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Seagrass ecosystem recovery: Experimental removal and synthesis of disturbance studies

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Abstract

Net global losses of seagrasses have accelerated efforts to understand recovery from disturbances. Stressors causing disturbances (e.g., storms, heatwaves, boating) vary temporally and spatially within meadows potentially affecting recovery. To test differential recovery, we conducted a removal experiment at sites that differed in thermal stress for a temperate seagrass (*Zostera marina*). We also synthesized prior studies of seagrass recovery to assess general patterns. Seagrass shoots were removed from 28.3 m^2 plots at edge and central sites of a meadow in South Bay, Virginia, USA. We hypothesized faster recovery for edge plots where greater oceanic exchange reduces thermal stress. Contrary to our hypothesis recovery was most rapid in the central meadow matching control site shoot density in 24 months. Recovery was incomplete at the meadow edge and estimated to require 158 months. Differences in recovery were likely due to storm-driven sediment erosion at the edge sites. Based on data from prior recovery studies, which were primarily on monospecific meadows of *Zostera*, seagrasses recover across a broad range of conditions with a positive, nonlinear relationship between disturbance area and recovery time. Our experiment indicates position within a seagrass meadow affects disturbance susceptibility and length of recovery. Linking this finding to our literature synthesis suggests increased attention to spatial context will contribute to better understanding variation in recovery rates.

The stability and resilience of coastal ecosystems is threatened by several features of global change including climate warming, sea-level rise, changes in storm frequency and severity, and species invasions (Orth et al. 2006; Short et al. 2011; Unsworth et al. 2015). Collectively, these features often create disturbances that either result in recovery or shifts to a different ecosystem state. Recovery is an attribute of ecosystem stability (Ives and Carpenter 2007) wherein mechanisms that maintain resilience promote the return of a disturbed system to a prior baseline equilibrium. Analyses of recovery are important for understanding how ecosystems might remain stable and whether these systems are showing signs of degradation (e.g., slowed recovery) indicating possible pending transformations.

In the context of coastal environments, seagrass meadows are among the most threatened ecosystems, as annual loss rate accelerated from <1% to 7% during the 20th century (Waycott et al. 2009), representing an estimated global net loss of 19.1% since 1880 (Dunic et al. 2021). Drivers of seagrass decline include mechanical (e.g., shell fishing, anchoring, coastal development), and environmental (e.g., eutrophication, anoxia, wasting disease, storm, heatwave) processes (Berger et al. 2020; Dunic et al. 2021). These factors can affect seagrass across scales, from rapid changes in molecular and cellular processes to changes in life histories or loss of aboveground and belowground biomass over large areas (O'Brien et al. 2018). Aboveground loss may reduce ecosystem resilience by enhancing feedbacks (e.g., increased bed shear stress that increases sediment suspension and reduces light and/or seed banks) that promote state change (Unsworth et al. 2015; Carr et al. 2016; Reidenbach and Thomas 2018). Losses of seagrass reduce coastal ecosystem services related to food production, coastal protection, sediment stabilization, water purification, fisheries maintenance, tourism, and recreation (Ramesh et al. 2019). In addition, seagrasses store organic matter at high rates, thereby acting as long-term carbon sinks

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Additional Supporting Information may be found in the online version of this article.

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that contribute to carbon sequestration and markets (Duarte et al. 2005; Fourqurean et al. 2012; Oreska et al. 2020).

Although large net losses have occurred, seagrasses often recover following disturbance based on prior experimental and observational studies (Williams 1988; Rasheed 1999; Aoki et al. 2021). These studies of disturbance–recovery dynamics are temporally (i.e., weeks to decades) and geographically extensive (*see* below), include mono- and mixed-species beds, and represent diverse disturbance scales and types. Studies document recovery by both clonal growth (Macreadie et al. 2014; El-Hacen et al. 2018) and seed recruitment (Lee et al. 2007; Qin et al. 2016). Furthermore, some studies observed a nonlinear recovery trajectory after disturbance (Short 1983; Lundquist et al. 2018), while others observed linear recovery (McGlathery et al. 2012; Qin et al. 2016). Despite the breadth of seagrass disturbance–recovery studies, there has been no synthesis of recovery patterns and mechanisms.

In addition to the study of recovery, seagrass losses have spurred research on restoration to reverse habitat loss and interest in how these systems respond to various disturbances. The coastal bays of Virginia, USA, are home to a large successful seagrass restoration project, which began in 1999 and now spans ~ 36 km^2 of meadow area (Orth et al. 2020). Shoot density increased linearly during restoration after an initial lag period and eventually leveled off after 9 yr (McGlathery et al. 2012). Subsequently in 2015, a marine heatwave (MHW) caused ~ 90% reduction in *Zostera marina* shoot density, 20% reduction in sediment carbon stores, and shifted the metabolism in some parts of the meadow to net heterotrophy (Berger et al. 2020; Aoki et al. 2021). Spatial patterns in shoot density loss were not uniform, as the damage was confined to the meadow interior, while the meadow edge had no loss of shoot density or canopy cover. Follow-up studies provided evidence of a thermal gradient between the meadow edge and interior (Berger et al. 2024) and a hindcast sediment temperature model suggested the MHW induced a sediment heatwave that exceeded the seagrass thermal stress threshold in the meadow interior but not at the meadow edge (Tassone and Pace 2023*a*). Nonetheless, the disturbed seagrass recovered ~ 2–4 yr following the heatwave disturbances based on aerial canopy cover imagery and annual summer (June or July) shoot density counts (Aoki et al. 2021). The lack of heatwave effects at the meadow edge suggests this area may be more resilient to heatwaves than the meadow interior.

In this study, we designed an experiment to evaluate the aspects of a MHW disturbance by removing aboveground *Z. marina* biomass from central and edge locations of the same 20.3 km^2 restored Virginia seagrass meadow that experienced the June 2015 MHW. We asked (1) is recovery faster at sites with greater oceanic exchange (i.e., meadow edge) and thus lower thermal stress (Berger et al. 2024) and (2) what is the recovery trajectory pattern? We hypothesized that (1) faster recovery at the meadow edge due to lower heat stress (Aoki et al. 2021; Berger et al. 2024) and (2) the shape of shoot density recovery would be linear without a lag. To provide context for the experiment and explore general patterns, we synthesized results of seagrass recovery from prior studies to summarize spatial scales of experimental and observational research, time to recovery, and factors related to recovery.

