







SPECIAL FEATURE:
HONORING CHARLES H. PETERSON, ECOLOGIST

Bivalve facilitation mediates seagrass recovery from physical disturbance in a temperate estuary

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Abstract. Rapid global degradation of coastal habitats can be attributed to anthropogenic activities associated with coastal development, aquaculture, and recreational surface water use. Restoration of degraded habitats has proven challenging and costly, and there is a clear need to develop novel approaches that promote resilience to human-caused disturbances. Positive interactions between species can mitigate environmental stress and recent work suggests that incorporating positive interactions into restoration efforts may improve restoration outcomes. We hypothesized that the addition of a potential facultative mutualist, the native hard clam (*Mercenaria mercenaria*), could enhance seagrass bed recovery from disturbance. We conducted two experiments to examine the independent and interacting effects of hard clam addition and physical disturbance mimicking propeller scarring on mixed community *Zostera marina* and *Halodule wrightii* seagrass beds in North Carolina. Adding clams to seagrass beds exposed to experimental disturbance generally enhanced seagrass summer growth rates and autumn shoot densities. In contrast, clam addition to non-disturbed seagrass beds did not result in any increase in seagrass growth rates or shoot densities. Clam enhancement of autumn percent cover relative to areas without clam addition was most prominent after Hurricane Dorian, suggesting that clams may also enhance seagrass resilience to repeated disturbances. By June of the next growing season, disturbed areas with clam additions had greater percent cover of seagrass than disturbed areas without clam additions. Beds that were disturbed in April had higher percent cover than areas disturbed in June of the previous growing season. Our results suggest that the timing and occurrence of physical disturbances may modify the ability of clams to facilitate seagrass resiliency and productivity. Understanding when and how to utilize positive, interspecific interactions in coastal restoration is key for improving restoration success rates.

Key words: bivalve; coastal restoration; disturbance; facilitation; propeller scar; seagrass; Special Feature: Honoring Charles H. Peterson; Ecologist.

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INTRODUCTION

A rising awareness of the declining health and functioning of the planet's coastal ecosystems has occurred in recent years (Jackson et al. 2001, Lotze et al. 2006, Worm et al. 2006, Oliver et al. 2015). Coastal habitat loss is driven in part by an increasing number of natural and anthropogenic disturbances that can hinder ecosystem service provision or result in total ecosystem loss (Short and Wyllie-Echeverria 1996, Halpern et al. 2008). As coastal habitats become increasingly degraded or lost entirely, the need to develop novel and effective restoration techniques is clear (Waycott et al. 2009, Beck et al. 2011, Cullen-Unsworth and Unsworth 2016). To recover vital ecosystem functions and services, researchers and practitioners have invested in a variety of approaches to restore coastal ecosystems, but an understanding of how to ensure long-term sustainment and resilience of restored ecosystems has lagged behind (Lotze et al. 2006, van Katwijk et al. 2009, Zhang et al. 2018).

Improving restoration outcomes for foundation species (*sensu* Dayton 1972) is of particular interest to restoration ecologists (Byers et al. 2006, van Katwijk et al. 2009, Gedan et al. 2014). Foundation species play a large role in maintaining their habitat, in part by incorporating facilitative and mutualistic interactions to ameliorate abiotic and biotic stressors to create favorable conditions within the system (Dayton 1972). As foundation species, seagrasses benefit both human and natural communities via the provision of many ecological functions, including providing refuge and food for juvenile and adult animals (Heck and Orth 1980, Peterson et al. 1984, Peterson 1986, Heck et al. 1997, Heck and Valentine 2006, Goshima and Peterson 2012); stabilizing sediments and reducing erosion (Fonseca and Fisher 1986, Potouroglou et al. 2017); reducing flow and attenuating wave energy to protect nearshore habitats and infrastructure (Fonseca et al. 1982, Peterson et al. 2004, de Boer 2007); storing carbon (McLeod et al. 2011, Fourqurean et al. 2012); and reducing human and marine pathogens in the water column (Lamb et al. 2017). Degradation and loss of seagrasses are so severe that it has been dubbed a "global crisis" (Orth et al. 2006); thus, restoration efforts have increased dramatically in recent decades, but

seagrass restoration has proven to be both challenging and costly (Cunha et al. 2012, Bayraktarov et al. 2015, van Katwijk et al. 2016).

Restoration is particularly difficult in areas where seagrass has been entirely lost or where environmental quality has degraded to the point that the site is no longer suitable for the establishment of seagrasses (van Katwijk et al. 2009). Attempts to restore or accelerate recovery in seagrasses impacted by small-scale disturbances, such as propeller scarring, have included nutrient addition, supplemental planting of colonizing species, and biophysical stabilization, with varied success (Hall et al. 2006, Marion and Orth 2010, Kenworthy et al. 2018). Although often relatively small in scale, propeller scarring in seagrass beds can cause substantial economic and ecological losses, particularly when beds are exposed to repeated scarring events or to both scarring and major storms, such as hurricanes (Fonseca and Bell 1998, Whitfield et al. 2002, Engeman et al. 2008, Orth et al. 2017). For example, propeller scars in Florida exposed to a strong hurricane grew in size by 63% and only 11% of the seagrass coverage returned five years after the hurricane (Whitfield et al. 2002). These repeated disturbances can create physical instability in seagrass beds by uprooting shoots and severing rhizome connections, making them more vulnerable to further disturbances. For these beds, recovery is often slower than the initial decline, in some cases making it nearly impossible for a seagrass bed to recover naturally (Scheffer et al. 2001, Beisner et al. 2003, O'Brien et al. 2017). It is therefore critical to develop and rigorously test conservation approaches which improve local environmental conditions and promote the resilience of existing habitats to disturbance in order to maintain the ecosystem's ecological and economic value (Reynolds et al. 2016).

There is a growing movement among coastal restoration researchers and practitioners to understand which ecological relationships and functions provide innate resiliency and prevent significant degradation and loss of habitats experiencing stress (Silliman et al. 2015, Derksen-Hooijberg et al. 2017, Renzi et al. 2019). For example, several studies have shown that mussels promote saltmarsh resiliency to and recovery from physical and climatic disturbances via deposition of nutrient-rich waste and providing

structure which reduces soil salinity stress and enhances water storage capacity (Angelini et al. 2016, Derksen-Hooijberg et al. 2017). Many of the seagrass restoration strategies most widely employed today, including large-scale planting or seeding (Marion and Orth 2010) and use of laboratory-germinated seeds (Bird et al. 1994), are reactive practices designed to be implemented after the habitat has already been severely degraded or lost entirely. However, the proactive incorporation of positive, interspecific interactions into seagrass conservation and restoration (Zhang et al. 2021) after small-scale disturbances may have the potential to change the trajectory of recovery for seagrass ecosystems.

