



Eelgrass (*Zostera marina*) Recovery Affected by Disturbance Timing on Mechanically Harvested Oyster Culture Beds

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Abstract

Amid global seagrass declines and increasing human demands of coastal habitat, it is critical to mitigate the loss of seagrass habitat through understanding seagrass resilience following large-scale disturbance. Although seagrasses often respond to disturbance through increased sexual or asexual reproduction, past research on the cosmopolitan *Zostera marina* (eelgrass) is highly variable in terms of whether recovery occurs, and whether seeds or clonal growth is the primary contributor. In Willapa Bay, Washington state, we studied eelgrass recovery following large-scale disturbance on six adjacent oyster culture beds (~ 10,000 m² in area) that were harvested using mechanical methods (i.e., dredging). We found that recovery potential and mode are heavily affected by the timing of disturbance. In the 200 and 400 days post-disturbance, beds disturbed during the early growing season (EGS; January–April) were estimated to have more than double the vegetative shoot density of beds disturbed during the late growing season (LGS; May–September). We also found a higher contribution of new shoots from seedlings following EGS relative to LGS disturbance, with up to 71% of shoots following EGS disturbance occurring from seedling origin. Consistent with eelgrass life history, spring seedling densities were positively affected by flowering shoot densities the previous summer. Clonal reproduction (i.e., branching) was negatively affected by a disturbance within the past 4 months, likely from physical damage, but also showed negative density dependence, meaning that higher branching rates were observed at lower shoot densities. Overall, this work emphasizes the importance of seedlings to seagrass recovery and demonstrates that *Z. marina* has higher recovery when disturbed (here by mechanical harvest of shellfish) during EGS versus LGS time periods. These findings provide straightforward guidelines for the management of anthropogenic disturbance on eelgrass beds to reduce permanent habitat loss and can also guide restoration efforts of eelgrass beds.

Keywords Eelgrass · Resilience · Disturbance · Shellfish aquaculture

Introduction

Seagrasses are marine angiosperms that provide essential nearshore habitats for fish and invertebrates, as well as offer shoreline protection by sediment stabilization and dissipation of wave energy. Seagrasses are in global decline due to a multitude of stressors including coastline development, nutrient runoff, sedimentation, extreme weather events exacerbated by climate change, fishing and aquaculture practices, disease, and physical disturbances (Orth et al. 2006; Short

et al. 2014). Bioregional rates of decline vary; however, between 1879 and 2009, a loss of 29% of known seagrass extent occurred, with rates of decline accelerating since 1990 (Waycott et al. 2009; Dunic et al. 2021). Furthermore, in a world with a growing human population, many are looking towards the sea for more sustainable food solutions (Gentry et al. 2017; Costello et al. 2020). Amidst global stressors and expanding mariculture practices, there is a need to enhance the resilience of seagrass ecosystems—the ability to withstand repeated disturbances without switching to an alternative stable state—through research and management (Holling 1973; Horan et al. 2011; Unsworth et al. 2015).

In Washington state, including Willapa Bay, oyster farming and eelgrass (*Zostera marina*) have overlapped for over a century (Dumbauld et al. 2009). The state is unusual in that intertidal lands can be privately owned, contributing to the strong socioeconomic and cultural importance of

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the shellfish industry that makes Washington a leader in shellfish production in the United States (van Senten et al. 2020). There are multiple methods of growing oysters, including “ground” or “on-bottom” culture, a primary and historically utilized method in the region, where oysters are grown directly on the sediment, often intermixed with eelgrass. Dredge implements used during oyster harvest or bed maintenance result in disturbance events characterized by the removal of eelgrass vegetative tissue as well as damage or removal of below-ground rhizomes (Tallis et al. 2009). Soft, organic-rich surface sediment is also removed in the process to create optimum conditions for growing oysters on the sediment surface. Past research shows that space competition between oysters and eelgrass is minimal below a density of ~20% shell cover (Wagner et al. 2012). While it is known that dredging activity is a substantial disturbance to co-occurring seagrass (Erftemeijer and Lewis 2006), previous work reveals that seagrass can return to full density; however, recovery periods are variable and generally longer than recovery following manual harvest methods (Tallis et al. 2009; Ferriss et al. 2019). Some oyster farmers report employing dredging techniques that they observe to be less harmful to eelgrass (“Local” or “Farmers’ Ecological Knowledge”), which supports the continued co-occurrence of eelgrass and oysters.