Methods

Study site

Along the Virginia portion of the Delmarva Peninsula is a series of 14 coastal barrier islands with a Northeast–Southwest orientation that parallel the mainland. Since 1987, the area from the edge of the mainland to the ocean edge of the barrier islands has constituted a protected region known as the Virginia Coast Reserve. The Virginia Coast Reserve is 1 of 28 National Science Foundation Long-Term Ecological Research Network sites. Between the barrier islands and mainland are shallow lagoons (typically average depth = 1–2 m; Fagherazzi and Wiberg 2009) where subtidal seagrass meadow restoration has been ongoing since 1999. South Bay contains one seagrass meadow located landward of Wreck Island that has been successfully restored and covers approximately 20.3 km^2 (Orth et al. 2020; Fig. 1).

The physical structure of seagrass in South Bay alters the hydrodynamic environment and water quality conditions (Hansen and Reidenbach 2012, 2013). This in turn affects sedimentation and carbon accumulation rates (Oreska et al. 2017; Zhu et al. 2022). The water residence time within South Bay varies between 12 and 80 h, with longer residence times as distance from the northern oceanic inlet increases (Safak et al. 2015). Similarly, water and sediment temperature vary with distance from the northern oceanic inlet such that summer water temperature is, on average, 0.7°C warmer in the central meadow relative to the meadow edge (Tassone and Pace 2023*a*; Berger et al. 2024; Berger and Berg 2024).

Experimental design

In June 2020, triplicate paired seagrass treatment and control plots, each with a circular shape and 6 m diameter, were established at two locations (i.e., central meadow and meadow edge) approximately 1.4 km apart within South Bay (Fig. 1). These locations were selected due to their observed differences in seagrass canopy cover and shoot density following the June 2015 MHW (Berger et al. 2020; Aoki et al. 2021). As the predominant flow direction in South Bay is N–S (Hansen and Reidenbach 2013), control and treatment plots were placed E–W to maintain hydrodynamic similarity and minimize variability among plots. Central sites had a linear orientation, while edge sites had a triangular orientation due to the presence of other ongoing research in the area and the distance to the meadow edge (distance to meadow edge at edge sites was ~ 50 m). Control and treatment pairs were spaced 20 m apart edge-to-edge to minimize any potential impact of the treatment on the control plots, while maintaining similar depth,

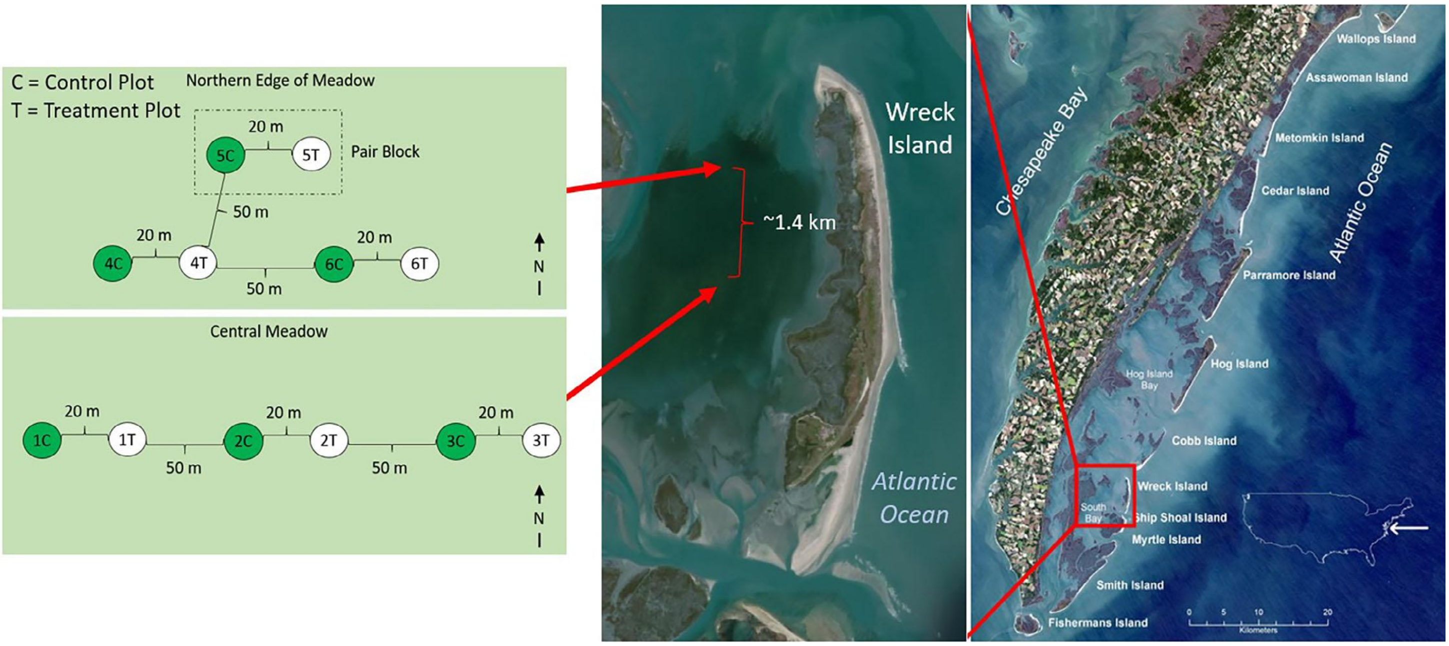

Fig. 1. Location of the seagrass experiment along with site location and plot layout. Each plot was circular with a 3-m radius. Paired plots consisted of control (no seagrass removal) and treatment (aboveground seagrass removal), which were spaced 20 m edge-to-edge, with plot pairs spaced 50 m edge-to-edge. Differences in layout design were due to water depth, ongoing research in the area, and distance to meadow edge.

seagrass density, and hydrodynamic properties (e.g., flow velocity and direction). Each pair block was separated by 50 m edge-to-edge to further minimize any potential impact from flow disruption within the treatment plots and from working within each pair block. Within treatment plots, seagrass was manually removed by hand, pulling out aboveground seagrass biomass, on June 5, 2020 (Commonwealth of Virginia Marine Resources Commission permit # 2020-0277). The relatively small number of replicates in our experimental design was necessary for three reasons: (1) seagrass is protected by federal, state, and local government regulations which actively seek to minimize damage to these ecosystems; (2) the need to not disturb other ongoing long-term projects in the meadow; and (3) field conditions limited safe access to day light hours and sampling time to low tide periods. These requirements and the comparatively large size of our experimental plots, which was part of the design, necessitated the limited replication.

