 2011). Integrating coastal acidification into estuarine ecosystem dynamics is critical to predict future ecosystem structure; however, ecosystem response is dependent upon substrate and habitat type.

Benthic habitats within estuaries are generally net heterotrophic with the marked exception of seagrass meadows (Caffrey 2004, Rheuban et al. 2014, Wallace et al. 2021). Seagrasses form highly autotrophic environments drawing down pCO_2, while elevating dissolved oxygen (DO), pH_T (total H^+ ion scale), CO_3^{2-} and aragonite saturation (Ω_{Ar}; Hendriks et al. 2014, Wallace et al. 2021). Laboratory experiments have demonstrated statistically significant benefits for seagrasses exposed to environmentally relevant increases in pCO_2 (Buapet et al. 2013, Invers et al. 1997, Koweek et al. 2018, Lowell et al. 2021, Lowell et al. 2026, Palacios and Zimmerman 2007, Zimmerman et al. 2015, Zimmerman et al. 2017, Zimmerman et al. 1997). Seagrass meadows currently support commercial fisheries valued at ~ $19,000 ha^{-1} (Capistrant-Fossa and Dunton 2024, Costanza et al. 1997, Mtwana Nordlund et al. 2016) and should now be assessed for any facilitative co-benefits for marine calcifiers living within or adjacent to seagrass meadows under changing carbon regimes (Kapsenberg and Cyronak

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2019). Understanding how seagrasses and by comparison unvegetated benthos respond to changes in carbonate chemistry induced by coastal acidification is necessary to predict long term changes to marine fisheries.

Given that seagrasses often occur adjacent to vulnerable calcifying communities, any amelioration in carbonate chemistry could have positive feedbacks for associated species (Gillis et al. 2014, Ricart et al. 2021a, Scott-Askin et al. 2025). Available research remains inconclusive, making it difficult to determine if and how seagrass-modulated water will affect associated calcifiers (Cossa et al. 2024). Some modeling and in situ studies suggest that primary production by intact luxuriant seagrass meadows can positively influence overlying seawater carbonate chemistry (Hendriks et al. 2014, Scott-Askin et al. 2025). Calcifiers located downstream from seagrass beds may experience ~18% higher rates of calcification due to projected increases in pH (~ 0.4 pH units) and Ω_{Ar} (~3 units; Unsworth et al. 2012). Additional studies demonstrate that the seagrass, *Halodule wrightii*, may mitigate the negative effects of ocean acidification by increasing calcification of the crustose coralline algae, by 1.6 fold (Bergstrom et al. 2019). Yet, nighttime respiration in some seagrass meadows may outpace daytime production resulting in net heterotrophic environments in future oceans (Cossa et al. 2024, Invers et al. 1997, Olivé et al. 2016, Rasmusson et al. 2017, Van Dam et al. 2019). Regardless, variation among coastal habitats and their associated buffering capacities can influence the growth and survival of marine calcifiers (Cossa et al. 2024, Leung et al. 2022). As CO_2 increases in the water column due to ocean uptake from the atmosphere, the rate of change can be attenuated by the initial conditions of the habitat's carbonate system (Xue et al. 2025). Photosynthesis within seagrass meadows may exert a strong buffering effect (Bergstrom et al. 2019, Cossa et al. 2024), although the interactive effects of seagrass production and marine calcifiers measured in situ is largely missing from the literature (but see Cox et al. 2015, 2017a, 2017b), making these studies highly valuable for bolstering our understanding of a community-wide response.

Few studies have manipulated the interaction of pCO_2 and seagrass in situ (but see: Arnold et al. 2012, Campbell and Fourqueran 2013, Cox et al. 2015, Takahashi et al. 2015, Cox et al. 2016, Cox et al. 2017a, Cox et al. 2017b). In situ CO_2 experiments have traditionally been confined to natural sources of CO_2 enrichment, but the development of Free Ocean CO_2 Enrichment systems allowed for stable control of seawater carbonate chemistry (Gattuso et al. 2014, Stark et al. 2019). Few systems have been implemented due to logistical, technical, and financial constraints. This study adapted the FOCE design to target estuarine response to future shifts in carbonate chemistry, while also assessing how commercially important bivalves responded across two habitat types. This approach exposed bivalves to the natural, dynamic cycling of the water column incorporating natural variations in food source and sediment biogeochemistry. This contrasts with traditional ocean acidification research examining organisms under static treatments with controlled inputs of food and nutrients (Cornwall and Hurd 2016). The strength of FOCE systems is their ability to capture holistic community-level responses to altered carbonate chemistry, allowing for unique insight into the effects of coastal acidification.

The aims of this study were twofold: 1) to investigate the spatial extent of seagrass-modified water to determine if seagrass meadows can serve as localized refugia in changing carbon regimes and 2) to quantify the early life stage growth and survival of multiple species of bivalves in coastal environments where acidification will likely occur over the 21st century. We hypothesize that seagrasses will ameliorate carbonate chemistry in a highly localized environment. We

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hypothesize that low pH/high CO_2 will negatively impact growth and mortality across all assessed bivalves. However, we hypothesize that seagrasses will locally ameliorate carbonate chemistry, thereby facilitating growth of commercially important bivalves under acidified conditions. Finally, we hypothesize that unvegetated substrate will exacerbate acidified conditions resulting in deleterious changes to growth and mortality for all assessed bivalves.

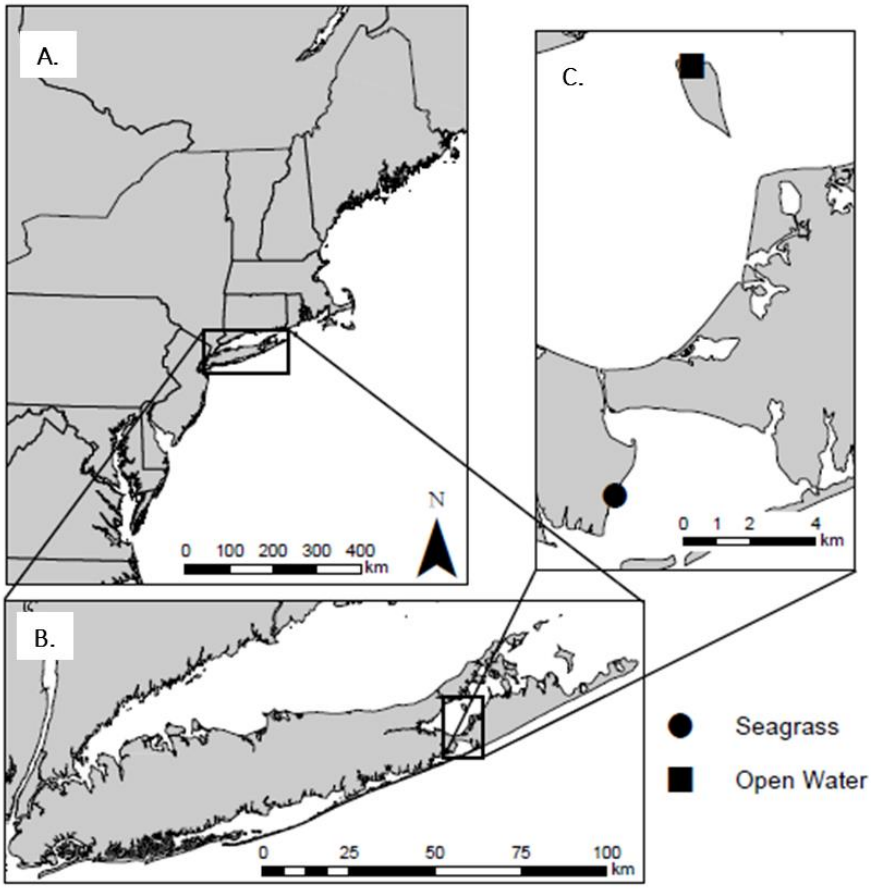

Figure 1: Map of A) Northeast US and B) Long Island. C) In situ CO_2 enrichment experimental site in a seagrass bed indicated by black circle and open water site indicated by black square.

2 Methods

2.1 Spatial Mapping

Inter- and intra-spatial variability in carbonate chemistry was assessed using two high-resolution mapping cruises conducted in a seagrass habitat and an open-water estuary.

To assess how seagrass primary productivity modulates overlying seawater chemistry, a 75-point sampling grid incorporating a patchy eelgrass (*Zostera marina* L.) habitat was surveyed for fine scale differences in carbonate chemistry. The seagrass experimental site was within the surveyed area (40.854320, -72.500859; Fig. 1) and was chosen for ease of

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surveying, homogeneity of depth (< 1 m), and comparably homogenous shoot density (539.2 ± 202.11 m^2) and leaf area (163.11 ± 41.16 mm^2; Figs.1 & 2). At each point, discrete samples were taken from 10 cm above the sediment — seawater interface using a Masterflex E/S Portable Sampler and PVC sampling pole with intake at 10 cm above the substrate (Fig. 2). Water was passed into a sampling reservoir where measurements for temperature (°C), conductivity (µS cm^{-1}), DO (optical; mg L^{-1}), pH on the National Bureau of Standards scale (pH_{NBS}), and pH_T (Honeywell Durafet pH Sensor) were recorded. Every third site was measured for pH_T and a complementary sample for dissolved inorganic carbon (DIC) was taken using borosilicate BOD bottles (300 mL) and preserved with 100 µL of supersaturated mercuric chloride ($HgCl_2$). Discrete water samples were held at 4°C until analyzed (for description of DIC analysis, see Section 2.4). Each point was georeferenced using a Trimble Geo Xm Geoexplorer (Serial Number: 50393-50). Aerial imagery was collected using a DJI Phantom 4 Pro drone and georeferenced to place markers with known coordinates (Fig. 2).