Several seagrass and bivalve species interact positively with one another as facultative mutualists (Boström et al. 2006). Seagrass beds benefit associated bivalves by serving as a refuge from predation, providing a source of sediment oxygen, and minimizing exposure to bacterial pathogens (Peterson et al. 1984, Wall et al. 2008, Goshima and Peterson 2012, Lamb et al. 2017). The hard clam, *Mercenaria mercenaria*, has been shown to have elevated survivorship and densities within *Zostera marina* beds relative to those within adjacent unvegetated substrate (Peterson et al. 1984, Peterson 1986, Irlandi 1997). Bivalves, in turn, have been shown to increase seagrass productivity and survivorship in some cases (Reusch et al. 1994, Peterson and Heck 2001a, Gagnon et al. 2020). Bivalves benefit seagrasses by enhancing sediment nutrient content via the biodeposition of feces and pseudofeces, thereby potentially fertilizing seagrasses (Reusch et al. 1994, Peterson and Heck 1999, 2001b, Newell and Koch 2004, Lotze et al. 2006). Bivalves also enhance water column clarity via suspension feeding, which allows for increased light penetration and higher seagrass photosynthetic and growth rates (Wall et al. 2008). Additionally, by providing habitat for epiphytic grazers and directly feeding on epiphyte propagules in the water column, bivalves can also help control eutrophication and algal blooms, thereby reducing deleterious fouling on seagrass blades (Peterson and Heck 2001a, Cerrato et al. 2004). In some seagrass beds, lucinid bivalves host sulfide-oxidizing bacteria in their gills which reduces the levels of toxic sulfide in the sediment and enhances seagrass aboveground biomass by

alleviating sulfide intrusion (van der Heide et al. 2012, van der Geest et al. 2020).

To determine whether artificial enhancement of the densities of *M. mercenaria*, a bivalve commonly found in seagrass beds within North Carolina's estuarine waters (Peterson et al. 1984), could facilitate seagrass bed resilience to disturbance, we conducted two experimental studies examining the independent and interacting effects of bivalve facilitation and physical disturbance on seagrass productivity and recolonization of disturbed areas. We proposed the following hypotheses: (1) The addition of *M. mercenaria* to undisturbed beds would increase seagrass productivity relative to control beds; (2) the addition of *M. mercenaria* to disturbed beds would increase seagrass productivity relative to disturbed beds without *M. mercenaria* addition; and (3) seagrass with clam additions would recolonize disturbed areas more rapidly and extensively than seagrass in disturbed areas without clam additions. Further, because past studies have confirmed that severe storms can act as repeated disturbances that cause propeller scars to expand or persist (Fonseca and Bell 1998, Whitfield et al. 2002), we also sampled before and after Hurricane Dorian, a Category 1 hurricane, to determine how seagrass percent cover was affected by the storm in our experimental treatments.

METHODS

Study area

We conducted two experiments in mixed community seagrass beds in Back Sound, North Carolina (Fig. 1). Both experimental sites are well-flushed, nutrient-limited systems with excellent water quality (NCDEQ 2018). Back Sound is a shallow, temperate estuary dominated by soft-sediment bottom; *Zostera marina* and *Halodule wrightii* are the dominant seagrass species present, although *Ruppia maritima* was seasonally abundant (Micheli et al. 2008; Appendix S1: Fig. S1). Our study sites are unique because Back Sound is located in the narrow band where *Z. marina* and *H. wrightii* range distributions overlap. *Z. marina* is a temperate species, ranging from the Arctic to North Carolina, and experiences seasonal summer heat stress at our study site which causes declines in growth rate and cover throughout the summer (Thayer et al. 1984). Although *Z. marina* is the

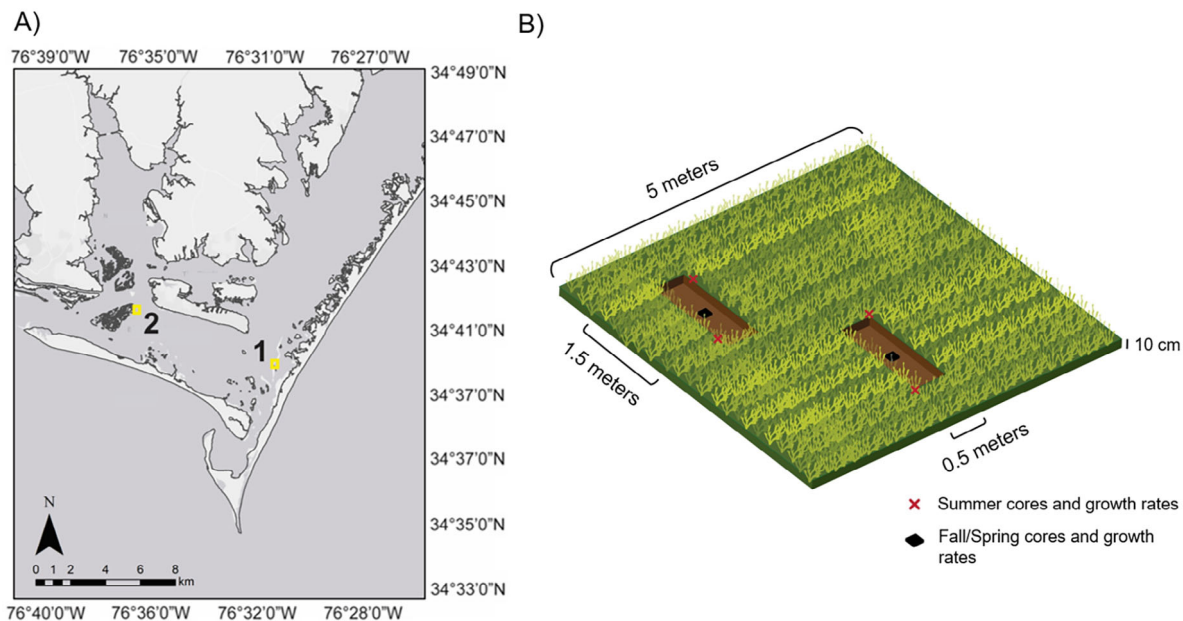


Fig. 1. (A) Back Sound, North Carolina, USA, showing the location of Experiment 1 and Experiment 2 and (B) the experimental setup of Experiment 2; two subplots with dimensions of 1.5 m \times 0.5 m were set up within each larger 25-m² experimental plot; for the disturbance treatments, the subplots were excavated to a depth of 0.1 m, and for clam addition treatments, clams were added along the border of each subplot. Summer 2019 growth rates and cores were sampled directly adjacent to the subplot edge. Fall 2020 and spring 2020 percent cover and cores were sampled from within the subplot interior.

dominant species in our beds until early June, *Z. marina* shoots were sparse by July in both of our experiments; therefore, July *Z. marina* growth and biomass samples could not be collected for some replicates. Conversely, *H. wrightii* is a tropical species which exists at its northern thermal limit in North Carolina and experiences increased growth, canopy height, and cover beginning in early June (Thayer et al. 1984, Zhang et al. 2021; S. E. Donaher, *personal observation*). Both of the experimental meadows consisted of annual *Z. marina* growth forms which senesce in late summer and rely on seed banks to regrow in the early spring and mixed annual-perennial *H. wrightii* which reaches a peak in mid-summer (Thayer et al. 1984, Jarvis et al. 2012).