Data collection

Z. marina shoots were counted monthly in situ between June–October 2020, May–October 2021, and April–October 2022 using a 0.25 m^2 quadrat. We focused on shoot density as our recovery metric for three reasons: (1) shoot density is a non-destructive variable to quantify, which was important for this multiyear study; (2) shoot density co-varies with seagrass biomass, productivity, and leaf length (McGlathery et al. 2012; Rheuban et al. 2014; Berger et al. 2024); and (3) shoot density was the most time and cost-effective variable to quantify given the large spatial scale of our study sites. Within each plot, shoots were counted at 0.5, 1.5, and 2.5 m from the edge of the plot at random orientations. Adverse weather prohibited sampling the central sites in September 2022. Water temperature was monitored at fixed positions 20 cm above the sediment surface at the center of each plot using Onset HOBO Pendant 64K temperature loggers. Water temperature was collected at 15-min intervals between April and October and hourly intervals between November and March. To further characterize differences between the central meadow and edge, benthic chlorophyll and surface water quality samples were collected (Supporting Information Table S1). Depth was measured at 15-min intervals using Onset HOBO Water Level Data Logger between October and November 2021 within five of the six pair blocks (two in the central meadow and three at the edge). Seagrass bed elevation was measured once in October 2022 along an 18-m N–S transect, centered on the middle of each plot, using an Emlid Reach RS2 RTK GNSS receiver with a factory-stated vertical precision of 1.4 cm. Lastly, hourly wind speed, wind direction, and barometric pressure were collected from a National Oceanic and Atmospheric Administration (NOAA) tide monitoring station at Wachapreague, Virginia (station ID: 8631044; 37.6078°N, 75.6858°W), which is 38 km north of South Bay. Wind speed was further categorized according to the Beaufort wind force scale (WMO 2012) to characterize a storm event in May 2022.

Statistical analysis

The recovery of shoot density for treatments relative to controls was determined using Welch's *t*-test for each monthly sampling at each location. To correct for multiple comparisons, p-values were adjusted using a 5% false discovery rate (Benjamini and Hochberg 1995). We tested for differences in shoot density among control plots within each site at each timepoint using a three-way ANOVA with pair block number (i.e., 1–3 for central and 4–6 for edge), meadow location, and collection date as the independent variables. Pairwise comparisons of the three-way ANOVA resulted in three statistically significant differences out of 108 tests therefore, samples were pooled among sites at each location prior to statistical analysis. Recovery rate and trajectory were determined based on the relative recovery of the central and edge treatment sites to their control sites. Relative recovery was derived for each month based on the mean shoot density of the treatment sites ($\overline{x}_{\text{ShootDensity,Treatment}}$) relative to the mean shoot density of control sites ($\overline{x}_{\text{ShootDensity,Control}}$) for each location.

$$\text{Relative Recovery} = \left(\frac{\overline{x}_{\text{ShootDensity,Treatment}}}{\overline{x}_{\text{ShootDensity,Control}}}\right) \times 100\%$$

All analyses were conducted in the R environment for statistical computing (R Core Team 2022) with code available on GitHub (https://github.com/spencer-tassone/SGRecovExp_LitSynthesis).

Literature synthesis

To put our disturbance–recovery experiment in context, we conducted a quantitative synthesis of English-language primary research articles on seagrass disturbance and recovery. The literature search was conducted for publications up to May 13, 2022, using the search terms "seagrass" and "recoloni*" in the Web of Science (WoS) database. The latter search term was selected based on studies of seagrass recovery from disturbance that tended to use the word "recolonization" rather than "recovery." This combination of search terms produced the most relevant number of studies. Of the 142 articles identified, 36 were relevant as determined from reading the abstract. All relevant research articles cited within the 36 originally identified manuscripts were further assessed, and 24 additional studies were identified, leading to a total of 60 primary research articles (Supporting Information Table S2). Studies with multiple treatments (e.g., different locations or depths) were treated independently, bringing the total number of observed disturbance and recovery comparisons to 137. Studies that were historical updates to previously published works were included in this review; however, in the case of updates, the prior results were excluded in favor of the longer-term observations. Articles were examined to identify study type (i.e., experimental or observational), geographic location, disturbance type, disturbance shape, disturbance area, total aboveground loss, recovery time, recovery trajectory pattern (i.e., linear or nonlinear), recovery mechanism (i.e., lateral clonal growth, seedling recruitment, or both) and total aboveground recovery (*see* Supporting Information for details). Recovery rates were derived by dividing recovery time by disturbance area. In efforts to make quantitative comparisons, recovery rates were only examined for those sites where the total aboveground loss was ≥ 80%, and recovery during the study period was ≥ 90%.

Results

Site conditions

The edge sites were, on average, 20 cm deeper (mean sea-level [MSL] depth = 1.5 m) than the central sites (MSL depth = 1.3 m), with both sites having an equal tidal range of 1.2 m (Supporting Information Table S1). Both sites are within the optimal depth range of 0.8–1.6 m MSL determined by the hydrodynamic–vegetation model of Carr et al. (2012*a*) and validated with long-term data (Aoki et al. 2020). Water temperature at the central sites was, on average, significantly warmer (mean ± SD = 21.2 ± 7.2°C) than edge sites (20.7 ± 6.9°C; p-value ≤ 0.001); however, edge sites were typically warmer (up to 4.2°C) than central sites during winter (December–February; Fig. 2). During summer (June–August), water temperature at the central sites followed a diurnal cycle, whereas the edge sites followed a semidiurnal and diurnal cycle, reflecting the greater influence of tides at the edge sites. These differences produced water temperature gradients of up to 8.9°C with the central sites warmer than the edge sites.