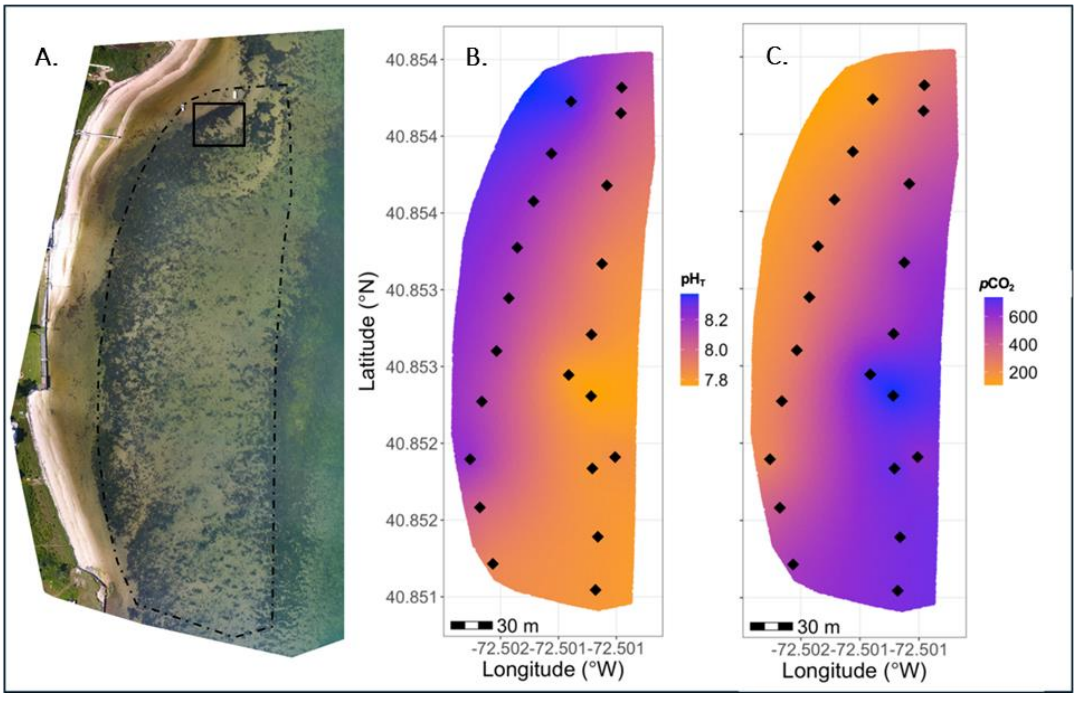

Figure 2: A) High resolution drone imagery of seagrass beds, B) pH_T, and C) pCO_2 levels encompassing a 950 m^2 region. Samples were collected at 10 cm above the sediment-water interface. The inset black box overlaying the imagery indicates the location of experimental chambers.

High-resolution surface mapping was conducted during August in the Peconic Estuary to characterize spatial variability of water quality parameters surrounding the unvegetated open water experimental site (Figs 1 & 3). In situ pCO_2 levels were measured using a Contros HydroC CO_2 sensor (Fig. 3). The HydroC measures pCO_2 levels via non-dispersive infrared spectrometry (NDIR) after dissolved gasses within seawater permeate a hydrophobic membrane and equilibrate with the inner pumped gas circuit (Fiedler et al. 2012, Fietzek et al. 2014). The HydroC was integrated into a continuous flow

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system that included a YSI EXO2 multiparameter sonde and a Sea-Bird Scientific (SBE) ocean pH sensor, enabling the measurements of surface water quality parameters at high spatiotemporal resolution (Fig. 3). Seawater for the continuous flow system was drawn from a rigid intake 1 m below the surface via laminar flow pump. All sensor packages were integrated via custom flow cells. The Contros HydroC pCO_2 sensor had the addition of a SBE 5T centrifugal pump that was affixed in-line to maintain constant flow and reduce bubbling over the sensor membrane. A polycarbonate sleeve was attached between the pump and the HydroC to evenly displace water across the sensor membrane and maintain overflow into the sensor chamber, enabling internal/external temperature equilibration (Wallace and Gobler 2021). All data was transmitted at 0.3–1 Hz and georeferenced using a BU-353 S4 GPS receiver, SiRF Star IV (Wallace and Gobler 2021). Discrete DIC samples (as described above) were collected from the continuous flow system via regulation of a Y-valve between the pump and the sensor array in which excurrent water was diverted for the collection of surface samples for analysis of parameters described above.

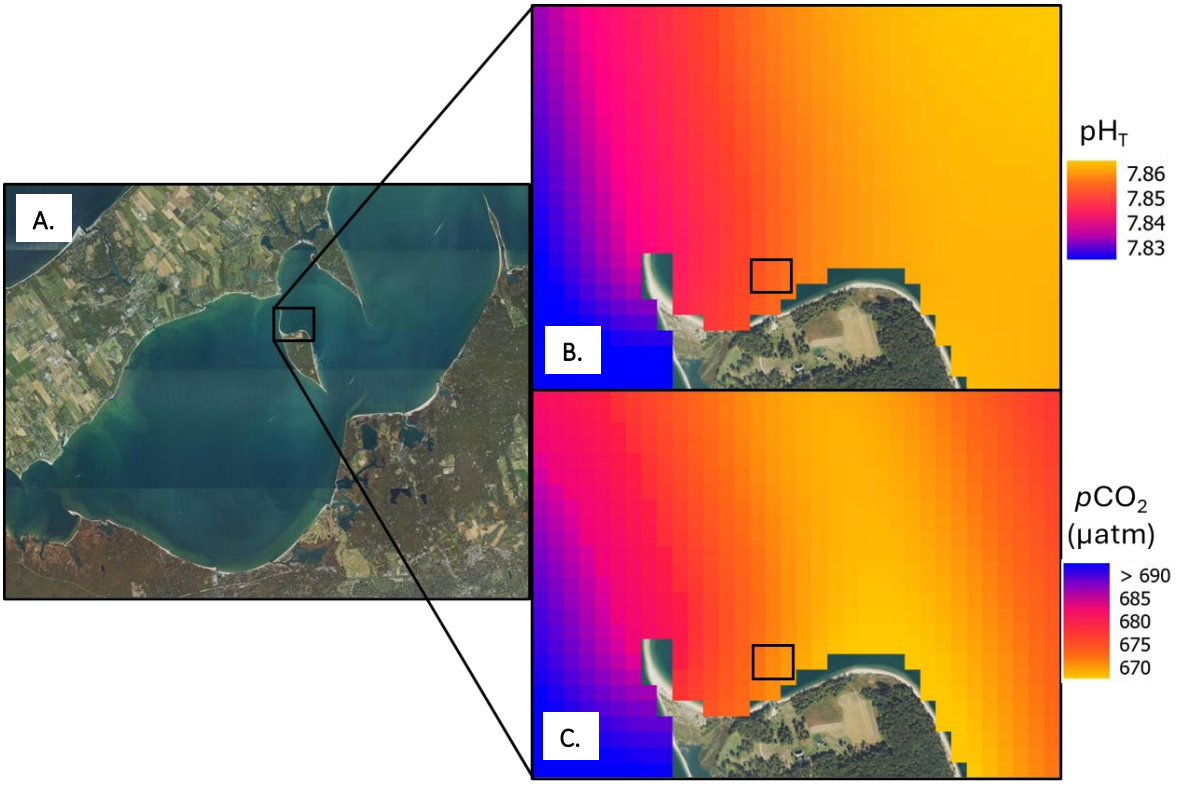

Figure 3: A) National Agriculture Imagery Program (NAIP) natural color imagery of the Peconic Estuary, 2022. B) Surface mapping of pH_T and C) pCO_2 in a 2.65 km^2 area surrounding the open water experimental region (60 m horizontal resolution). The inset black box indicates the location of the experimental chambers.

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2.2 In situ CO_2 enrichment system fabrication

An in-situ CO_2 enrichment system modeled after the FOCE systems (Barry et al. 2014, Gattuso et al. 2014, Kirkwood et al. 2015, Riebesell et al. 2010, Stark et al. 2019) was used to experimentally offset pH from ambient conditions (Fig. 4). The FOCE system was constructed from plexiglass sections sealed with SCIGRIP weld-on 16 cement (Figs. 4, S1, S2, S3, & S4). The system designed for this experiment deviated from previously published FOCE systems as it utilized a fixed injection of CO_2 to integrate into the diel cycling of the estuarine environment. The system maintained a target Δ pH offset allowing for manipulated pH to naturally oscillate with ambient seawater chemistry (Figs. 4 & 5). In doing so, we aimed to capture the natural variability of estuarine systems under future conditions reflective of coastal acidification (Pacella et al. 2018, Wallace et al. 2014)

To control carbonate chemistry, raw seawater was injected with pure CO_2 prior to being delivered into a single, sealed, time-delay, raceway path (~ 1 minute; Figs. 4A, S2A, & S4). This allowed for the dissociation and subsequent transformations in carbonate chemistry to occur prior to entering the incubation chamber (Kirkwood et al. 2015). The raceway path was 76 cm long, 51 cm wide, and 32 cm high, and consisted of four contiguous chambers (Figs. 4A, S2A, & S4). Seawater and CO_2 gas were pumped into the system using a Hydro centrifugal universal submersible pump (part #E160713). A Cole Parmer Gas Flow Proportioner system was used to deliver pure CO_2 gas by bubbling continuously inline at 140 mL min^{-1} (Fig. S3). In doing so, pH and Ω_{Ar} were effectively controlled for all experiments. Preliminary tank and field tests demonstrated that our target bubbling rate yielded pH levels 0.3 – 0.5 units below ambient conditions (Fig. 4B); a level of acidification commonly observed in eutrophic NY estuaries during the summer (Wallace et al. 2014, Wallace and Gobler 2021, Wallace et al. 2021).

Once treated, the acidified water passed through translucent valve-controlled Perspex tubing into one of three bottomless chambers; thus, allowing treated water to be in contact with the sediment (Figs. 4A, S1, & S2B). The design of the chamber allowed for an open wall amendment to accommodate natural variations in salinity, temperature, DO, and food supply, while also integrating potential changes generated by sediment biogeochemistry (Figs. 4A, S2B & C). The chamber (n = 3) measured 30.5 cm high by 29 cm wide; except for the wall receiving acidified water (Figs. 4A, S2B & C). This side wall extended an additional 5.7 cm past the chamber to accommodate the passageway designed to incorporate raw seawater (Figs. 4A & S2B). The volume of the chamber was 25.65 liters, which gave sufficient room to populate the space with study organisms. The top of the chamber was detachable (Figs. 4A, S1, S2B & C) to allow access to the inside of the chamber. An additional 3 chambers were designed and operated in parallel to those described above. Instead of receiving acidified treatment water, these chambers were circulated with ambient seawater to serve as experimental controls.