The clam addition only experiment (Experiment 1 herein) was located in a large contiguous intertidal seagrass bed near Cape Lookout, NC (34.668121, -76.509455), and the clam addition and disturbance experiment (Experiment 2 herein) were located in a moderately sized subtidal bed in the Rachel Carson Estuarine Reserve,

Beaufort, NC (34.698799, -76.595439; Fig. 1). To document the spatial characteristics of the experimental areas, we mapped the extent of the contiguous seagrass bed and the coordinates of the experimental plots and subplots with a Trimble R10 Integrated GNSS system in May 2018, June 2018, and July 2019 for Experiment 1 and April 2019 and July 2019 for Experiment 2 in the NAD83 coordinate system (Fig. 2). Elevation, used as a proxy for water depth, was measured and analyzed as a covariate in our analyses because depth has been shown to be an important variable controlling seagrass distribution, biomass, and growth (Duarte 1991, Enríquez et al. 2019). For Experiment 1, plot elevation ranged from -0.57 to -0.43 m with an average depth of -0.54 m relative to the North American Vertical Datum of 1988 (NAVD88). For Experiment 2, plot elevation ranged from -0.76 to -0.53 m with an average depth of -0.62 m NAVD88. We used Environmental Systems Research Institute (ESRI) ArcMap (version 10.3.2) to create maps and process elevation data.

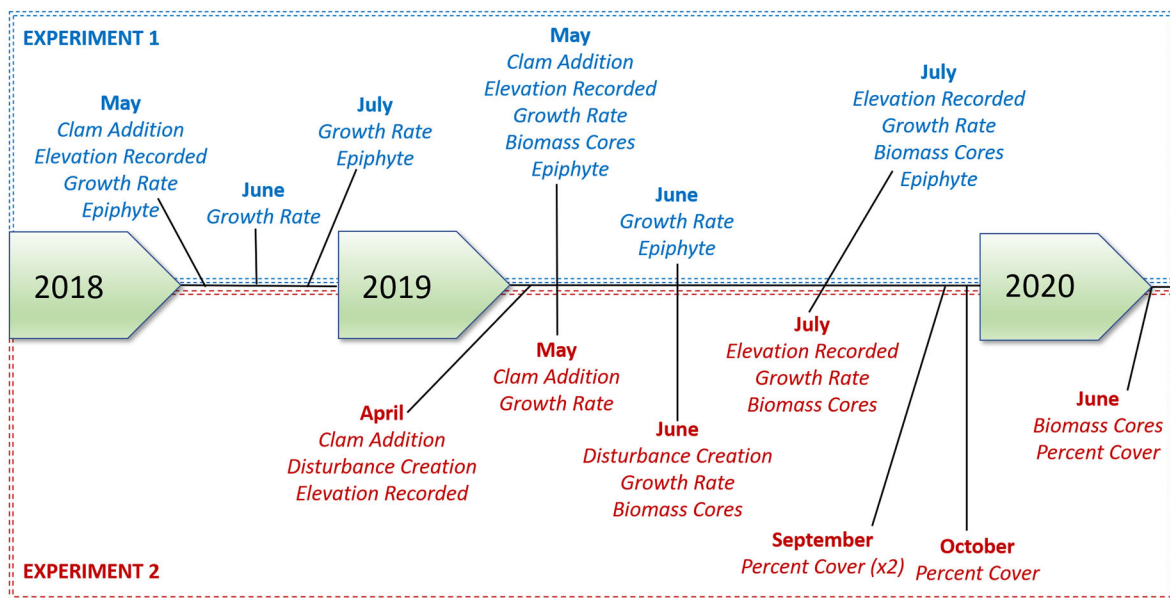


Fig. 2. A timeline of all experimental treatments and sampling. Experiment 1 (in blue) ran from May 2018 to July 2019 and Experiment 2 (in red) ran from April 2019 to June 2020.

Experiment 1

Experimental design and setup.—For Experiment 1, we examined the effects of adult *M. mercenaria* addition on summer seagrass growth rates, shoot densities, biomass, and epiphytic loads for both *Z. marina* and *H. wrightii*. Clams already in the bed were not removed. Both treatments (clam addition and control) had sixteen replicates for a total of thirty-two independent plots, each with an area 1 m². All clams for this experiment were collected from North River Marsh, NC, or Middle Marsh, NC, in 2018 or 2019; only clams between 100 and 300 g were used. Clams were added in May 2018 (2200 ± 100 g of wet clam biomass with shells per plot; 10 clams total) and May 2019 (2053 ± 41 g of wet clam biomass with shells per plot; 10 clams total). Clams were placed on the sediment and allowed to burrow autonomously. Adult *M. mercenaria* are known to be sedentary and do not exhibit large horizontal movement (Roberts et al. 1989). All sampled shoots were selected from within the experimental plots for this experiment (Fig. 1).

Field sampling.—1. *Biomass cores.*—Biomass cores were taken from near the center of each plot in May 2019 and July 2019 and analyzed for

Z. marina and *H. wrightii* shoot density, above-ground biomass, and belowground biomass (Fig. 2). For all core samples, we used a metal corer with a diameter of 10 cm that was pushed into the sediment to a depth of 15 cm. The core was extracted and sieved in the field to remove sediment, shells, and faunal biomass and stored frozen until processing. All cores were processed within sixty days of collection. To process, cores were thawed under warm running water and then carefully separated into the following categories: aboveground *Z. marina* biomass, aboveground *H. wrightii* biomass, and belowground biomass from both species as it was not possible to distinguish belowground biomass between the two species. Shoot count for each species was recorded for each core. Biomass samples were dried in a Fisher Scientific 180-L gravity convection oven at 60°C until fully dry and then massed.

2. *Growth rates.*—We measured summer growth rates for *Z. marina* and *H. wrightii* in 2018 and 2019 for Experiment 1. To quantify *Z. marina* growth rate, we used the leaf marking technique first put forth by Zieman (1974) and modified by Dennison (1990). A random location was selected within the treatment plot, and all *Z. marina*

shoots within a three-inch diameter of that random location were pricked completely through the sheath below the meristem using a pushpin. Marked shoots were collected fourteen days later, as this is on the order of the plastochrone interval, or the time required for the appearance of new growth, for the leaves of both species (15.3 d for *Z. marina* and 16.5 d for *H. wrightii*; Hemminga and Duarte 2000). Samples were brought back to the University of North Carolina's Institute of Marine Science (UNC IMS) where they were processed within twenty-four hours. Up to five shoots were used for each treatment plot or subplot per sampling point. New growth was defined as any tissue below the scar created from the pushpin puncture and was separated from the old biomass. Belowground biomass was discarded. Samples were dried in a Fisher Scientific 180-L gravity convection oven at 60°C until fully dry and then weighed. The growth rate (GR) was calculated as:

$$\text{GR} = \frac{\text{new biomass (g)}}{(\text{number of shoots} \times \text{days between pricking and collection})} \quad (1)$$

Due to the small size of *H. wrightii*, it was not possible to mark leaves using the method described above, and thus, we used the clipping method from Virnstein (1982). A location within the plot was selected randomly during each sampling point and the shoots were trimmed with scissors flush to the sediment in a triangular area roughly ~40 cm². The trimmed area was marked, and we returned after fourteen days to collect trimmed shoots for processing in the laboratory. Up to five shoots per plot or subplot were processed. Growth was determined from the average height of all processed shoots.