Seagrass recovery experiment

Shoot density removal at the edge and central treatment plots was 85% ± 6% and 93% ± 1% effective, respectively. Treatment site shoot density remained low (≤ 76 shoots m^{-2}) throughout 2020, while control sites senesced after July (Fig. 3). In 2021, shoot density recovery within treatment sites was significantly greater (p-values ≤ 0.009) at the central sites relative to the edge sites for June and July, with an estimated marginal mean difference of 61 and 56 shoots m^{-2} for the 2 months, respectively. Additionally, in 2021, the peak relative recovery at the central and edge treatment sites occurred in July prior to seasonal senescence and were 54% and 43%, respectively (Fig. 4). At the beginning of the second growing season (April 2022), treatment sites at the central and edge locations had similar shoot densities (p-value > 0.05); however, by May 2022 central treatment sites were significantly greater than edge treatment sites by 83 shoots m^{-2}. Central treatment sites reached and maintained control site shoot density by June 2022 (Fig. 3). Conversely, in 2022 the edge treatment site's mean shoot density was less than the previous year's mean shoot density. Furthermore, the mean shoot density at the edge treatment sites declined after June 2022, whereas the edge control sites senesced after July 2022.

The relative recovery of shoot density increased linearly at the central treatment sites. Densities were no longer significantly different from control sites after 24 months. In contrast, for the edge treatment sites, the linearly estimated 100%

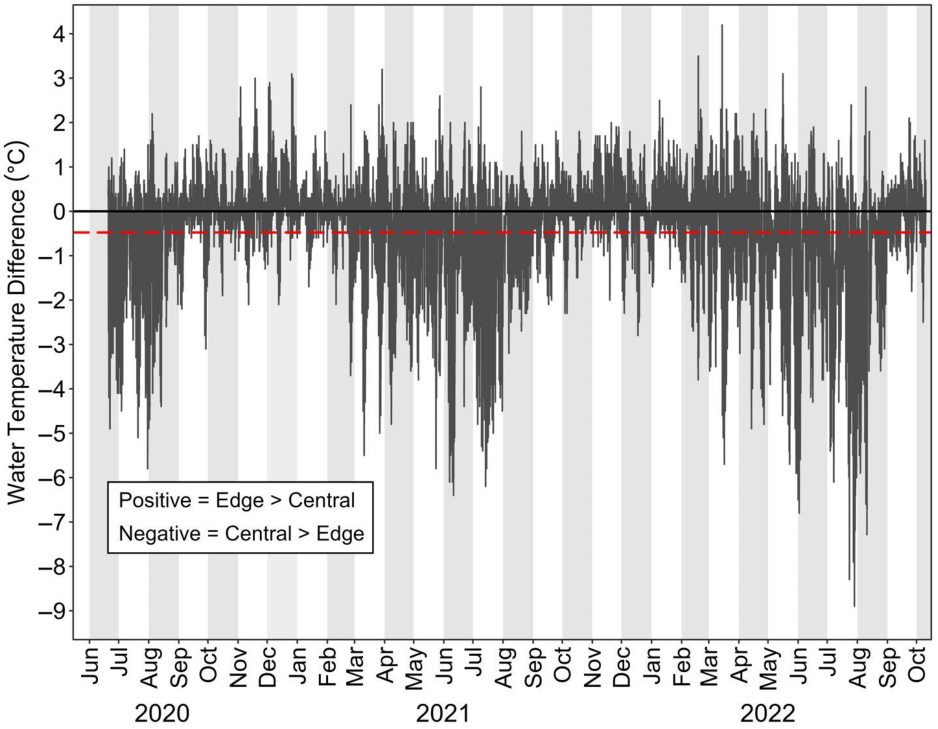

Fig. 2. High-frequency (≤ 1 h) water temperature difference between central and edge meadow locations. Temperature was collected at 15-min intervals between spring and fall (April–November) and hourly in the winter (December–March). The red dashed line indicates the overall mean difference.

relative recovery time was 158 months (Fig. 4). Between May 6, 2022 and May 12, 2022, a nor'easter moved through the Virginia Coast Reserve that produced 59% and 48% of the year's total Gale and Near Gale force winds (Supporting Information Fig. S1). By October 2022, the bed elevation within the meadow edge treatment plots were depressed on average by 9.4–10.4 cm based on elevation measurements across transects that extended 6 m north and south of each plot edge (Fig. 5). No significant depression was observed within the central treatment plots.

Literature synthesis

Seagrass disturbance and recovery studies have been conducted across all continents except Antarctica, including 16 countries that span the northern and southern hemispheres and the Atlantic, Pacific, and Indian Ocean basins (Fig. 6). The most common category of seagrass disturbance (58%) cited among the 60 studies considered were physical disturbances, such as shellfishing, trawling, hull grounding, propeller/anchor scarring, explosions, grazing, ice scour, and land reclamation (Supporting Information Fig. S2). Additional categories of seagrass disturbance included chemical (i.e., eutrophication, anoxia), light availability (i.e., turbidity caused by dredging), climate (i.e., marine heatwaves, cyclone), disease (i.e., wasting disease), and natural mass mortality (i.e., breakdown of a mutualistic relationship with a bivalve). Of the 72 recognized seagrass species (Short et al. 2011), 47% ($n = 34$) were included in this synthesis, with *Z. marina* and the *Zostera* genus receiving the greatest attention. Most studies (53%) provided evidence that recovery was linear over time, while 17% suggested nonlinear recovery, and the remaining were not classified (Supporting Information Fig. S3).

Of the 60-seagrass disturbance and recovery studies considered, 45% ($n = 27$) were experimental and 55% ($n = 33$) were observational. Most experimental and observational studies were conducted within monospecific meadows (52% and 61%, respectively; Supporting Information Fig. S4). Observational disturbances were typically irregularly shaped (73%) whereas experimental disturbances were typically square shaped (70%) or circular (19%; Supporting Information Fig. S5). The disturbance scale among experimental and observational studies varied by nine orders of magnitude, ranging between 0.01 m^2 and 1220 km^2, with median experimental and observational disturbance areas of 0.25 and 124,900 m^2, respectively (Supporting Information Fig. S6). Recovery time ranged from 0.5 to 1188 months. Log-transformed recovery time was significantly positively correlated with log-transformed disturbance area ($R = 0.50$, p-value < 0.001; Fig. 7). Of the 119 studies where percent recovery could be determined, 85 had > 50% recovery while 5 had little to no recovery (< 5%) during the study period. Recovery rates varied considerably among studies but were not significantly different among latitudinal regions ($\mathrm{median}_{\mathrm{Tropics}} = 0.04$, $\mathrm{mediam}_{\mathrm{Subtropics}} = 0.11$, $\mathrm{median}_{\mathrm{Temperate}} = 0.17\ \mathrm{m}^2\ \mathrm{month}^{-1}$;