The wall opposite to the side receiving treatment water had an outflow port affixed with a BlueRobotics M100 brushless motor. Simulating tidal velocity was deemed critical to maintaining environmental realism; therefore, flow rates were maintained at a mean ambient water velocity calculated from measured tidal cycles (~2.9 cm sec^{-1}; Wallace et al.

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2021). Target water velocity was maintained across all replicates. The resulting turnover rate (17.5 cycles min^{-1}) allowed for complete replenishment of treatment water 3.4 times every hour.

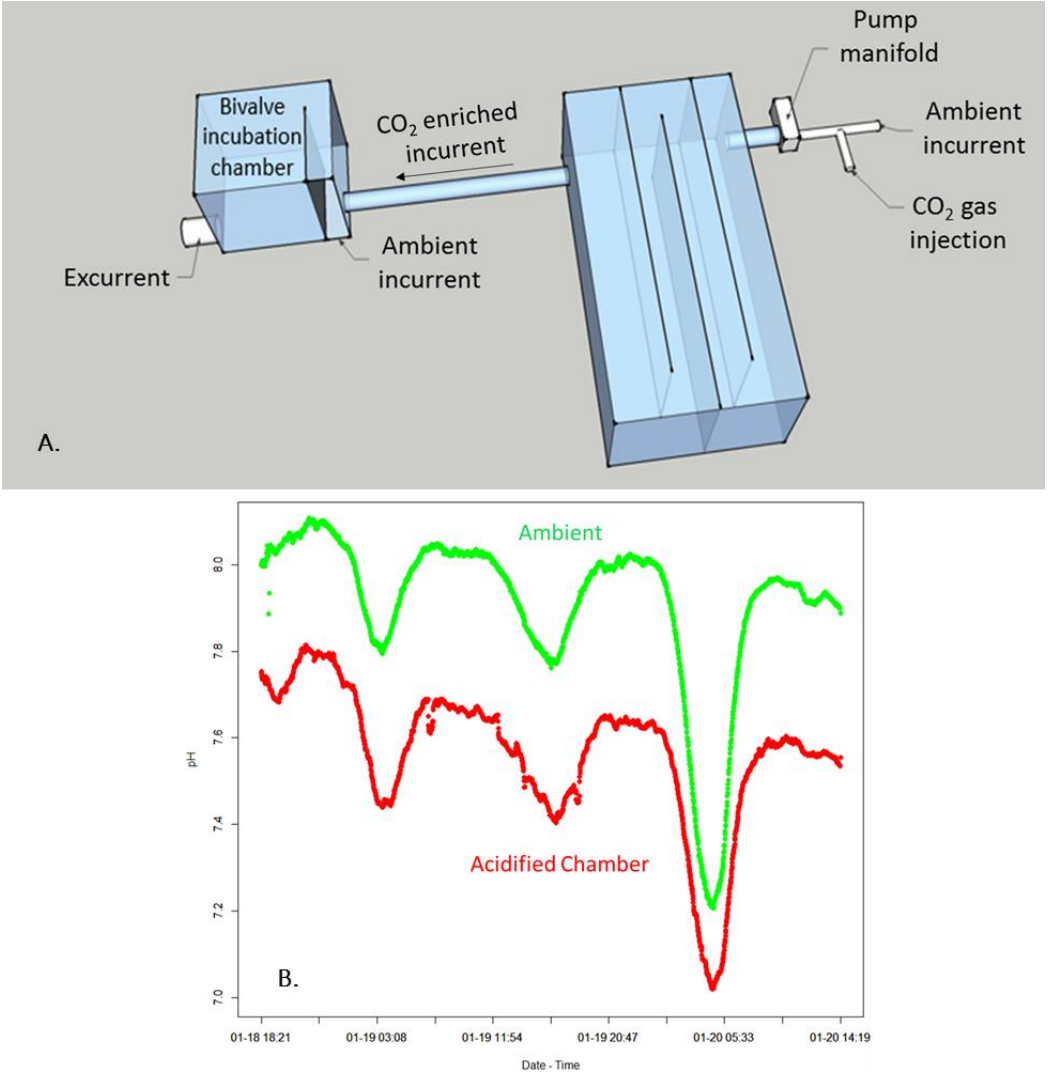

Figure 4: A) Schematic of in situ water chemistry control system showing injection and mixing system that delivered CO_2-enriched seawater to the incubation chambers. B) Resulting pH from multiday deployment within test tank (see figure S4) where ambient seawater was continuously delivered from adjacent embayment.

2.3 High-frequency monitoring

Given the complex and novel nature of this system, a series of instrumentation were used to generate high frequency time series data to capture the diel cycling of both ambient and acidified treatments. For each ambient and CO_2 chamber, an SBE SeaFET V2 Ocean pH sensor was initially embedded within the side wall (Figs. S1 & S4A) to

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continuously record pH_T. Once pH was determined to be stable in each chamber, the sensors were removed from the side wall and integrated into the outflow piping, to measure pH at 20-minute intervals during the experimental incubation (Fig. 5). Dissolved oxygen (DO) and conductivity data loggers (Onset: HOBO® U24-002-C and U-26-001) were installed in each chamber to continuously record temperature, salinity, and DO (Fig. S1C). In addition, a telemetry array using a YSI EXO2 water quality sonde parameterized to temperature (°C), conductivity (µS cm^{-1}), DO (optical; mg L^{-1}), pH on the National Bureau of Standards scale (pH_{NBS}), and chlorophyll *a* fluorescence (RFU) was established on site to continuously monitor real-time ambient water chemistry outside the experimental chambers at 20-minute intervals.

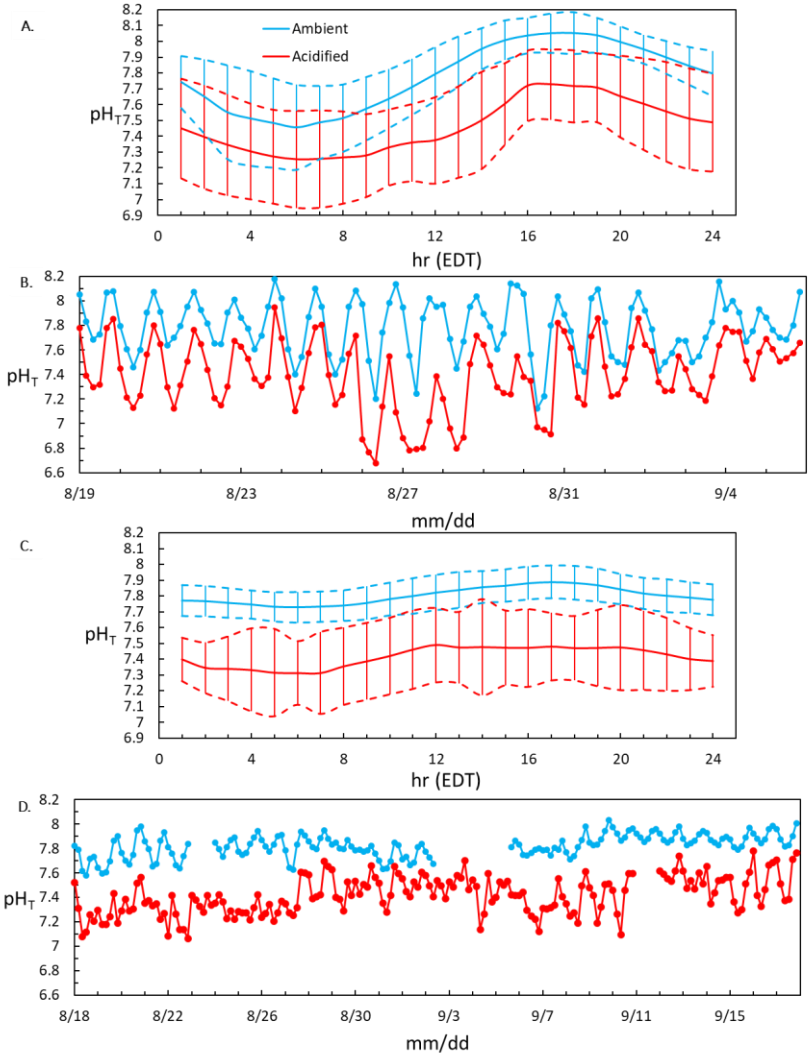

Figure 5: A) Diel patterns of pH_T ± SD (mean hourly) and B) four hour binned mean pH_T in ambient and acidified treatment chambers at the seagrass site for the duration of the experiment. C) Diel patterns of pH_T ± SD (mean hourly) and D) four hour binned mean pH_T in ambient and acidified treatment chambers at the unvegetated site for the duration of the experiment.

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2.4 Acute exposure to ecologically relevant levels of acidification – Bivalve response

To compare juvenile bivalve growth and survival under experimentally acidified conditions, two in situ CO_2 enrichment experiments were performed. The first experiment was conducted within a seagrass meadow located in east Shinnecock Bay (40.86001, -72.49834; Fig. 1) from August to September (8/19 – 9/6). This site was chosen because previous studies indicated that it was net autotrophic (Wallace et al. 2021). The investigators made a conscious decision to exclude seagrass from the chambers due to difficulties with standardizing shoot density and shoot morphometrics across 6 distinct mesocosms. The decision was justified by spatial mapping indicating a robust zone of influence within and adjacent to the meadow (Wallace et al. 2021 & Fig. 2). An additional experiment was performed in an open water site in the Peconic Estuary (40.97672, -72.46638; Figs. 1 & 3) from August to September (8/11 – 9/18). Both locations were shallow (< 2m), easily accessible, with coarse sediment, and likely to remain saturated with respect to $CaCO_3$ through the experimental season as demonstrated by previous studies (Wallace et al. 2021).

For all experiments, bay scallops, *Argopecten irradians*, and Eastern oysters, *Crassostrea virginica*, were selected due to their historic importance for Northeastern fisheries. Two size classes of bay scallop, *A. irradians,* (initial lengths: 5 and 11 mm) were replicated across both experiments. However, due to lack of availability, one size class (initial lengths: 10 mm) were used for Eastern oysters, *Crassostrea virginica*. The investigators chose to include two sizes of bay scallops in the experiments as juvenile sensitivity to abiotic parameters changes through its life history (Dupont et al. 2010). Larger juveniles are thought to be more robust than their younger, smaller counterparts (Gobler et al. 2014). The size classes of Eastern oysters reflect the smallest size class available at the start of the experiment.