3. *Epiphytic load*.—We estimated the epiphytic load on *Z. marina* and *H. wrightii* shoots using epiphytic chlorophyll *a* as a proxy (see Parsons et al. 1984) in May 2018, July 2018, May 2019, June 2019, and July 2019 (Fig. 2). We haphazardly selected four individual seagrass blades of each species from each plot (except for *Z. marina* during both July sampling points, where only one shoot was collected due to few *Z. marina* shoots remaining in the meadow and the high load of epiphytic biomass on the *Z. marina* shoots by this point in the summer). Shoots were

carefully floated into a Ziploc bag with a small amount of seawater and stored in a cool, dark container for transport to UNC IMS and processed within twenty-four hours.

In the laboratory, each sample was transferred to a sorting pan with a small amount of filtered seawater. Blades were carefully scraped to remove all epiphytes using a glass microscope slide, and the total surface area of each blade was recorded. The epiphytes and seawater were vacuum-filtered through a Whatman GF/F 0.7-μ filter and frozen for no longer than eight weeks before they were extracted. The filters were sonicated in 90% acetone for sixty seconds and extracted for 12–24 h in a freezer. Chlorophyll *a* concentration was measured on a Turner Designs Trilogy Laboratory Fluorometer, and chlorophyll concentrations were normalized to seagrass surface area.

Experiment 2

Experimental design and setup.—For Experiment 2, we examined the independent and interacting impacts of a disturbance simulation of physical excavation (similar in size and shape to propeller scars caused by recreational vessels) and addition of adult *M. mercenaria* on seagrass productivity and recovery. Each treatment (clam-only, disturbance-only, clam and disturbance crossed, and control) had eight replicates for a total of thirty-two independent plots. Each square plot was 25 m² and within each plot were two 0.75-m² subplots where all treatments were applied and sampling was conducted (Fig. 1). Physical disturbance in the subplots of the disturbance-only or clam and disturbance treatments was administered by excavating the entire subplot by hand to a depth of 10 cm and until all seagrass biomass was removed. To determine the effects of disturbance timing on recovery, one subplot within the larger plot was excavated during April 2019 (hereinafter referred to as the early-season disturbances) and one subplot was excavated in June 2019 (hereinafter referred to as the late-season disturbances). Any resident or experimental clams recovered during excavation were returned to the subplot. All excavations were conducted under CAMA permit #01-2019 and NERRS permit #4-2019.

Clams were added in April and May 2019 along the border of the subplots of the clam-only or clam and disturbance crossed treatments with

a total of 3873 ± 206 g/plot of wet clam biomass (with shells; 20 clams total). All clams for this experiment were collected from North River Marsh, NC, or Middle Marsh, NC, in 2019 and weighed between 100 and 400 g. As in Experiment 1, clams were placed on the sediment and permitted to self-bury. Sampling for 2019 seagrass growth rates and biomass cores was conducted directly adjacent to the edge of the 0.75-m² treatment subplots in the remaining seagrass and sampling of the fall 2019 and spring 2020 biomass cores and percent cover were conducted within the 0.75-m² treatment subplot (Fig. 1).

Field sampling.—1. *Biomass cores.*—Biomass cores were taken in June 2019, July 2019, and June 2020 and analyzed for *Z. marina* and *H. wrightii* shoot density, aboveground biomass, and belowground biomass (Fig. 2). Cores from the first year of the experiment were taken from the outside edge of subplots to determine the effects of disturbance and clam addition on neighboring shoots. Cores taken in June 2019 were collected from 1.5-month-old early-season disturbance subplots; July 2019 cores were collected from 1-month-old late-season disturbance subplots. At the conclusion of the experiment in June 2020, seagrass had recolonized to some extent into all disturbed subplots; therefore, cores for aboveground and belowground biomass and shoot densities were taken from within all subplots. Sample processing protocol was the same as described for Experiment 1.

2. *Growth rates.*—Growth rates for *Z. marina* and *H. wrightii* were measured in Summer 2019 following similar protocols to Experiment 1. To quantify *Z. marina* growth rate, a random location was selected along the outside edge of the subplots and all *Z. marina* shoots within a three-inch diameter of that random location were pricked completely through the sheath below the meristem. For *H. wrightii*, a random location along the outside edge of the subplot and the shoots were trimmed with scissors flush to the sediment in a triangular area roughly ~40 cm².

3. *Percent cover.*—We estimated seagrass percent cover to assess seagrass regrowth into experimentally disturbed areas and compared it to percent cover of non-disturbed areas with and without clam additions. Percent cover of the entire subplot was recorded three times in the fall of 2019 (3 September, 16 September, and 2

October) and once in the spring of 2020 (6 June) (Fig. 2). Between the two September sampling points, Hurricane Dorian made landfall along the North Carolina coast as a Category 1 hurricane on 6 September 2019.

Statistical analyses

All statistical analyses were performed in R statistics software version 4.0.0 (R Core Team 2014). Prior to all analyses, Shapiro-Wilk's and Levene's tests were performed to ensure that data met the assumptions of normal distribution and homogeneity of variance, respectively. Growth data for *Z. marina* in Experiment 2 were found to violate both assumptions. A square-root-transformation was applied to this data, diagnostic tests were re-run, and it was confirmed that the transformed data conformed to assumptions of the planned parametric analyses.

For Experiment 1, separate analysis of covariance (ANCOVA) tests were used to examine the effects of the categorical variable of treatment (clam addition or control) and the continuous covariate of elevation on *Z. marina* and *H. wrightii* growth rate, aboveground biomass, epiphytic load, and combined species belowground biomass. For Experiment 2, separate ANCOVA tests for the late- and early-season disturbances were used to test for the effects of the two categorical treatment variables (clam addition and disturbance presence) and the continuous covariate of elevation on *Z. marina* and *H. wrightii* growth rate, aboveground biomass, and combined species belowground biomass directly adjacent to the subplots for all 2019 sampling. The same procedure was used to analyze the percent seagrass cover and 2020 biomass cores within the subplots. Occasionally, replicate samples were not able to be collected or analyzed for each response variable due to uncontrollable circumstances (i.e., unable to locate subplots in inclement weather, oven malfunction, etc.). All ANCOVA tests were conducted using the *lm* function within the built-in R package *stats*. Where significant (<0.05 or <0.1 level) independent or interaction terms were detected, Tukey's test for post hoc multiple comparison analysis for fixed effects was conducted using the *multcomp* procedure for simultaneous inferences in general parametric models from the R package of the same name (Hothorn et al. 2008).

RESULTS

Biomass cores

In Experiment 1, one year after the experiment was initiated, the shoot density, aboveground biomass, and belowground biomass of both seagrass species trended higher in clam addition plots in May, but not in July; however, these differences were not statistically significant (Fig. 3; Appendix S1: Table S1).