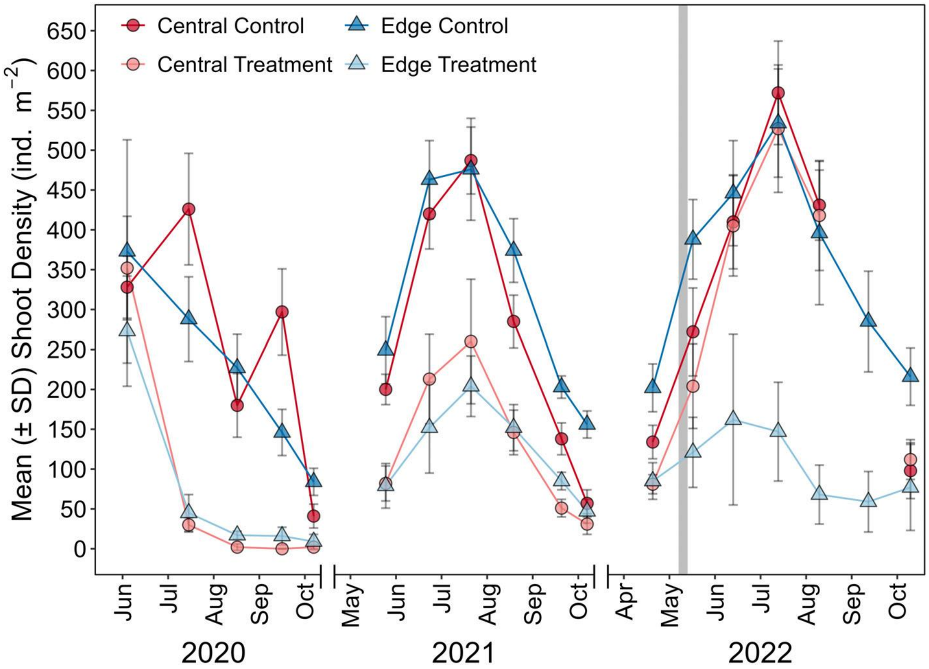

Fig. 3. Mean (± SD) shoot density for control and treatment groups among the central (circle) and edge (triangle) locations of the South Bay, Virginia, seagrass meadow. Removal of seagrass from the treatment plots occurred on June 5, 2022 after the first sampling. The gray shaded area represents the May 6–12, 2022 storm.

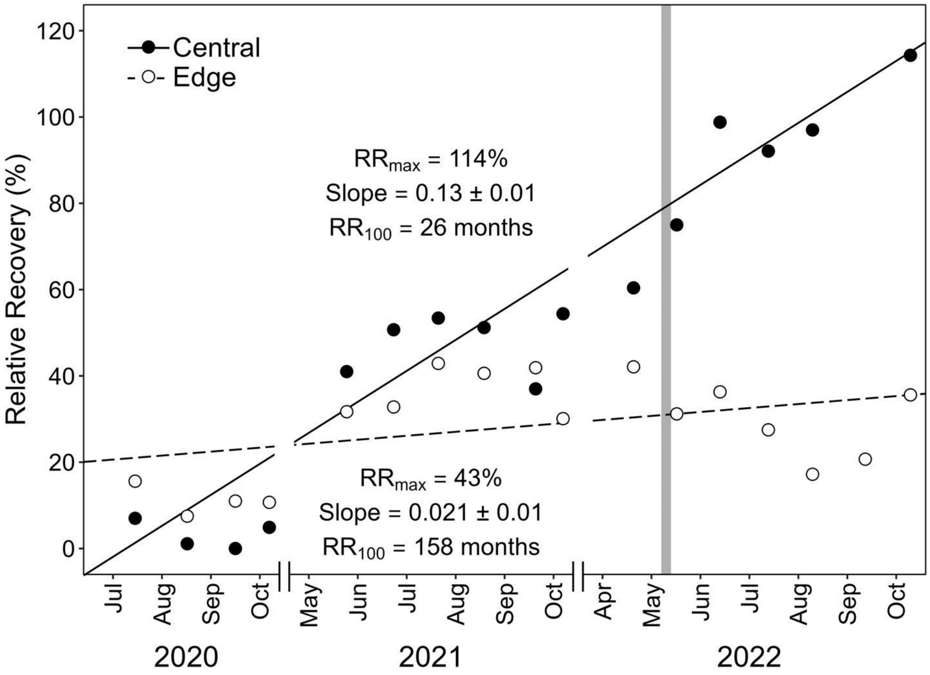

Fig. 4. Relative recovery (RR) of the treatment groups for the central (black) and edge (white) locations. The solid black line represents the linear recovery trend for the central sites, while the dashed line represents the linear recovery trend for the edge sites. The gray shaded area represents the May 6–12, 2022 storm.

Supporting Information Fig. S7). The dominant recovery mechanism cited for experimental and observational studies was lateral clonal growth (56% and 30%, respectively; Supporting Information Fig. S8). While none of the experimental studies cited seedling recruitment as the lone recovery mechanism, two studies provided evidence of both seedling recruitment and