A. irradians and *C. virginica* were obtained from the East Hampton Town shellfish hatchery located within the Peconic Estuary watershed, 50 km east of our Peconic Estuary experiment site. The East Hampton Town shellfish hatchery utilizes broodstock originating from the Peconic Estuary.

At the start of each experiment, all shellfish were tagged using Bee tags (The Bee Works, Ontario, Canada) and photographed to scale. Images were analyzed using Fuji Image Processing software. Bivalve height/length (hinge - ventral margin) measurements were made to the nearest 0.01 mm. Once imaged, 15 individuals per species were placed in 3 mm mesh bags and placed in triplicate across each chamber (three control: three treatment). The bags were affixed to the top of the chambers using aquarium grade suction cups attached to custom PVC sleeves (Fig. S1C). At the conclusion of each experiment, all shellfish were photographed and measured for height/length to the nearest 0.01mm. Growth rates were normalized to µm day^{-1}. During each experiment, water samples were collected for analysis of chlorophyll *a*. These values were used as proxies for bivalve food availability and to complement real time in situ measurements of chlorophyll *a* fluorescence. Both seawater collected outside the chamber and within all chambers was collected in triplicate and filtered through 0.2 µm (47mm) polycarbonate membrane filters. Filters were frozen and analyzed within two weeks for chlorophyll *a* quantification using a non-acidification method on a Turner Designs© Trilogy Laboratory Fluorometer with an excitation wavelength of 485 nm and

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an emission wavelength of 685/10 nm. The concentrations of chlorophyll *a* were not significantly different between the chambers or between the chambers and ambient conditions ($p > 0.05$; ANOVA).

2.5 Carbonate Chemistry

During each in situ CO_2 experiment, weekly discrete measurements of environmental conditions (temperature, salinity, DO) were made during the afternoon (~15:00 local time) using a YSI 556 MultiProbe System and measurements of pH_T were made using a Honeywell DuraFET III pH electrode (Ion Selective Field Effect Transistor; ISFET) integrated to a Honeywell Analytical Process Analyzer (APT) 4000PH series. pH_T measurements were used to confirm the integrity of the SeaFET calibration and were used for downstream calculations in carbonate chemistry.

A rubber valve was embedded into the wall of each incubation chamber to allow for discrete water samples to be extracted via a syringe or peristaltic pump (Fig. S2B). Discrete water samples (300 mL) for DIC analysis were collected at least 2x weekly using borosilicate glass BOD bottles. To remove aeration, water was allowed to overflow the bottle by two full volumes. Samples were preserved on site using 100 mL of saturated $HgCl_2$ solution and sealed with Apiezon L ultra-high vacuum grease. DIC samples were analyzed within two weeks of sample collection by coulometric titration using a UIC Inc. CM5017O coulometer interfaced to a VINDTA 3D delivery system. As a quality assurance measure, certified reference material generated by Dr. Andrew Dickson's lab (University of California San Diego, Scripps Institution of Oceanography) was analyzed immediately before and after sample titration, yielding full recovery during this study (99.99% ± 0.05). Additional carbonate system parameters were calculated from measured levels of DIC, pH_T, temperature, and salinity using CO2SYS. Published values of phosphate, silicate, boron (Lee et al. 2010), sulfate (Morris and Riley 1966), and fluorine (Riley 1965), as well as the dissociation constant of potassium fluoride (Dickson and Riley 1979), the dissociation constant of potassium sulfate (Dickson 1990), the solubility coefficient of CO_2 (Weiss 1974), the vapor pressure of H_2O above seawater (Weiss and Price 1980), and the first and second dissociation constants of carbonic acid in seawater (Millero 2010) were used in addition to measured values (pH_T, salinity, temperature) to calculate pCO_2, alkalinity (A_T), Revelle factor (Rf), and Ω_{Ar}.

2.6 Statistics

All statistical analyses were conducted in R Statistical Software with data analysis and visualization performed using the 'tidyverse' package (Wickham et al. 2019, v 2025.09.2+418; R Core Team 2024). Spatial packages are noted as used. Prior to all analyses, residuals were plotted to assess normality and homogeneity of variance using R base package. If data was normally distributed, parametric testing was used. An alpha (α) of 0.05 was used to determine significance for all analyses. Pairwise comparisons were explored when significance with main effects was found. All *p* values were corrected with Holm-sidak *p* value adjustment. All values are reported as means (±SD).

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2.6.1 Spatial modeling

Spatial data surrounding the seagrass site was assessed for semivariance, adjusted with optimal nugget size, and then fit to a spherical model. Ordinary kriging using the 'sf' package in R was used to spatially interpolate water chemistry within a 950 m^2 matrix (Pebesma and Bivand 2023). Differences with respect to pH and DO were compared between sand and seagrass using a One-Way ANOVA. High resolution horizontal survey points of pCO_2 were interpolated using a diffusion kernel technique with an additive raster barrier in the Geostatistical Analyst extension in ArcGIS Pro 3.6. This interpolation method uses a distance metric (optimally varying kernel) that calculates the cost of travel from one cell of the matrix to the next (Krivoruchko and Gribov 2004). This method factored in areas with insufficient data or areas that have non-transparent barriers (i.e. coastlines) for chemical propagation (Gribov and Krivoruchko 2011). Furthermore, this interpolation was able to smooth data that was anomalous over short distances (i.e. peaks/troughs due to bubbling and/ or caused by wave action moving intake vertically in the water column) that would not necessarily have been removed using a standard kriging method.

2.6.2 Carbonate chemistry with respect to substrate and treatment

Within substrate, One-way ANOVA was used to determine significant differences between carbonate chemistry for ambient and acidified treatments. A Two-Way ANOVA was used to determine significant differences between substrate and treatment. When significance was found as a main effect, pairwise comparisons were used and adjusted using Holm-Sidak *p*-value adjustment. Non-parametric analysis is noted as used.

Parameter	Open Water	Seagrass	
		Inside	Outside
Temperature (°C)	28.41 ± 0.17	24.96 ± 1.22	25.23 ± 1.16
Salinity (psu)	29.15 ± 1.21	30.84 ± 0.08	30.82 ± 0.07
A_T (µmol kg^{-1})	1948.64 ± 64.24	2063.3 ± 84.09	2060.6 ± 66.01
DIC (µmol kg^{-1})	1856.29 ± 22.91	1804.72 ± 105.64	1831.33 ± 106.23
pCO_2 (µatm)	681.07 ± 34.54	403.6 ± 181.62	484.7 ± 230
Rf	13.25 ± 0.39	10.57 ± 2.14	10.9 ± 2.37
Ω_{Ar}	1.67 ± 0.47	3.02 ± 1.05	2.68 ± 0.96
pH_T	7.84 ± 0.02	8.05 ± 0.18	7.98 ± 0.18
DO (mg L^{-1})	6.75 ± 0.3	9.48 ± 1.65	8.40 ± 1.20

Table 1: Summary of recorded seawater chemistry for spatial maps recorded in figure 2 and figure 3. Reported values are representative of discrete water samples taken for DIC analysis (n = 25). Values are reported as mean ± SD for temperature (°C), total alkalinity (A_T; µmol kg^{-1}), dissolved inorganic carbon (DIC; µmol kg^{-1}), partial pressure of carbon dioxide (pCO_2; calculated), Revelle factor (Rf), saturation state of aragonite (Ω_{Ar}), pH_T (total H+ scale) and Dissolved Oxygen (mg L^{-1}).

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2.6.3 In situ CO_2 enrichment experiments – Bivalve response

Bivalve data was partitioned into three datasets: 5 mm bay scallops, 11 mm bay scallops, and 10 mm oysters. Each dataset was assessed for outliers (as defined by Q3 + 1.5xIQR or Q1 – 1.5xIQR; IQR = interquartile range) with respect to growth rate and mortality. Extreme outliers (i.e., 3xIQR) were removed from analyses to improve both QQ plot and model fit. Growth rate was calculated as final length minus initial length divided by the number of days deployed (µm day^{-1}). Mortality rate was defined as the number of dead animals divided by the total number of animals deployed. Both growth and mortality rate were analyzed using One-Way and Two-Way ANOVAs to compare within and across experiments. For Two-way ANOVAs, both substrate (seagrass vs. open water estuary) and treatment (ambient vs. acidified pH) were treated as fixed effects. When a main effect was found, pairwise comparisons were adjusted using Holm-sidak *p*-value adjustment.

3. Results

3.1 Spatial mapping

The seagrass survey comprised an area of approximately 928.82 m^2. Averaging across the survey matrix, depth was 0.52 ± 0.28 m, pH_T was 8.01 ± 0.18, DO was 9.25 ± 1.62 mg L^{-1}, pCO_2 was 445.6 ± 202.6 µatm, and Ω_{Ar} was 2.84 ± 1.03. There is a notable range of recorded pCO_2 values between the seagrass and open estuary sites. Within the densely populated, shallow edge of the seagrass meadow, values ranged from 150 – 280 µatm with the outer, more sparsely populated edge of the meadow corresponding to 500 – 750 µatm (Fig. 2 & Table 1). Examining localized differences between seagrass and sand-cover bottom at this site revealed clear differences with respect to carbonate chemistry and dissolved oxygen. With respect to the seagrass habitat, pH_T was 8.05 ± 0.18, dissolved oxygen was 9.48 ±1.65 mg L^{-1}, pCO_2 was 403.6 ± 181.62 µatm and Ω_{Ar} was 3.02 ± 1.05 (Table 1). With respect to the sandy bottom habitat, pH_T was 7.98 ± 0.18, DO was 8.40 ± 1.20 mg L^{-1}, pCO_2 was 484.7 ± 230 µatm, and Ω_{Ar} was 2.68 ± 0.96 (Table 1). There were significantly higher levels of pH_T (One-way ANOVA; $F_{(1,24)} = 7.70$; $p = 0.007$) and DO (One-way ANOVA; $F_{(1,24)} = 6.79$; $p = 0.01$) within the seagrass habitats compared to the regions without seagrass.