In Experiment 2, during June 2019 sampling of early-season disturbances (i.e., disturbances created in April), aboveground *Z. marina* biomass was lowest adjacent to disturbances with clam addition and highest adjacent to disturbances without clam additions ($P = 0.06$; Fig. 4i; Appendix S1: Table S2). Late-season disturbances (i.e., disturbances created in June) were associated with reduced adjacent *Z. marina* shoot densities ($P = 0.049$; Fig. 4b) but increased adjacent *H. wrightii* shoot densities ($P = 0.056$; Fig. 4f; Appendix S1: Table S2) in July 2019. Clam addition, regardless of disturbance, had the opposite effect of disturbance and was associated with significantly lower adjacent *H. wrightii* shoot densities in July 2019 ($P = 0.026$; Fig. 4f). June 2019 combined species shoot density marginally increased with increasing elevation ($P = 0.079$; Appendix S1: Fig. S2, Table S2).

By June 2020, *Z. marina* shoot densities and aboveground biomass within early-season disturbed subplots with and without clam additions were comparable to control and clam addition subplots (Fig. 4c,k). Late-season disturbances had higher *Z. marina* aboveground biomass and shoot densities than control or clam addition subplots (aboveground biomass, $P = 0.020$; shoot density, $P = 0.090$; Fig. 4d,i). *H. wrightii* shoot densities in disturbance subplots were not statistically different than control or clam addition subplots (Fig. 4g,h). *H. wrightii* aboveground biomass in both early- and late-season disturbance subplots without clam addition was lower than control subplots (early season, $P = 0.073$; late season, $P = 0.012$; Fig. 4o,p). Combined species belowground biomass was lower in control subplots than clam-only and disturbance-only subplots for both early- and late-season disturbances (early-season, $P = 0.006$; late-season, $P = 0.080$; Fig. 4s,t; Appendix S1: Table S2). June 2020 *H. wrightii* aboveground biomass and shoot density in

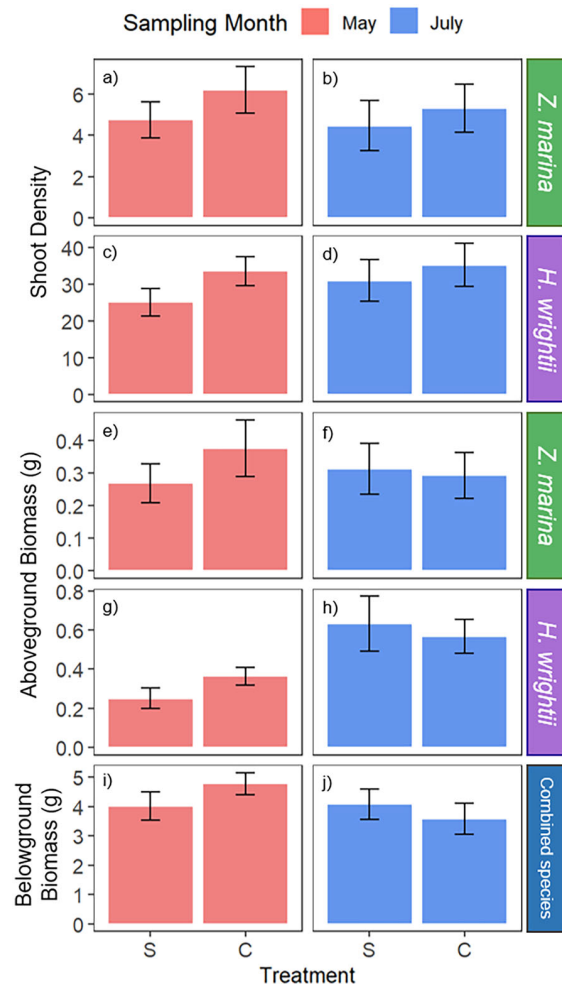


Fig. 3. Experiment 1 biomass cores (78.5 cm²) by treatment (S—control; C—clam addition) taken in May 2019 (left column) and July 2019 (right column) for (a, b) *Z. marina* shoot density, (c, d) *H. wrightii* shoot density, (e, f) *Z. marina* aboveground biomass, (g, h) *H. wrightii* aboveground biomass, and (i, j) combined species belowground biomass. Bars represent standard error.

late-season disturbances increased with increasing elevation (aboveground biomass, $P = 0.048$; shoot density, $P = 0.048$; Appendix S1: Table S2).

Growth rates

For Experiment 1, there was no effect of clam addition on summer growth rates except for *H. wrightii* growth in May 2019, where clam addition plot growth rates were 10% lower