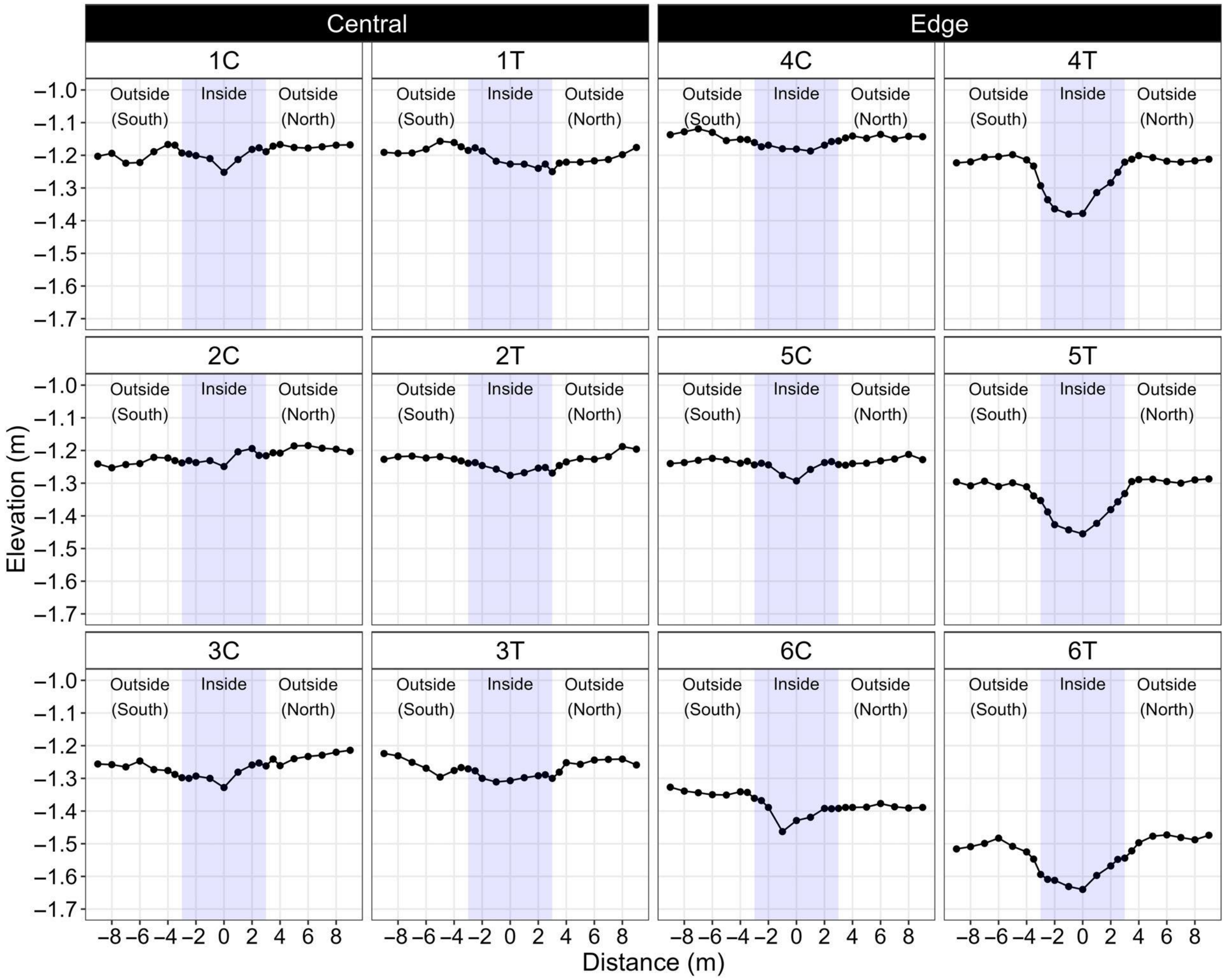

Fig. 5. Bed elevation of control and treatment groups between sites relative to NAVD88 vertical datum. Sites 1–3 are from central South Bay, and sites 4–6 are from the meadow edge. The C indicates control groups, and T represents treatment groups where seagrass was removed. Measurements were collected along a N–S transect, with the shaded areas representing data from within the plots and non-shaded areas representing areas outside the plots. Note the depressions in the edge treatment sites.

lateral clonal growth as co-contributors to recovery. Conversely, four observational studies cited seedling recruitment as the lone recovery mechanism, while five indicated both seedling and clonal growth as contributors to recovery.

Discussion

Seagrass recovery experiment

Our initial hypothesis was that seagrass recovery would be quicker at the meadow edge relative to the meadow center based on patterns of loss following the June 2015 MHW and observed water temperature differences (Aoki et al. 2021; Berger et al. 2024). However, after 24 months shoot density at the central treatment plots matched control plot values, whereas recovery was incomplete and estimated to take 158 months at the edge sites. Without a major MHW during the experimental period, the recovery rate of the central treatment sites agreed with annual shoot density counts and aerial photography of South Bay that indicated recovery occurred 2–4 yr following the June 2015 MHW (Berger et al. 2020; Aoki et al. 2021). While recovery rates were similar during the first growing season, differences in recovery times between locations were likely due to storm-driven sediment erosion at the edge treatment locations during the second growing season between the April and May 2022 sampling periods. Hourly meteorological records from the nearby NOAA Wachapreague tide monitoring station provided evidence of a strong nor’easter passing through the Virginia Coast Reserve between May 6, 2022 and May 9, 2022, which produced Gale and Near Gale force winds between May 8, 2022 and May 12, 2022. This wind event produced 59% and 48% of the Gale and Near Gale winds, respectively, for 2022. In shallow coastal areas, waves and bed shear stress that erode sediments respond strongly to wind events (Lawson et al. 2007; Zhu et al. 2022). While seagrass meadow edges attenuate wave energy and near-bottom currents, they are exposed to stronger hydrodynamic conditions than meadow interiors (Granata