The open water mapping survey was conducted throughout the entirety of the Western Peconic Estuary (Fig. 3A), where the 2.65 km^2 region examined during this study focused on the area of interest surrounding the in situ experimental location (Fig. 3B). Due to the homogeneity of this embayment, no statistically significant differences were observed across the survey region. Temperature and salinity were stable surrounding the open water site, where the average temperature was 28.41 ± 0.17°C, salinity was 29.15 ± 1.21, and DO was 6.75 ± 0.3 (Table 1). The open estuary site has a significantly smaller range in pCO_2 (670 – 690 µatm; Fig. 3) indicating a less dynamic, more biogeochemically stable environment.

A_T was > 100 µmol kg^{-1} higher at the seagrass site than what was observed at the open water site, where DIC was higher and more stable (1856.29 ± 22.91 vs 1804.72 ± 105.64; see Table 1). The mean Rf during the open water cruise was also higher and more stable when compared with the seagrass site (13.25 ± 0.39 vs 10.57 ± 2.14, respectively), where both pH_T and Ω_{Ar} were significantly lower at the open water site (Table 1).

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Treatment	Ambient	Ambient	Acidified	Acidified
Substrate	Seagrass	Open water	Seagrass	Open water
Temperature (°C)	23.79 ± 2.36	22.77 ± 1.56	23.06 ± 2.44	23.23 ± 1.90
Salinity (psu)	29.77 ± 0.76	29.24 ± 0.12	29.60 ± 0.82	29.23 ± 0.12
A_T (µmol kg^{-1})	1956.08 ± 55.22	1963.93 ± 26.44	2032.83 ± 131.9	1950.8 ± 63.51
DIC (µmol kg^{-1})	1747.96 ± 14.0	1807.71 ± 22.78	1981.92 ± 128.79	1922.23 ± 64.43
pCO_2 (µatm)	426.95 ± 132.04	538.77 ± 64.81	1329.73 ± 265.15	1542.35 ± 358.11
Rf	11.03 ± 1.94	12.47 ± 0.70	16.64 ± 1.19	17.00 ± 0.54
Ω_{Ar}	2.39 ± 0.71	1.87 ± 0.21	1.01 ± 0.27	0.82 ± 0.17
pH_T	7.99 ± 0.11	7.89 ± 0.05	7.56 ± 0.08	7.49 ± 0.09
Chl-*a* (µg L^{-1})	7.07 ± 4.07	3.49 ± 0.9	6.04 ± 2.73	2.19 ± 0.59

Table 2: Summary of recorded seawater chemistry across both substrates and treatments representative of discrete water samples taken for DIC analysis. Values are reported as mean ± SD for temperature (°C), total alkalinity (A_T; µmol kg^{-1}), dissolved inorganic carbon (DIC; µmol kg^{-1}), partial pressure of carbon dioxide (pCO_2; calculated), Revelle factor (Rf), saturation state of aragonite (Ω_{Ar}), pH_T (total H^+ scale), and Chlorophyll *a* (Chl-*a*; µg L^{-1}).

3.2 In situ CO_2 enrichment experiment in a seagrass bed

For the first experiment, conducted within a seagrass meadow, there was no statistical difference between continuous water quality measurements made in the seagrass site compared to the ambient chambers (salinity, chlorophyll *a*, temperature, DO, A_T, DIC, pH_T, pCO_2; refer to Tables 2, S1; Fig. S5; $p > 0.05$, One-Way ANOVA), demonstrating the control chambers reflected ambient conditions.

During experiment 1, mean salinity was 29.65 ± 0.78, mean temperature was 23.32 ± 2.37°C, and mean chlorophyll *a* was 6.41 ± 3.18 µg L^{-1} (Table 2). Mean daily differences in pH_T between ambient and acidified chambers was statistically significant and averaged 0.43 ± 0.03 units (Table 2; Fig. 5; $F_{(1,15)} = 76.56$; $p < 0.0001$; One-Way ANOVA). Mean pH_T measured 7.99 ± 0.11 for the ambient treatments and 7.56 ± 0.08 for the acidified treatments. Mean DIC and pCO_2 was 426.95 ± 132.03 µatm in ambient treatments and were significantly lower than the acidified treatments (DIC = 1981.92 ± 128.78 µmol kg^{-1}; pCO_2 = 1329.73 ± 265.15 µatm; DIC: $F_{(1,15)} = 19.11$; $p < 0.0001$; One-Way ANOVA; pCO_2; Table 2; $F_{(1,15)} = 60.06$, $p < 0.0001$; One-Way ANOVA). The mean Ω_{Ar} in the acidified treatment was low but saturated in $CaCO_3$ during the incubation period (mean Ω_{Ar} = 1.01 ± 0.27) while mean Ω_{Ar} in the ambient treatment chambers was significantly higher, 2.39 ± 0.71 (Table 2; $F_{(1,15)} = 34.93$, $p < 0.001$; One-Way ANOVA). Finally, the Rf in the ambient treatment (Rf = 11.03 ± 1.94) was significantly lower (Rf: Table 2; $F_{(1,15)} = 55.26$, $p < 0.0001$; One-Way ANOVA) than the acidified treatment (16.64 ± 1.19). A_T, salinity, chlorophyll *a*, and temperature were not statistically different between treatments (Table 2; $p > 0.05$; One-Way ANOVA).

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Species	Size Class (mm)	Open water: Ambient	Open water: Acidified	Seagrass: Ambient	Seagrass: Acidified
A. irradians	5	355.4 ± 92.3	170.8 ± 74.2	260.2 ± 177.6	187.6 ± 116.9
A. irradians	11	273.8 ± 160.6	151.9 ± 93.3	312.9 ± 95.2	241.0 ± 40.4
C. virginica	10	429.2 ± 139.9	321.0 ± 133.7	392.3 ± 148.4	322.9 ± 131.0

Table 3: Summary of growth rate (µm day^{-1}) for bivalves as it relates to substrate (Open water estuary vs. Seagrass) and seawater treatment (Ambient vs. Acidified). Values are represented as mean ± SD.

Two size classes of *A. irradians* (initial lengths: 5 and 11 mm) and one cohort of *C. virginica* (initial length: 10 mm) were deployed during this experiment. Both species and size classes exhibited statistically significant differences in growth rate (µm day^{-1}) and/or mortality (%) between treatments (Figs. 6 - 8). Growth rates of the smaller cohort of *A. irradians* were not different between treatments (Fig. 6, Table 3; $F_{(1,42)} = 2.29$; $p > 0.05$; One-Way ANOVA). The larger *A. irradians* cohort exposed to higher pCO_2 conditions exhibited significantly slower growth rates under acidified conditions compared to the control (Fig. 7, Table 3; $F_{(1,48)} = 9.48$; $p < 0.001$; One-ANOVA). *C. virginica* also had slower growth under acidified conditions (Fig. 8, Table 3; $F_{(1,78)} = 4.83$; $p = 0.03$; One-Way ANOVA). The smaller *A. irradians* cohort (5 mm initial length) experienced significantly higher mortality rates under acidified conditions (Fig. 6, Table 4; $F_{(1,5)} = 16.84$; $p < 0.01$; One-Way ANVOA) as did *C. virginica* (Fig. 8, Table 4; $F_{(1,5)} = 2.56$; $p < 0.05$; One-Way ANOVA). There were no differences in mortality for the 11 mm *A. irradians* cohort across treatments (Fig. 7, Table 4, $F_{(1,5)} = 0.00$; $p > 0.05$; One-Way ANOVA).

Species	Size Class (mm)	Open: Ambient	Open: Acidified	Seagrass: Ambient	Seagrass: Acidified
A. irradians	5	43.3 ± 5.7	55.6 ± 9.6	2.6 ± 4.4	28.9 ± 10.2
A. irradians	11	16.6 ± 15.3	10.0 ± 10.0	13.3 ± 23.1	13.3 ± 15.3
C. virginica	10	1.1 ± 1.9	2.3 ± 1.9	0.0 ± 0.0	17.8 ± 19.2

Table 4: Summary of mortality (%) for bivalves as it relates to substrate (Open water estuary vs. Seagrass) and seawater treatment (Ambient vs. Acidified). Values are represented as mean ± SD.

3.3 In situ CO_2 enrichment experiment in the open water site

For the second experiment at the open water site in the Peconic Estuary, there was no statistical difference between continuous water quality measurements made in the open water site compared to the ambient chambers (salinity, chlorophyll *a*, temperature, DO, A_T, DIC, pH_T, pCO_2; refer to Tables 2, S1; Fig. S6; $p > 0.05$, One-Way ANOVA), demonstrating the control chambers reflected ambient conditions.

During experiment 2, the average salinity was 29.24 ± 0.12, mean temperature was 22.77 ± 1.56°C and mean chlorophyll *a* was 3.49 ± 0.9 µg L^{-1} (Table 2, Fig. S6). The mean pH_T in the ambient chambers was 7.89 ± 0.05 and was

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significantly higher than the acidified treatments (pH_T of 7.49 ± 0.09; Fig. 5C & D, Table 2; $F_{(1,41)} = 235.16$; $p < 0.0001$; One-Way ANOVA) whereas mean DIC and pCO_2 levels in the ambient chambers were (1807.71 ± 22.78 µmol kg^{-1}; 538.77 ± 64.81 µatm) significantly lower than the acidified chambers (1922.23 ± 64.43 µmol kg^{-1} and 1542.34 ± 358.11 µatm: DIC; $F_{(1,41)} = 46.68$; $p < 0.0001$, One-Way ANOVA; pCO_2: $F_{(1,41)} = 46.68$; $p < 0.0001$, One-Way ANOVA). Subsequently, Ω_{Ar} was unsaturated in the acidified chambers (0.82 ± 0.17) compared to supersaturated conditions (Ω_{Ar} = 1.87 ± 0.21) within the ambient chambers (Table 2; $F_{(1,41)} = 327.9$; $p < 0.0001$, One-Way ANOVA). Finally, the Rf followed similar patterns where the ambient treatment (Rf = 12.47 ± 0.7) was significantly lower (Rf: Table 2; $F_{(1,41)} = 560.19$, $p < 0.0001$; One-Way ANOVA) than the acidified treatment (17.00 ± 0.54). A_T, salinity, chlorophyll *a*, and temperature were not different between treatments (Table 2: $p > 0.05$; One-Way ANOVA).