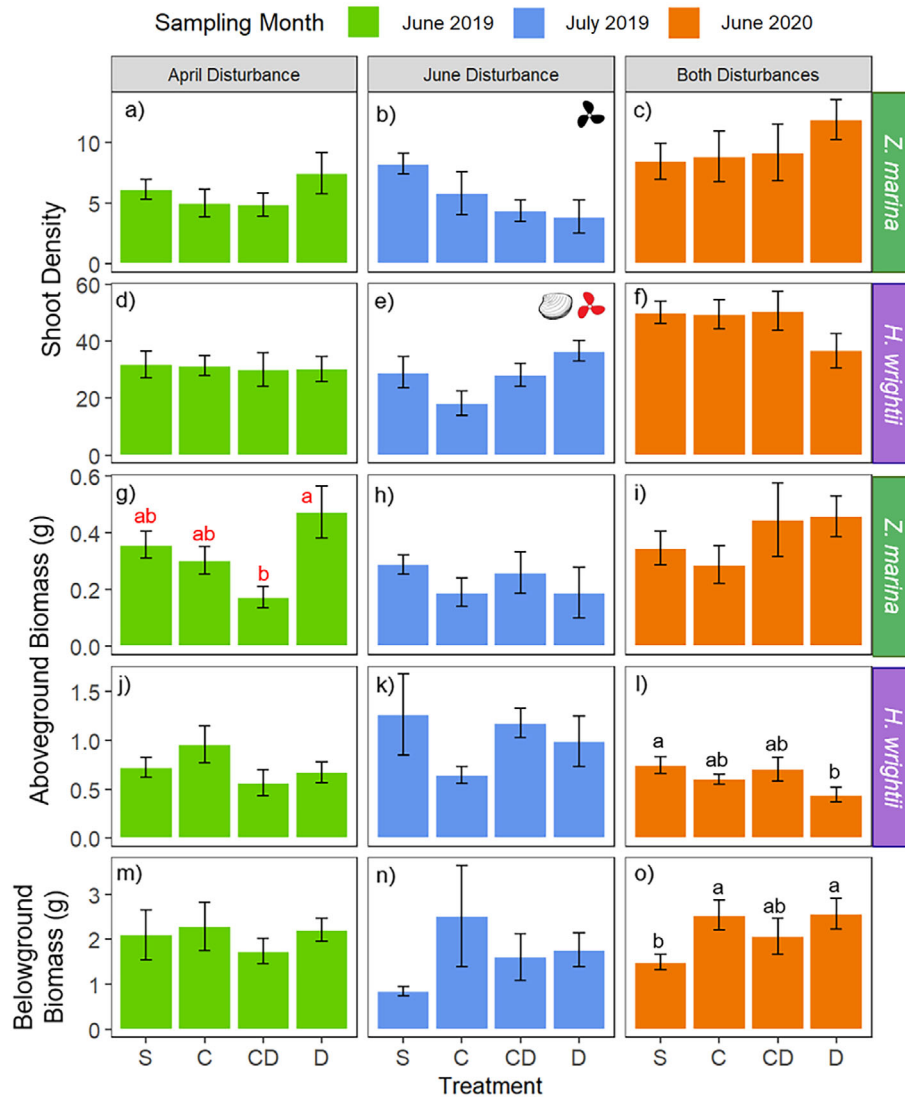


Fig. 4. Experiment 2 biomass cores (78.5 cm²) by treatment (S—control; C—clam addition; CD—clam/disturbance; D—disturbance only) taken in (left) June 2019 for April disturbances, (middle left) June 2019 for June disturbances, (middle right) June 2020 for April disturbances, and (right) June 2020 for June disturbances for (a–c) *Z. marina* shoot density, (d–f) *H. wrightii* shoot density, (g–i) *Z. marina* aboveground biomass, (j–l) *H. wrightii* aboveground biomass, and (m–o) combined species belowground biomass. The clam symbol indicates there was a statistically significant effect of clam addition at the 0.05 significance level. The propeller image indicates there was a statistically significant effect of disturbance at an alpha of 0.05 (black) or 0.10 (red). Lowercase letters indicate clam and disturbance treatment interaction at alpha of 0.05 (black) or 0.10 (red).

relative to control plots ($P = 0.027$; Appendix S1: Fig. S3, Table S3). *Z. marina* growth rates increased with decreasing elevation in July 2018 ($P = 0.050$) and May 2019 ($P = 0.043$), and *H. wrightii* growth rates increased with decreasing

elevation in July 2019 ($P = 0.004$; Appendix S1: Fig. S4, Table S3).

In Experiment 2, disturbances with clam addition had qualitatively higher adjacent *Z. marina* growth rates than disturbances without clam

addition for both disturbances across all sampling months, although this was only statistically significant for early-season disturbance subplots sampled in May ($P = 0.027$; Fig. 5; Appendix S1: Table S4). *Z. marina* growth rates were lower adjacent to disturbances without clams than control subplots for early-season disturbances sampled in June ($P = 0.050$; Fig. 5; Appendix S1: Table S4.) We were not able to collect enough *Z. marina* from early-season disturbances due to seasonal die-offs to examine differences between treatments in July. Clam addition to disturbances also increased adjacent *H. wrightii* growth rates relative to disturbances without clams for late-season disturbance subplots sampled in July ($P = 0.004$; Fig. 5; Appendix S1: Table S4). Interestingly, while not statistically significant, clam addition also appeared to slightly reduce growth rates relative to controls for both species across all sampling months (Fig. 5). *Z. marina* June growth rates increased with increasing elevation ($P = 0.049$) and *H. wrightii* May growth rates

decreased with increasing elevation ($P = 0.006$; Appendix S1: Fig. S2, Table S4).

Epiphytic load—Experiment 1

There was no reduction of epiphytic load due to the clam treatment for any of the sampling points (Appendix S1: Fig. S5). In fact, epiphytic load increased on *H. wrightii* shoots with clam addition during the May 2018 sampling period and on *Z. marina* shoots with clam addition during the July 2018 sampling period (*Halodule*, $P = 0.075$; *Zostera*, $P = 0.034$; Appendix S1: Fig. S5, Table S5). Epiphytic load did not change with elevation, regardless of species, sampling month, or treatment.

Seagrass percent cover—Experiment 2

By September 2019, all *Z. marina* was gone from the bed; therefore, fall percent cover observations consisted entirely of *H. wrightii*. For both September 2019 sampling points, average seagrass percent cover was higher in non-disturbance

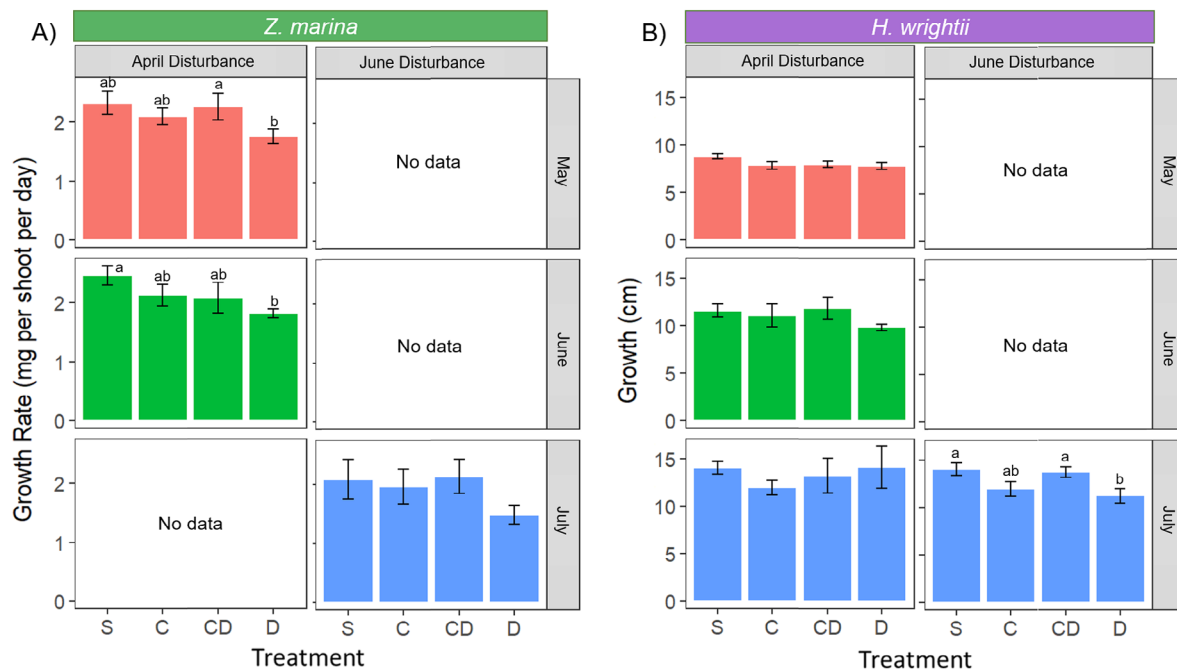


Fig. 5. Experiment 2 growth rates in summer 2019 of (A) *Z. marina* and (B) *H. wrightii* adjacent shoots by treatment (S—control; C—clam addition; CD—clam/disturbance; D—disturbance only) for disturbances created in April and June (top panel) for the three sampling months (side panel). Plots disturbed in June were not sampled until July; therefore, growth rates are not reported for May and June. Not enough *Z. marina* was present in April disturbances due to seasonal die-offs for collection. Symbols are as in Fig. 3.