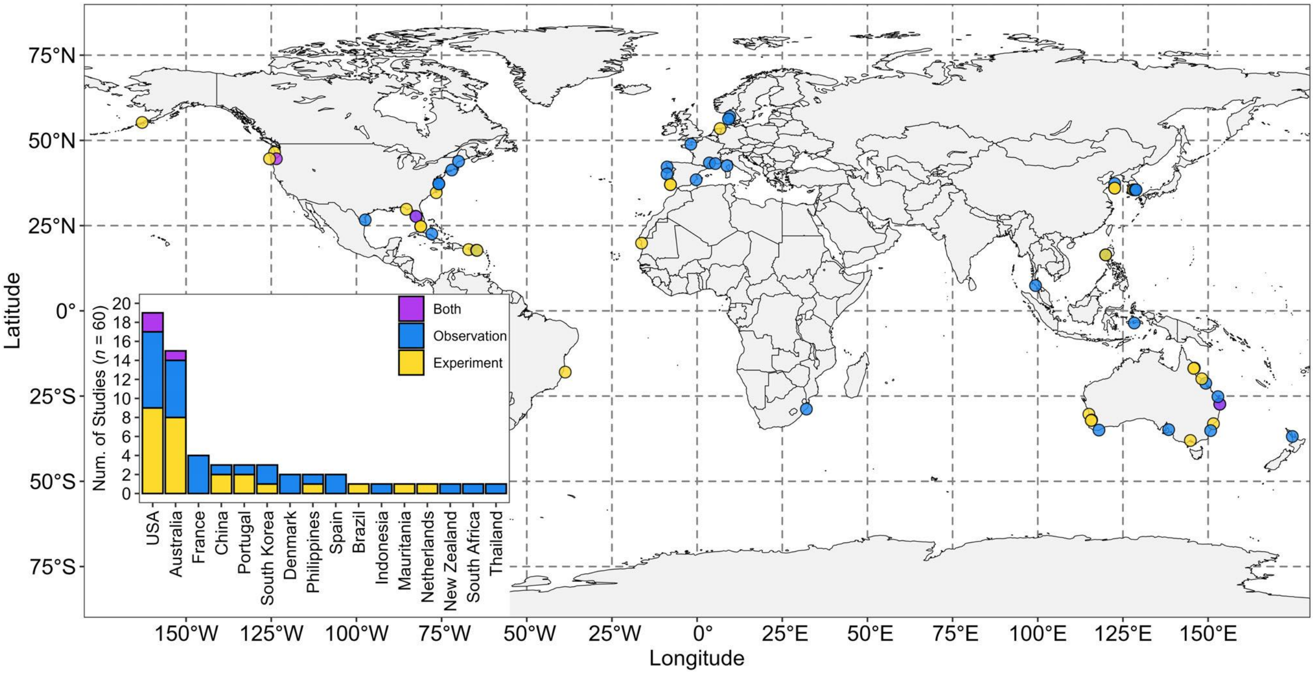

Fig. 6. Seagrass disturbance and recovery study locations and distribution (inset) among countries. The inset does not cover any study locations.

et al. 2001; Hansen and Reidenbach 2012; Zhu et al. 2021). In April 2022, shoot density at the edge control sites (202 ± 30 shoots m^{-2}) was likely abundant enough to reduce current flow such that bed shear stress did not erode control sites. Conversely, shoot densities within the edge treatment sites were low (mean = 85 ± 23 shoots m^{-2}) and likely unable to reduce current flow resulting in high bed sheer stress, sediment erosion, and decreased bed elevation within the edge treatment sites (Hansen and Reidenbach 2013; Zhu et al. 2022). Reproductive seagrass shoots develop in South Bay between April and May, so it is likely but uncertain that this storm produced high current flows near the meadow edge that advected seedlings and damaged rhizomes during sediment erosion thereby limiting the recovery potential of the 2022 growing season at those sites. Additionally, the greater depth within the edge treatment sites following the storm may have further limited recovery by reducing underwater light availability. Previous studies have provided evidence that severe storm events can induce strong currents that erode vegetated sediments which result in extensive seagrass loss and mortality (Williams 1988; Oprandi et al. 2020).

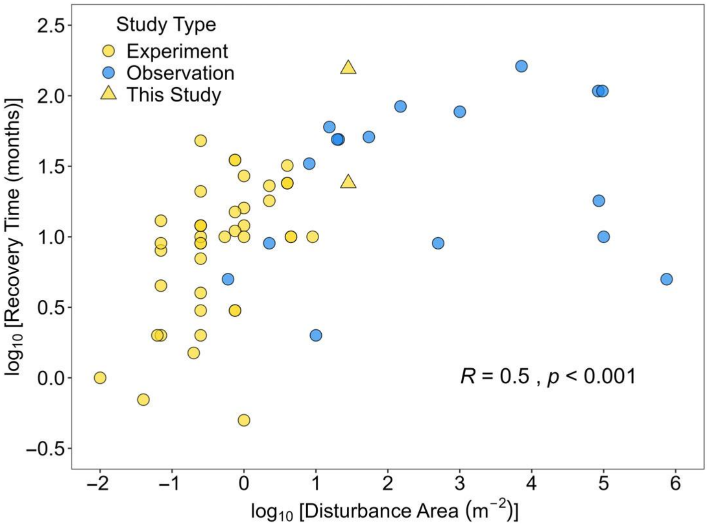

Fig. 7. Correlation of log transformed recovery time as a function of log transformed disturbance area. Results from our disturbance–recovery experiment are triangle shaped with the circle shapes coming from the literature synthesis.

The experiment and long-term observations indicate factors that influence the ability of seagrass shoots to persist differ from the factors that influence regrowth. These results indicate how different mechanisms (i.e., storms, heat) can cause different responses and recoveries such that stability varies spatially. Berger et al. (2024) provided evidence that seagrass density along a thermal stress gradient was up to 65% greater in areas with greater thermal relief (i.e., tidal cooling). Furthermore, Tassone and Pace (2023*a*) provided evidence that MHW can induce sediment heatwaves that exceed the thermal stress threshold for seagrass suggesting heat impacts the entire plant, not just the aboveground portion. Seagrass in the central meadow recovered as rapidly as 2 yr in response to the June 2015 MHW and to experimental removal. While considering the mechanisms of recovery was beyond the scope of the present study, clonal growth and seedling recruitment likely explain this rapid recovery when conditions are favorable, as was the case in the central meadow following the MHW and experimental removal. Furthermore, we did not set out to measure hydrodynamics of our study sites; however, the unexpected May 2022 nor'easter provided the opportunity to consider how storm erosion could differentially impact recovery of the meadow treatment sites. So, while not directly observed, we speculate that the limitation of seagrass recovery at the meadow edge was likely due to hydrodynamic forces that affected clonal growth and seedling recruitment. Thus, seagrass stability (i.e., ability to recover to prior equilibria) appears to differ between the meadow edge and central meadow. The former appears more susceptible to storms, the latter more exposed to heat stress (Berger et al. 2024).

The relative recovery of shoot density at both locations was linear. The linear recovery trajectory for shoot density supports prior annual observations from within South Bay that followed seagrass shoot density during meadow restoration efforts (McGlathery et al. 2012). However, unlike recovery following South Bay meadow restoration, there was no initial lag in shoot density, which increased at both locations throughout the first post-disturbance growing season. This suggests that mature seagrass meadows possess greater stability than young or newly restored meadows, analogous to forested systems of varying stand age (Sohn et al. 2016). Prior studies suggest it is likely that both seedling recruitment and lateral clonal growth, from remaining shoots and those just outside the plot boundaries, contributed to recovery. Measurement of clonal growth or seed recruitment were beyond the scope of this study, making it difficult to estimate the contribution of each to the observed recovery. Nevertheless, *Z. marina* lateral clonal growth rates range from 0 to $2.26\ \mathrm{m\ yr^{-1}}$ (Castorani and Baskett 2020 and references therein) indicating how lateral growth of about $1\ \mathrm{m\ yr^{-1}}$ could have led to recovery. Most (80–90%) *Z. marina* seedlings disperse within ≤ 7.1 m of their origin (Orth et al. 1994) indicating the potential for seed deposition to contribute to recovery of the 6-m diameter plots. While uncertainty remains regarding the recovery process, these lateral growth rates and seedling dispersal distances suggest that treatment sites benefitted from close proximity to undisturbed areas that promoted rapid shoot density recovery. However, these biological recovery mechanisms were offset by sediment erosion at the edge sites during the second growing season, resulting in a net-zero gain in shoot density between the first and second growing seasons. Nonetheless, seedling recruitment and lateral clonal growth from undisturbed areas will likely be important for the lagged recovery of the edge treatment sites.