Like the seagrass experiment, two size classes of bay scallops (*A. irradians*; 5 and 11 mm) and one size class of Eastern oysters (*C. Virginica;* 10 mm) were deployed for experiments and all cohorts grew significantly faster in ambient treatments compared to the acidified chambers (Figs. 6 - 8; $p < 0.05$; One-Way ANOVA). The oysters in the ambient chambers grew ~100 µm d^{-1} faster than oysters grown in the acidified chambers (Fig. 8A, Table 3; $F_{(1,168)} = 21.33$; $p < 0.001$; One-Way ANVOA). Similarly, 5 mm scallops grew almost twice as fast in ambient treatments compared to acidified treatments (Fig 6A, Table 3; $F_{(1,34)} = 20.84$; $p < 0.0001$; One-Way ANVOA). The larger bay scallop cohort grew almost two times faster under ambient conditions than acidified conditions (Fig 7A, Table 3; $F_{(1,40)} = 8.81$; $p < 0.005$; One-Way ANVOA). There were no significant differences in mortality amongst bivalves in relation to treatment (Figs. 6 - 8, Table 4; $p > 0.05$; One-Way ANOVA).

3.4 Comparison of carbonate parameters across substrate and treatment

A series of Two-Way ANOVAs was utilized to understand how substrate and treatment affect carbonate chemistry across two distinct habitats. Salinity and temperature were not significantly different across substrate and treatment ($p > 0.05$; Two-Way ANOVA). However, when assessing pH_T as a function of substrate and treatment, we found significant main effects for substrate ($F_{(1,56)} = 4.806$; $p < 0.001$; Two-Way ANOVA) and treatment ($F_{(2,56)} = 154.88$; $p < 0.0001$; Two-Way ANOVA). Most importantly, there was no significant difference between low pH_T treatments across substrates ($p > 0.05$; Two-way ANOVA). Furthermore, there were no significant differences between ambient-high pH treatments across substrate ($p > 0.05$; Two-way ANOVA), indicating that we successfully replicated pH across substrates and treatments. This trend continued with pCO_2 (substrate: $F_{(1,56)} = 0.73$; $p < 0.01$; treatment: $F_{(2,56)} = 88.37$; $p < 0.0001$; Two-Way ANOVA), DIC (substrate: $F_{(1,56)} = 3.09$; $p < 0.05$; treatment: $F_{(2,56)} = 34.11$; $p < 0.001$; Two-Way ANOVA), Rf ($\chi^2 = 15.86$, df = 3, $p < 0.0001$; Kruskal-Wallis), and Ω_{Ar} ($\chi^2 = 42.48$, df = 3, $p < 0.001$; Kruskal-Wallis). However, A_T followed a different trend where substrate ($F_{(1,56)} = 0.05$; $p < 0.05$; Two-Way ANOVA), not treatment ($F_{(2,56)} = 2.62$; $p = 0.11$; Two-Way ANOVA) was a significant main effect. Pairwise comparisons revealed that under acidified conditions, the seagrass meadow had significantly higher A_T compared to the open estuary site ($p < 0.01$).

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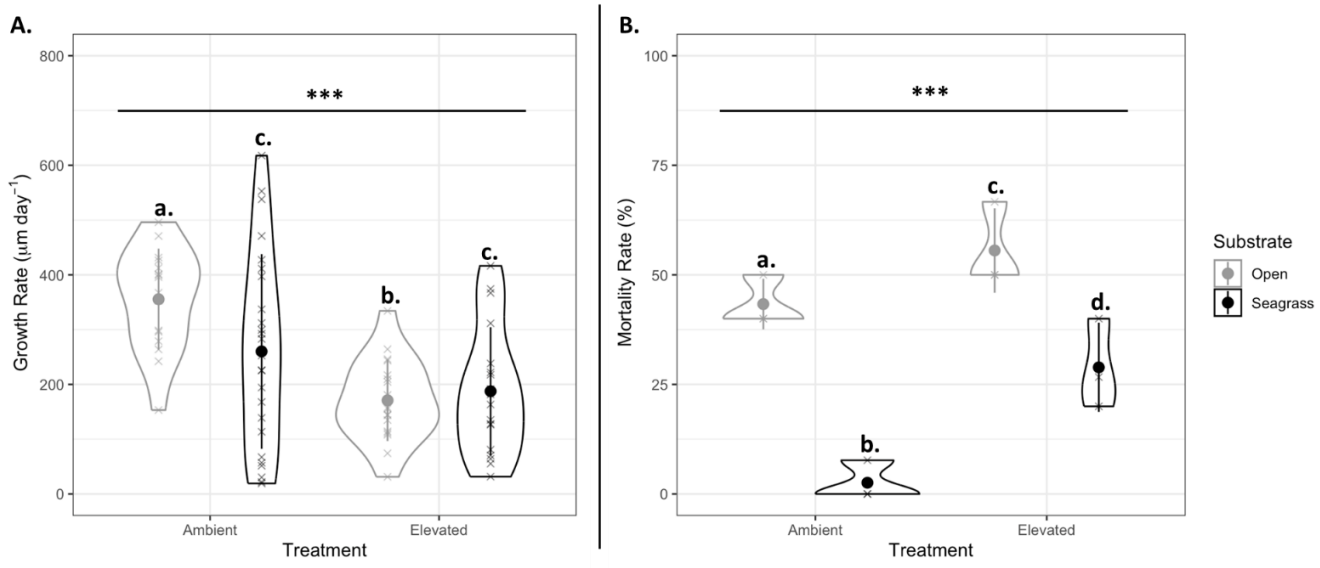

Figure 6: Growth rate and mortality of 5 mm bay scallops as it relates to substrate and treatment. A) Growth rate (µm day^{-1}) of 5 mm bay scallops. Bar indicates a highly significant effect of treatment on growth rate. Pairwise comparisons are noted via lettering. B) Mortality of 5 mm bay scallops. Bar indicates a highly significant effect of treatment on mortality. *** $p < 0.05$; ** $p < 0.1$; *** $p < 0.001$*

3.5 Comparison of bivalve response to substrate and treatment

A series of Two-Way ANOVAs was utilized to understand how substrate and treatment affect the growth and survivorship of the experimental organisms. For 5 mm bay scallops, treatment was a significant factor in determining growth rate (Fig. 6A, Table 3; $F_{(1,73)} = 17.18$; $p < 0.05$; Two-Way ANOVA). Pairwise comparisons indicated that there was a highly significant effect of treatment on growth in the open estuary site (Tables 3, S2, & S3; $p < 0.001$); however, there was no significant effect of treatment on growth when 5 mm bay scallops were grown in seagrass (Tables 3, S2, & S3, $p > 0.5$). For 11 mm bay scallops, growth rate was significantly impacted by substrate (Fig. 7, Tables 3, S4, & S5; $F_{(1,85)} = 8.27$; $p < 0.05$; Two-Way ANOVA) and treatment (Fig. 7, Tables 3, S4, & S5; $F_{(1,85)} = 18.35$; $p < 0.05$; Two-Way ANOVA). As with 5 mm bay scallops, for the 11 mm bay scallops there was a highly significant effect of treatment on growth in the open estuary site (Table S5; $p < 0.001$) that was not observed in seagrass (Table S5, $p > 0.05$). Interestingly, under acidified conditions, 11 mm bay scallops grew significantly faster within seagrass than in an open estuary (Tables 3 & S5; $p < 0.01$). Finally, Eastern oysters exhibited a significant effect of treatment on growth (Fig. 8A, Tables 3, S6 & S7; $F_{(1,242)} = 29.4$; $p < 0.001$; Two-Way ANOVA). Like the bay scallops, Eastern oysters were significantly affected by acidified conditions in the open estuary site (Tables S6 & S7, $p < 0.001$). This was not observed in the seagrass (Table S7, $p > 0.05$).

With respect to mortality, all bivalves demonstrated mortal sensitivity to acidification. For 5 mm bay scallops, there were significant effects of substrate (Fig. 6B, Tables 4, S8 & S9; $F_{(1,8)} = 54.7$; $p < 0.001$; Two-Way ANOVA) and treatment

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(Fig 6B**,** Tables S8 & S9; $F_{(1,8)} = 17.9$; $p < 0.01$; Two-Way ANOVA) on morality. The 5 mm bay scallops survived significantly better in the seagrass meadow than open water estuary site under ambient CO_2 conditions (Tables 4 & S9 X; $p < 0.001$). However, within seagrass, acidified conditions significantly increased mortality in 5 mm bay scallops (Tables 4 & S9; $p < 0.01$). Interestingly, the presence of seagrass significantly improved survivorship for 5 mm bay scallops under acidified conditions (Tables 4 & S9, $p < 0.01$). There were no significant effects of treatment or substrate on mortality for 11 mm bay scallops or Eastern oysters (Fig. 7, 8, Tables 4, S10, S11; $p > 0.05$; Two-Way ANOVA).

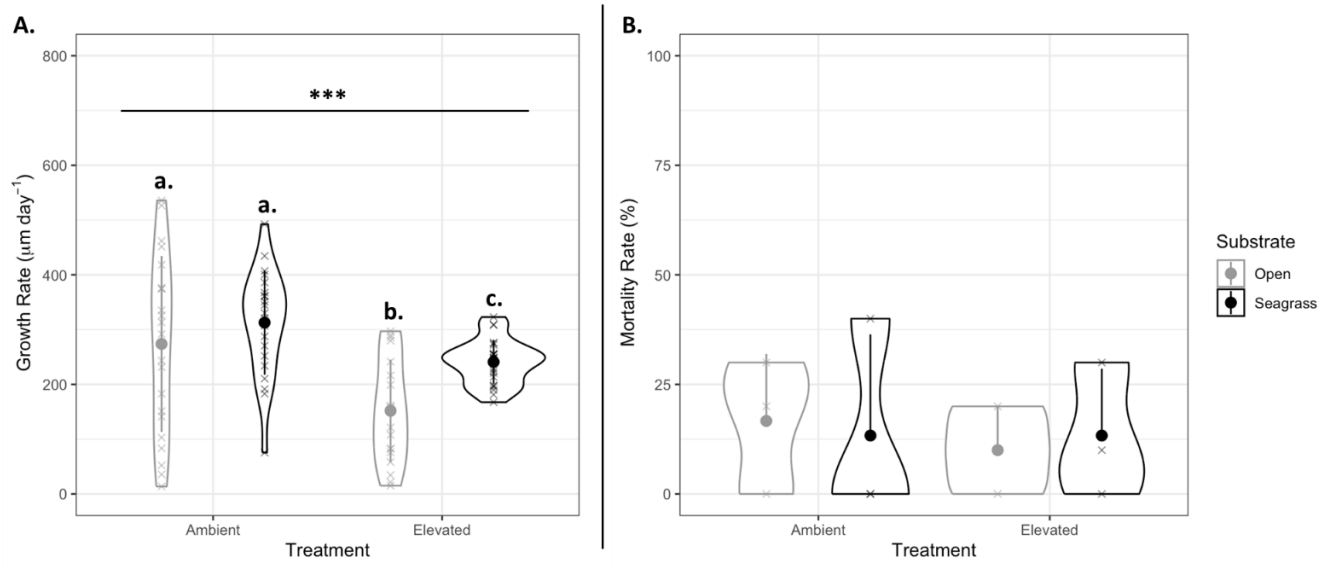

Figure 7: Growth rate and mortality of 11 mm bay scallops as it relates to substrate and treatment. A) Growth rate (µm day^{-1}) of 11 mm bay scallops. Bar indicates a highly significant effect of treatment on growth rate. Pairwise comparisons are noted via lettering. B) Mortality of 11 mm Bay Scallops. No significant effect of treatment or substrate on mortality. *** $p < 0.05$; ** $p < 0.1$; *** $p < 0.001$*