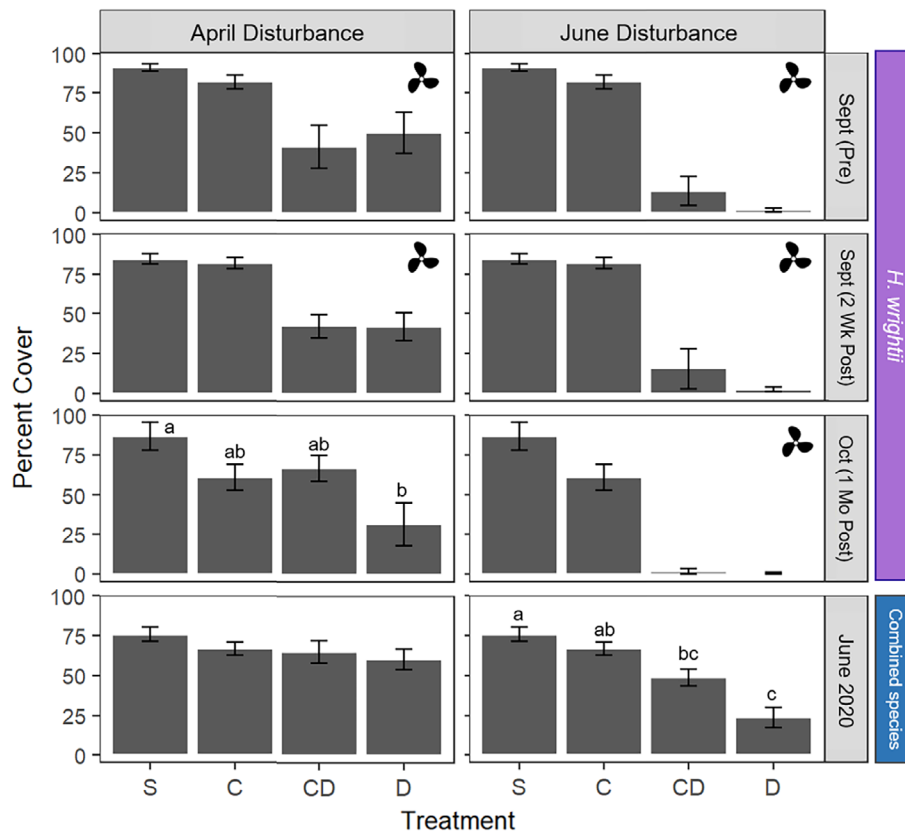


Fig. 6. Experiment 2 percent cover in fall 2019 and summer 2020 by treatment (S—control; C—clam addition; CD—clam/disturbance; D—disturbance only) for disturbances created in (left) April 2019 and (right) June 2019 during the (top) September 2019 pre-Dorian, (middle top) September 2019 two weeks post-Dorian, (middle bottom) October 2019 one month post-Dorian, and (bottom) June 2020 sampling points. Symbols are as in Fig. 3.

treatments than in disturbance treatments, regardless of clam addition, for both early-season ($P < 0.001$) and late-season disturbances ($P < 0.001$; Fig. 6; Appendix S1: Table S6). There was no evidence of Hurricane Dorian affecting seagrass percent cover in any treatment plots immediately post-storm (Fig. 6). In October 2019, average seagrass percent cover was higher in control subplots than disturbance-only subplots for early-season disturbances ($P = 0.018$; Fig. 6). In October, late-season disturbances had lower percent cover compared to control or clam addition subplots ($P < 0.001$; Appendix S1: Table S6). There was almost no seagrass cover for late-season disturbances by October 2019.

In June 2020, one year after the late-season experimental disturbances were created, both *Z. marina* and *H. wrightii* were present in the bed

and percent cover observations included both species. Early-season disturbances with and without clam addition returned to pre-disturbance levels of percent cover. Late-season disturbance subplots, regardless of clam addition, had lower percent cover than control subplots ($P < 0.001$), but this was more pronounced for disturbances without clams ($P < 0.010$; Fig. 6; Appendix S1: Table S6). Percent cover was higher for early-season disturbances than late-season disturbances across all sampling months ($P < 0.001$; Appendix S1: Table S7).

DISCUSSION

In contrast to previous studies demonstrating that bivalves can enhance seagrass productivity (Peterson and Heck 1999, 2001b, Wall et al. 2008),

our results from two field experiments did not uniformly support the hypothesis (*H1*) that the addition of a native bivalve, *M. mercenaria* (hard clam), to undisturbed seagrass beds would increase seagrass productivity. Clam additions did not consistently increase, and in some cases even decreased, standing biomass, growth rates, and percent cover of *Z. marina* and *H. wrightii* in undisturbed plots (Figs. 3, 6). Therefore, clam additions may actually reduce or inhibit *Z. marina* and *H. wrightii* productivity in otherwise undisturbed seagrass beds. This may be due to space competition within the sediment between clams and seagrass, or an indicator of clam burrowing causing small-scale, localized disturbance. However, clams did qualitatively enhance seagrass aboveground biomass and shoot density in May 2019 for Experiment 1, which was conducted in a shallower bed exposed to higher levels of thermal and desiccation stress (Fig. 3). This suggests that facilitation may occur during seasonal growth periods, but not during die-off periods associated with high abiotic stress.

Our results did support *H2* and *H3* that the addition of hard clams to disturbed beds would enhance neighboring productivity and recolonization of disturbed areas, although the strength of this correlation varied by species and disturbance timing. Clams may enhance seagrass resiliency to repeated pulse disturbances by increasing post-disturbance seagrass growth rates and recolonization of physically disturbed areas within a meadow (Figs. 5, 6). Incorporation of interspecific facilitation into the Menge-Sutherland model has shown stress amelioration via facilitation to be most impactful at medium to high levels of environmental stress. Our results align with this paradigm, with bivalve facilitation appearing to be most beneficial under higher-stress conditions and less beneficial, or even harmful, under lower-stress conditions (Menge and Sutherland 1976, Bruno et al. 2003).

Our study demonstrated that physical disturbances, such as propeller scarring, can have consistent deleterious effects on seagrass productivity and recolonization (Figs. 5, 6). Propeller scars can create bare patches within seagrass beds by uprooting shoots and severing the rhizome connections (Zieman 1976, Byron and Heck 2006). Severing connections between clones in the rhizome could increase physiological stress and

limit resource sharing among clones (Thayer et al. 1984, Marbá et al. 2006, Schwarzschild and Zieman 2008, Kaldy et al. 2013). Seagrass has been shown to allocate more energy to the production of belowground biomass to increase resiliency after a disturbance (Peterson et al. 2002, Connolly et al. 2018). We found that belowground biomass was higher for both clam addition and disturbance treatments compared to controls one-year post-disturbance (Fig. 4). The exception to this was early-season disturbances with clam addition, supporting our hypothesis that clam addition can speed the recolonization and resiliency of physical disturbances. Evidence for hurricanes as a major disturbance for seagrass meadows is conflicting, with some studies describing huge meadow losses (Preen et al. 1995, Congdon et al. 2019), no impact (Byron and Heck 2006, Anton et al. 2009), or mixed effects (Carlson et al. 2010). One study found that a Category 2 hurricane increased the size of preexisting disturbances caused by vessels within a seagrass bed and that large disturbances created by boats are non-resilient to hurricanes (Whitfield et al. 2002). We found that Hurricane Dorian, a Category 1 hurricane, did not reduce *H. wrightii* percent cover, nor did it increase the size of the experimental disturbances (Fig. 6). The lack of impact on the beds may be because Hurricane Dorian hit North Carolina near high tide and moved over the state within 24 h, suggesting that the seagrass beds may have been buffered from Dorian's storm surge and category 2 winds (Avila et al. 2019).