Literature synthesis

Experimental disturbances have largely been conducted on small spatial scales of $< 1\ \mathrm{m^2}$ in contrast to our plots of $28.3\ \mathrm{m^2}$. Experimental seagrass disturbances on larger spatial scales better characterize recovery from large disturbance events and how in situ processes influence recovery rates. However, for the predominately smaller-scale studies, lateral clonal growth has been cited as the dominant seagrass recovery mechanism. This is likely due to the greater perimeter to area ratio of small disturbances relative to large disturbances. Additionally, recovery rates of small experimental disturbance areas likely do not adequately represent the range of physical forcings, such as hydrodynamics, that are experienced in large disturbances (Carr et al. 2016; El Allaoui et al. 2016). Furthermore, different types of disturbances likely impact recovery, with environmental disturbances (e.g., heat, disease) potentially selecting for specific traits while mechanical disturbances may not exert selective pressures (Puijalon et al. 2011). Differences in the physical forcings and disturbance type among small-scale experiments and large-scale observational studies likely contribute to the positive, nonlinear relationship between recovery time and disturbance area, suggesting that recovery rates become increasingly slow as disturbance area increases. Additionally, disturbance area thresholds exist at which natural recovery is no longer possible, as was observed in the Virginia Coast Reserve following a concurrent pandemic slime mold disease and hurricane that eliminated seagrass from the system for 70+ yr (Orth et al. 2020). Experimental efforts should further consider not only the disturbance area, but the volume of sediment disturbed, the effects of increased disturbance frequency, how different disturbance types affect trait-based selection, how ecosystem function and community composition recover alongside seagrass, and the impact of targeted restoration actions (e.g., seeding, sediment in-filling, transplants) on large disturbance areas. Studies of the kind proposed will necessitate long-term monitoring and considerable experimental effort, but will provide a greater understanding of seagrass stability as the frequency of pulsed disturbances increases (Webster et al. 2005; Oliver et al. 2018; Smale et al. 2019).

Seagrass disturbance–recovery studies have provided insights into recovery rates and mechanisms across all continents except Antarctica, where seagrass is not known to occur (McKenzie et al. 2020). However, these studies have not been well distributed among the world's coastlines, with a limited representation of islands and oceanic regions such as the Indian Ocean, South Atlantic, and Eastern Pacific. Furthermore, disturbance–recovery studies have only been conducted in 16 of the 191 countries (8.4%) with seagrass meadows (Short et al. 2007; McKenzie et al. 2020). This limited biogeographic representation that covers less than half (47%) of known seagrass species suggests the need to prioritize disturbance–recovery studies in underrepresented regions and on species with low representation. Expanding the range of studies will provide a better understanding of the stability of these keystone species.

Seagrass recovery and resilience

The extensive studies of seagrass recovery indicate that these systems are resilient to disturbances large and small. In conceptual terms, this means the seagrass state is a strong attractor, and there is likely a broad and deep stability landscape that sustains the seagrass state. Our experimental results, coupled with prior long-term observations (Berger et al. 2020; Aoki et al. 2021), support this view and indicate that the seagrasses in the Virginia Coast Reserve can recover from MHWs and likely from hydrodynamic disturbances. However, there are few long-term studies where shallow subtidal areas transition from seagrass to bare or vice versa and maintain those states (as opposed to recover). Such a state shift occurred in the Virginia Coast Reserve in the 1930s and was reversed with concerted restoration efforts beginning in 1999 (Orth et al. 2012, 2020), aided by the reserve's protected status that limits external pressures thereby establishing favorable conditions for restoration (Hemraj et al. 2024). Prior modeling research in the Virginia Coast Reserve identified bistable states between seagrass and bare sediment at a depth of 1.6–1.8 m due to reduced underwater light availability (Carr et al. 2012*b*). However, at shallow depths, *Z. marina* is subject to high water temperatures (> 30°C) in summer that exceed their thermal tolerance (28.6°C), potentially limiting their distribution (Aoki et al. 2020; Berger and Berg 2024). Nonetheless, there remains a limited understanding of the stability landscape of shallow subtidal bare sediments that might otherwise support seagrass and how these habitats interact with seagrass habitats following state shifts (McGlathery et al. 2013).

The frequency of seagrass disturbance and recovery rate should be emphasized in future studies. If mechanisms that maintain seagrass state at locations are altered by an increased frequency and intensity of forcings like MHWs and high wind events (Wiberg 2023), then disturbance may result in slowing recovery rates—an indicator of declining resilience (Carr et al. 2012*a*; Scheffer et al. 2015; El-Hacen et al. 2018). Long-term studies have the potential to reveal such changes. In the specific case of the Virginia Coast Reserve, *Z. marina* is near the southern limit of its distribution (Jarvis et al. 2012) and may become increasingly temperature-stressed as the local climate warms. The current seagrass state might give way to alternates like bare sediment, microalgae/macroalgae, and/or the establishment of subtropical seagrasses. Additionally, sea-level rise within the Virginia Coast Reserve is accelerating and is among the fastest rates on the North American coast (Sallenger et al. 2012; Blum et al. 2021). Current rates of sediment accumulation in seagrass meadows (Greiner et al. 2016; Oreska et al. 2017) are sufficient to keep pace with sea-level rise (Aoki et al. 2020). However, as sea-level rise accelerates, the spatial resilience of *Z. marina* will likely change as intertidal bare sediments become subtidal and deeper areas become light-limited.

Data availability statement

The seagrass shoot density time series (Tassone and Pace 2022*a*), water temperature time series (Tassone and Pace 2022*b*), discreet benthic chlorophyll and surface water quality data (Tassone and Pace 2022*a*, 2022*c*), sediment elevation transects (Tassone 2023), and literature survey data (Tassone and Pace 2023*b*) are publicly available on the Environmental Data Initiative (EDI) data repository. Code used to run all analyses and produce all figures are available at https://github.com/spencer-tassone/SGRecoveryExp_LitSynthesis.

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Conflict of Interest

The authors declare that this research was conducted with no financial or commercial conflict of interest.

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