4. Discussion

Experiments capable of manipulating the carbonate system in coastal habitats provide valuable insight into both species and ecosystem responses to predicted, future ocean conditions as well as current coastal ocean acidification. Over a two-year period, an *in-situ* CO_2 enrichment system was used to alter carbonate chemistry and examine the subsequent growth and survival of two bivalve species in two coastal habitats. Results demonstrated that even brief periods of acidification, at levels currently occurring in estuaries (Wallace and Gobler 2021, Wallace et al. 2021) and expected to become more common in the future (Çelekli and Zariç 2024, Doney et al. 2020), significantly decreased the growth and survival of common North Atlantic bivalves. However, the presence of seagrass altered the fate of bivalves exposed to acidification.

The CO_2 enrichment system developed for this project effectively altered carbonate chemistry and maintained a pH offset within the range of conditions predicted for the future coastal ocean (Findlay et al. 2025, IPCC 2013, 2021, Shi and Li 2024) while maintaining the natural diel, tidal, and seasonal variations in the surrounding water column and the ambient

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chambers. Although controlled laboratory experiments have examined bivalve growth and survival under future predicted acidified conditions (Bressan et al. 2014, Pernet et al. 2025, Stevens and Gobler 2018, Thomsen et al. 2015), and field studies have manipulated CO_2 in situ to assess effects on corals and urchins (Barry et al. 2014, Georgiou et al. 2015), no field study has examined bivalve growth and survival under acidified conditions with the carbonate system altered in situ. Though advantageous, the lack of control during such experiments requires accurate characterization of many additional field parameters via intense sampling and integrative high-frequency sensing equipment. This experimental design introduces the diverse range of dynamic (diel, tidal, and seasonal) conditions that organisms experience in their natural habitat and is likely more representative of how organisms will respond under future climate change scenarios compared to static laboratory experiments where a single variable is altered.

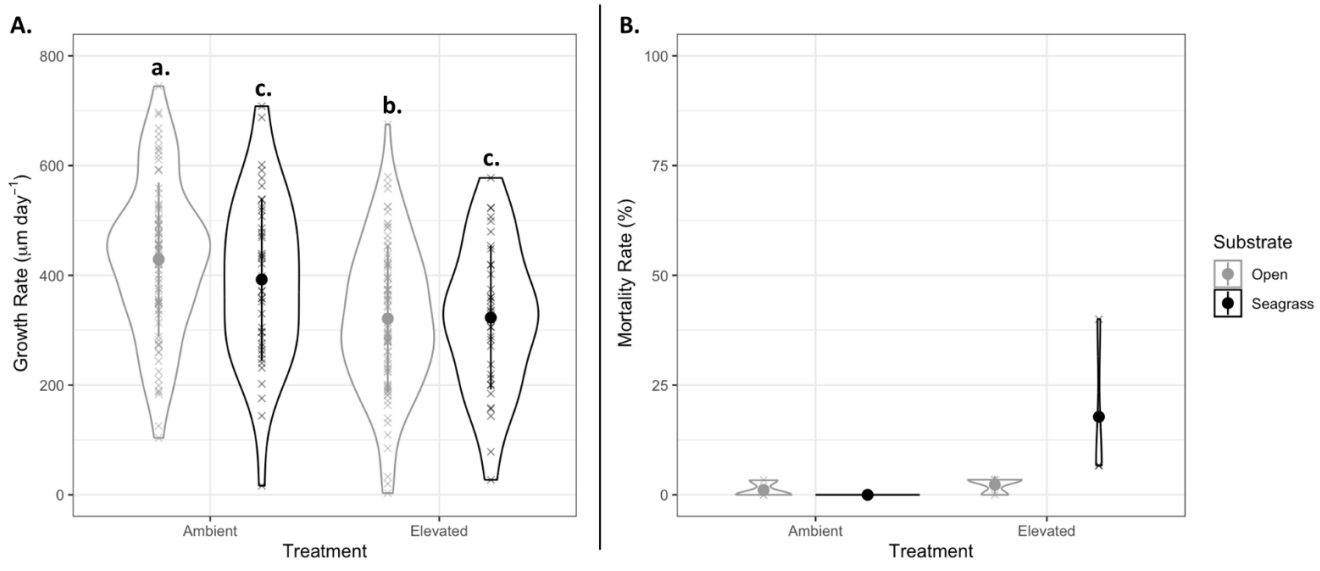

Figure 8. Growth rate and mortality of 10 mm Eastern oysters as it relates to substrate and treatment. A) Growth rate (µm day^{-1}) of 10 mm Eastern oysters. Growth rate was not significantly affected by treatment in the seagrass meadow. B) Mortality of 10 mm Eastern oysters. No significant effect of treatment or substrate on mortality. ***p < 0.05; ** p < 0.1; ***p < 0.001***

4.1 Seagrass CO_2 enrichment experiments

Seagrass beds are typically net autotrophic environments (Caffrey 2004, Wallace et al. 2021), and essential habitats that can both sequester and store carbon (Berg et al. 2019, Duarte et al. 2010). The uptake of CO_2 within seagrass habitats can increase pH of the surrounding seawater, increasing buffering capacity both within seagrass ecosystems and in adjacent habitats (Awaluddin et al. 2025, Cyronak et al. 2018, Hendriks et al. 2014, Ricart et al. 2021b, Unsworth et al. 2012). Beyond the response of organisms living within seagrass beds, understanding the chemical modification of seawater within the beds as acidification intensifies can enable improved ecosystem modeling of future scenarios. Cruises conducted in waters surrounding the seagrass experiment revealed a significantly higher buffering capacity (Rf < 11), or lower Rf, compared with waters surrounding the open water experiment (Rf > 13). Furthermore, regions located farther from the dense beds, yet within

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the same vicinity, showed elevated Rf values, suggesting a potential "halo" effect associated with dense seagrass meadows. Increases in Rf result from the fractional change in pCO_2 in relation to the fractional change in DIC (Egleston et al. 2010, Hauck and Völker 2015, Revelle and Suess 1957). During this study, acidified treatments yielded Rf values comparable to those currently observed in high latitude surface waters, regions that play a critical role in global carbon uptake (Broecker et al. 1979, Feely et al. 2018, Hauck and Völker 2015, Sabine et al. 2004). Although the experimental increase of CO_2 in this system decreased the buffering capacity in the seagrass meadow experiment, increasing the Rf from ~11 to ~16, Rf values remained lower than those in acidified open water treatments, while Ω_{Ar} remained saturated on average. A study by Pacella et al. (2018) reported that under future climate change scenarios (year 2100; IPCC 2013, IPCC 2021), diel ranges of pH_T and pCO_2 will increase but the range of Ω_{Ar} may decrease by > 0.3 units in a temperate seagrass meadow. These modeled results are consistent with observations from acidified chambers during this study, where mean Ω_{Ar} was 1.38 units lower than in ambient chambers, standard deviation decreased by 0.44, and the ranges of pH_T and pCO_2 increased. Although these results indicate that this refuge habitat is susceptible to future acidification, it is likely that unvegetated habitats may be at greater risk and dependent on the system's initial buffering capacity (Cai et al. 2017, Xue et al. 2025). Regardless, the chemical response in both habitat types was sufficient to negatively impact North Atlantic bivalve populations (Grear et al. 2020). Amplitude attenuation of Ω_{Ar} will also likely occur both seasonally and on diel timescales in many coastal regions as increasing pCO_2 reduces carbonate ion (CO_3^{2-}) concentrations resulting in a decreased buffer capacity (Kwiatkowski and Orr 2018, Pacella et al. 2018). Although the anticipated chemical modulations (Pacella et al. 2018) and effects of future acidification in seagrass habitats established here exhibited similarities, the response of submerged aquatic vegetation (SAV) to increasing CO_2 concentrations over extended temporal periods is not fully understood (Palacios and Zimmerman 2007, Takahashi et al. 2015, Ward et al. 2022, Young et al. 2018). Over extended temporal scales, healthy seagrass meadows may mitigate some of the observed carbonate chemistry changes via increased photosynthetic rates, expansion of habitat via increased growth, and carbon sequestration via increased burial rates (Alexandre et al. 2012, Bergstrom et al. 2019, Brodie et al. 2014, Job et al. 2023).

Experiments altering carbonate chemistry within a habitat can indicate the threat of ocean acidification to organisms in an ecosystem setting. Both the seagrass bed in Shinnecock Bay and the open water site in the Peconic Estuary are historically permissive for the robust growth and high survival of the bivalve species examined during this study (Tettelbach et al. 2013, Wall et al. 2013, Wall et al. 2011). When acidified conditions were experimentally applied, however, it resulted in significant declines in the survival of oysters and scallops during August, a period that coincides with other environmental stressors such as decreased dissolved oxygen concentrations (Wallace et al. 2021) and harmful algal blooms (Gobler et al. 2012, Griffith and Gobler 2020). This was especially evident during the seagrass deployment, where both juvenile oysters and the smaller cohort of scallops had significantly higher mortality rates in the acidified treatment. In contrast, there was no significant difference in mortality for the larger scallop cohort, evidencing the size- and age-dependent vulnerabilities of small bivalves to ocean acidification (Clements and George 2022, Cubillas et al. 2005, Green et al. 2004, Stevens and Gobler 2018).