One year after the late-season disturbances were created, we found that early-season disturbances had returned to pre-disturbance percent cover, regardless of clam addition, while late-season disturbances still had reduced percent cover, although clams qualitatively increased disturbance recolonization. This suggests that the timing of disturbance has important implications for recovery in North Carolina seagrass beds, with early-season disturbances potentially able to recover within a single year. Experimental disturbances created late in the growing season, after the *Z. marina* reproductive season, may have resulted in more disruption of and subsequent loss in seed bank accumulation than early-season disturbances, restricting *Z. marina* recovery in later-season disturbances (Livernois et al. 2017).

Regardless of disturbance timing, clam addition appears to mediate the recovery of these disturbance scars. In September 2019, all disturbances had reduced percent cover and we did not observe evidence of clam enhancement of seagrass recolonization of disturbed plots (Fig. 6). However, seagrass percent cover was nearly double for disturbances with clam addition relative to disturbances without clam addition for early-season disturbances sampled in October 2019 and late-season disturbances sampled in June 2020 (Fig. 6). This lends significant evidence to support *H3*, indicating that addition of the hard clam to disturbances can speed recolonization rates and extent within a year of disturbance. After a physical disturbance, seagrass may be released from competition with bivalves for nutrients and space, as is seen with megafauna grazers (Valentine et al. 1997, Moran and Bjorndal 2005), and able to benefit from the enhanced sediment nutrient content provided via bivalve biodeposition (Reusch et al. 1994, Newell and Koch 2004).

Only *H. wrightii* recolonized disturbed areas throughout the first growing season, despite early-season disturbances being created in April, theoretically early enough in the summer for *Z. marina* to recover via vegetative and even sexual regrowth, as it is the dominant species in North Carolina seagrass beds until early June (Jarvis et al. 2012). Further, adjacent *H. wrightii* growth rates increased with physical disturbance, confirming that *H. wrightii* is a colonizing species that is often able to utilize clonal growth to swiftly grow into gaps in the canopy and therefore may actually benefit from small-scale physical disturbances (Williams 1990, Gallegos et al. 1994, O'Brien et al. 2017). However, slower recolonization and reduced productivity post-disturbance suggest that *Z. marina* may be more vulnerable to disturbance, and ultimate long-term decline, than *H. wrightii* in our study region. This has important implications for the health and functioning of these seagrass beds as *Z. marina*-dominated beds may host greater densities of fish and invertebrates than *H. wrightii*-dominated beds in North Carolina (Micheli et al. 2008).

The net neutral and negative effects of clams on seagrass productivity in undisturbed beds in our experiments may be attributed to the clams

themselves acting as small-scale, localized physical disturbances, possibly due to the large size of clams used for the experiment. We suspect that burrowing by large clams can sever the rhizome network connecting shoots, similar to propeller scarring, and cause a resulting decline in seagrass productivity. Clam presence may also attract predators such as rays which have been shown to cause significant damage to *Z. marina* beds via bioturbation and cause additional disturbance to the system (Orth 1975). Additionally, large clams may compete with seagrass for space within the sediment, thereby having negative effects on seagrass productivity and resiliency (Gagnon et al. 2020). Finally, Castorani et al. (2015) demonstrated in a mesocosm experiment that some bivalve species have the potential to impede seagrass productivity in eutrophic systems by increasing sulfide stress in the sediment. The sediment conditions in our disturbed beds may have been inherently different than the sediment conditions in undisturbed beds, therefore regulating the effects of clams on seagrass productivity.

Other environmental conditions such as water depth (bed elevation was used as a proxy) also played a role in controlling seagrass productivity in our experiments, although this needs to be investigated further in future studies. Experiment 1 was conducted in a shallow, intertidal seagrass bed where the seagrasses were frequently aerially exposed at low tide and thus often experienced desiccation and thermal stress. *Z. marina* and *H. wrightii* late summer growth rates appeared to be enhanced more by the release from abiotic stress in the form of increasing water depth rather than bivalve facilitation in this bed (Appendix S1: Fig. S4). In contrast, enhanced productivity in Experiment 2 was occasionally correlated with shallower water depth. Experiment 2 was conducted in a deeper, subtidal bed where the seagrass was likely not as strongly heat-stressed (Appendix S1: Fig. S2). Water depth has been shown to limit or drive seagrass distribution and competition (Duarte 1991, Micheli et al. 2008). Our study suggests that a combination of environmental conditions and disturbance intensity may therefore regulate bivalve–seagrass interactions in a temperate estuary. As we did not directly measure sediment or seagrass nutrient content, we cannot directly

establish a causative mechanism for clam-affected seagrass productivity. Another primary limitation of this study was our inability to measure ambient clam densities and mortality in the system as quantification would have created significant disturbance to localized seagrass and compromised our experimental design. Although several clam shells were recovered in experimental plots after apparent predation by rays, we did not observe any evidence of ray bioturbation (e.g., pits) in the experimental subplots.

CONCLUSIONS

This study shows that the effects of hard clam interaction on seagrass in this temperate/subtropical system differ based on disturbance occurrence. Environmental stress models have shown that facilitation via stress amelioration is most impactful at medium to high stress levels (Menge and Sutherland 1976, Bruno et al. 2003) and our results confirm that physical disturbance within a seagrass bed can modify the strength and direction of the interaction of bivalves on seagrass. Clams facilitated seagrass productivity and recovery after a physical disturbance but not in undisturbed beds perhaps due to the subsequent release from space competition between clams and seagrass after a disturbance. Restoration practitioners wanting to incorporate bivalve facilitation into seagrass restoration design should be considerate of the environmental conditions of the bed. We also showed that the potential for rapid seagrass recovery in North Carolina is influenced by disturbance timing, with only the early-season disturbances recovering to pre-disturbance levels of percent cover within a single year. Managers should consider implementing special protections for seagrasses from vessel damage in mid- to late summer to best preserve ecosystem functioning. With the experimental evidence from both this study and the broader scientific literature suggesting that mutualisms should be utilized in marine conservation and restoration (Silliman et al. 2015, de Fouw et al. 2018, Renzi et al. 2019), it will become even more important to understand the environmental and physical context that leads to positive rather than negative bivalve–seagrass interactions. Researchers and practitioners should continue to investigate how bivalve size and life history

impact their efficacy as a potential seagrass facilitator. Additionally, it is imperative to develop a better understanding of the effects of site characteristics, particularly water depth and inundation time, on seagrass growth and recovery. Understanding when and how to utilize positive, interspecific interactions in coastal restoration could improve restoration success rates.

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DATA AVAILABILITY

Data are available from Dryad: <https://doi.org/10.5061/dryad.9cnp5hqh7>

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3804/full>