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Despite enhanced mortality of the smaller bivalves in the acidified treatment of the seagrass experiment, the growth rates of the survivors were unaffected by acidification. It is possible that the cohort of bivalves within the experiments contained a range of phenotypes with the surviving individuals being acidification-resistant individuals (Gobler and Talmage 2013, Waldbusser et al. 2016). Alternatively, mortality among the smaller bivalves may have facilitated growth of the remaining live individuals via highly localized, microscale buffering (Curtin et al. 2022, Melzner et al. 2011). This excess shell aggregation may have aided in shell formation and increased growth rates of surviving, neighboring individuals (Gazeau et al. 2007, Waldbusser et al. 2013), potentially highlighting the advantages of shell degradation in providing alkalinity buffering against future acidified conditions (Curtin et al. 2022, Waldbusser et al. 2013, Waldbusser et al. 2011).

4.2 Open water CO_2 enrichment experiments

The response of the carbonate system at the open water site to increased CO_2 differed in comparison to the seagrass site. While the CO_2 injection rates were consistent between sites during the same mid-summer period, a lower buffering capacity at the open water location (seagrass Rf = 11.03; open water Rf = 12.47) made this ecosystem more susceptible to acidification under higher CO_2 levels (Cai et al. 2017, Feely et al. 2018, Xue et al. 2025). Although Ω_{Ar}, and to a lesser extent pH, are important in determining bivalve sensitivities to acidification (Waldbusser et al. 2015), DIC/A_T ratios may be more effective in determining a coastal environments response to increasing atmospheric CO_2, providing valuable insight into mechanisms that can influence the buffer capacity of a given water body (Jiang et al. 2019, Sheu et al. 2009). The DIC/A_T ratio reflects the acid-base equilibrium state of seawater, with higher values indicating a greater fraction of CO_2 within the DIC pool and a more acidified system with reduced buffering capacity (Cai et al. 2020, Egleston et al. 2010). Sheu et al. (2009) found that in the West Philippine Sea, a 2% increase in the DIC/A_T ratio would result in a 10% increase in the Rf. During these experiments, the DIC/A_T ratio was 3% higher in the open water site than in the seagrass meadow, indicating a diminished capacity to withstand anthropogenic acidification (Cai et al. 2020). Another notable contrast between the two study locations was that ambient Ω_{Ar} was significantly lower at the open water site compared to the seagrass site (-0.52 Ω_{Ar}) suggesting that $CaCO_3$ secreting organisms living in the Peconic Estuary are presently more vulnerable to ocean acidification compared to the seagrass site (Waldbusser et al. 2015). In addition, the Rf was 13% greater for the open water site indicating that, along with a lower buffer capacity, the open water site had a lesser capacity to sequester CO_2 (Egleston et al. 2010, Sheu et al. 2009). When compared with the seagrass experiment, the chemical response to increased CO_2 in the open water chambers resulted in lower pH_T (-0.06), lower Ω_{Ar} (-0.19), and higher Rf (+0.36). Furthermore, the pH_T was 0.07 units greater within acidified chambers at the seagrass site, a further indication that the open water estuary was more vulnerable to acidification compared to the seagrass meadow.

The exacerbated response of the open water carbonate system to CO_2 enrichment translated into a significant bivalve response for both stages of juvenile bay scallops. The 5 mm bay scallops survived significantly better in eelgrass meadows when exposed to the acidified treatment. Furthermore, 11 mm scallops grown under acidified conditions in the Peconic Estuary grew significantly slower compared to their seagrass counterparts. Specifically, 11 mm bay scallops grew

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151.9 ± 93.3 µm d^{-1} in the acidified estuary treatment compared to 241.0 ± 40.4 in acidified seagrass treatments. In addition, all bivalve species including Eastern oysters incubated during this study exhibited significantly reduced growth under low pH conditions in the Peconic Estuary. As a large coastal embayment, the Peconic Estuary may be more prone to acidification as atmospheric CO_2 concentrations increase (Li et al. 2023). The Peconic Estuary has a larger potential surface area available for gas exchange coupled with higher ecosystem respiration rates (Wallace et al. 2021) making this system more vulnerable to acidification (Laruelle et al. 2017, Pacella et al. 2018).

Bivalves are differentially susceptible to acidification (Caillon et al. 2023, Gazeau et al. 2013, Ries et al. 2009). During this study, juvenile oysters were generally more resilient to acidification whereas bay scallops seemed to be less tolerant of acidification, a difference that is consistent with laboratory studies exposing scallops to chronic and diel cycles of acidification that emulate natural environmental variations (Kraemer and Gobler 2026, Schwaner et al. 2023, Stevens and Gobler 2018, White et al. 2013). This is particularly relevant given the collapse of the Peconic Bay scallop fishery in 2019–2020, which was one of only four U.S. fisheries, and the sole East Coast fishery, declared a commercial fishery disaster by the U.S. Department of Commerce during 2018–2020 (Tomasetti et al. 2023). A recent study demonstrated that the Peconic Estuary bay scallop population was at a 99% risk of collapse if exposed to pCO_2 levels exceeding 800 µatm (Grear et al. 2020); we documented mean pCO_2 levels approaching 700 µatm during this study, with summer pCO_2 in the western region of the estuary exceeding 800 µatm (Wallace et al. 2021). Given this and the findings presented here, it would seem Eastern oysters are more likely to resist future ocean acidification than bay scallops and thus may be a more appropriate fishery to target for wild harvest and aquaculture within this ecosystem.

4.3 Comparing across habitats: seagrasses provide refugia for juvenile bay scallops

In seagrass meadows, periods of net autotrophy can reduce pCO_2 resulting in carbonate conditions favorable for bivalves (Berg et al. 2019, Chou et al. 2023, Chou et al. 2025, Hendriks et al. 2014), however, such conditions may not be equally beneficial for all organisms. A recent study by Cossa et al. (2024) observed reduced growth rates of *Echinus esculentus* larvae when exposed to low pH conditions in the presence of seagrass, despite enhanced daytime calcification. In another study, this same species was found to have increased growth and survival under oscillating pH conditions when compared to static low pH conditions (Duvane and Dupont 2024). Consistent with these findings, juvenile scallop mortality during this study was significantly higher under depressed pH conditions at the open water site, despite this location exhibiting a more stable carbonate chemistry regime than the seagrass meadow. Seagrass meadows can mitigate the effects of ocean acidification during daylight hours but may enhance acidification during nighttime respiration (Scott-Askin et al. 2025, Wallace et al. 2021).

Seagrass meadows have been identified as a net source of A_T, thereby buffering the water column against increasing CO_2 concentrations (Scott-Askin et al. 2025). During the spatial mapping cruises, A_T was significantly higher within the seagrass bed. When CO_2 was introduced to the acidified seagrass chambers, mean A_T increased significantly, leading to a reduced difference between A_T and DIC (208.12 à 50.91 mol kg^{-1}). The difference between A_T and DIC ([A_T – DIC]) is often

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used as a proxy for buffering capacity of an ecosystem (Scott-Askin et al. 2025, Xue and Cai 2020). In the open water site, A_T remained relatively stable as DIC increased in the acidified chambers, decreasing [A_T – DIC] from 156.23 to 28.57 mol kg^{-1}. As anthropogenic CO_2 increases in the atmosphere, DIC will increase but A_T will not be affected, subsequently reducing [A_T – DIC] (Xue and Cai 2020). This reduction may be limited in seagrass habitats by A_T generation from seagrass beds and the surrounding sediment (Scott-Askin et al. 2025). The sediment in and around the seagrass beds examined during this study has higher organic carbon content than the open water site, and this may have contributed to a higher A_T flux as CO_2 increased (Chou et al. 2025, Lowell et al. 2026, Song et al. 2023). Elevated A_T at the seagrass site likely promoted higher growth rates of *A. irradians* and *C. virginica* in the acidified seagrass chambers relative to the acidified open-water chambers by increasing calcification rates, a process known to be influenced by ambient DIC and A_T (Comeau et al. 2017, Thomsen et al. 2015).

4.4 Managerial implications of in situ CO_2 enrichment experiments

Characterizing modulations in carbonate chemistry as well as the response of organisms to future climate stressors enables managers to better respond as habitats are altered. In situ chemical alterations can be considered an initial phase in the development of approaches for managing coastal species and ecosystem changes. In addition, these experimental systems may be altered to provide conditions more suitable for the growth of estuarine organisms (increase in DO and/or pH) further aiding managers and potentially commercial growers as future conditions begin to intensify as predicted (IPCC 2021). Collectively, the in-situ CO_2 enrichment experiments demonstrated the ability of seagrass beds to provide bivalve populations a refuge when exposed to acidification. As such, efforts to expand seagrass meadows in estuaries will provide resilience to bivalve populations as climate change intensifies this century. Moreover, the increased vulnerability of bay scallops to acidified conditions compared to Eastern oysters suggests oysters will be a more appropriate fishery target for aquaculture and restoration efforts as climate change advances in these estuaries.

4.5 Managerial implications of in situ CO_2 enrichment experiments

Estuarine systems are diverse, critical habitats that exhibit unique chemical responses to anthropogenic stressors that, in turn, alter bivalve growth and survival. Here, experimental acidification of coastal habitats significantly depressed growth rates and increased mortality of juvenile oysters and bay scallops during summer months. In larger temperate estuaries, bivalve populations may be especially vulnerable to increasing atmospheric CO_2 concentrations, facilitating CO_2 uptake and dissolution into water bodies that may be experiencing seasonal pH and DO minima. Many eutrophic estuaries are already experiencing acidification during the late summer which can negatively affect the growth and survival of juvenile bivalves. As anthropogenically induced global climate variations intensify and alter ocean chemistry, the likelihood of adverse impacts on populations of calcium carbonate secreting organisms in coastal zones will increase. Here, the comparative deployment of the in situ experimental CO_2 chambers across habitat types indicated seagrasses will represent an important refuge habitat for some bivalves as climate change accelerates.

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Author contributions

RW, RA, AL and CG designed the experiments, and RW, RA, and AL carried them out. RW prepared the manuscript with contributions from all co-authors.

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