Z. marina is widely distributed across the northern hemisphere, with recovery mechanisms that consist of (1) asexual branching from existing shoots and (2) the production of seeds and seedlings via flowering (O’Brien et al. 2018). Previous work documents variability in the recovery potential of *Zostera* species, with seedling contribution ranging from being the dominant recovery mechanism (Olesen and Sand-Jensen 1994; Jarvis and Moore 2010; Johnson et al. 2021) to playing little or no role (Boese et al. 2009; Macreadie et al. 2014). Seagrasses often enhance reproductive investment in response to disturbance (Cabaco and Santos 2012). Similarly, research in Willapa Bay has revealed elevated seedling densities in dredged seagrass beds compared to control and longline aquaculture beds, suggesting that seedlings contribute to bed recovery following dredging disturbance (Wisehart et al. 2007). Because seeds are negatively buoyant and rhizomes extend at < 1 m per year (Duarte 1991), damage to eelgrass on the oyster culture beds of several hectares cannot be rapidly recovered from eelgrass around the edges. Environmental factors certainly affect the success of recovery (Yang et al. 2013), but some baseline biological criteria, such as the existence of a seed bank or remaining adult shoots, must be met for recovery to be likely (Orth and McGlathery 2012). Understanding how timing, frequency, and severity of disturbance—the defining features of disturbance regimes (Lytle 2001)—interact with *Z. marina* phenology to determine if clonal shoots and/or

seedlings contribute to recovery allows us to hypothesize a 2-year framework to predict recovery potential. Eelgrass does not typically flower in the same year as germination, and the seed bank is short-lived (< 1 year) (Jarvis et al. 2014), so a bed needs to be undisturbed for more than a year for the next seed bank to form. We predict that seeds can persist through winter-time shellfish dredging and, if produced in the prior growing season, will contribute to recovery, with the greatest overall recovery when surviving adult shoots contribute to clonal reproduction (in cases of low or moderate severity disturbance). Following severe disturbance (i.e., no adult shoots remaining), recovery will require a seed bank, which may be absent in a high-frequency disturbance regime.

Due to the phenology of *Z. marina* life history, factors such as timing, frequency, and severity of a disturbance (i.e., shoot damage versus removal) can all affect whether a seagrass bed will demonstrate resilience or be subjected to a critical ecosystem tipping point (Unsworth et al. 2015; Horan et al. 2011; Holling 1973). Past experimental designs examine recovery of *Z. marina* from shoot removal or leaf damage at the small scale of meters (Fonseca et al. 1984; Boese et al. 2009; Soissons et al. 2016), with evidence that the timing, frequency, or magnitude of disturbance influences seagrass response (Ruesink et al. 2012; Soissons et al. 2016). Larger-scale studies track recovery following a single disturbance or die-off event (Plus et al. 2003; Jarvis and Moore 2010; Johnson et al. 2021). One study documents poor seagrass recovery following mechanical harvest (“dragging”) of commercial mussel beds, reporting long-term impacts on seagrass, with densities reduced to 2–3% of reference sites a year following disturbance, with an estimated 10.6-year recovery period (Neckles et al. 2005). Here, we seek to understand the recovery of eelgrass at an ecologically relevant scale (thousands of square meters) across multiple areas where disturbance events vary in frequency and seasonal timing. By considering the interaction of the phenology of *Z. marina* and disturbance timing, we test the underlying processes that determine if recovery is possible, or whether a seagrass bed has been pushed past an ecosystem tipping point. We also consider and hypothesize about the role of frequency, by examining cases where seagrass is disturbed repeatedly without a year (or more) to recover.

We utilized scheduled large-scale disturbances (~ 10,000 m² beds) accompanying the mechanical harvest of Pacific oysters (*Magallana gigas*) to study the recovery mechanisms of eelgrass and determine how seasonal timing of disturbance impacts resilience. The goal of this study is to quantify and identify how the interaction between disturbance timing and eelgrass life history affects resilience and to provide key takeaways that inform the management of planned disturbances to mitigate long-term damages to eelgrass populations. Our specific research questions are:

1. How does the timing of disturbance affect the recovery of eelgrass density?
2. How does the timing of disturbance affect the contribution of seedlings towards recovery?
3. How do flowering shoot density and oyster shell cover influence seedling recruitment (spring seedling density)?
4. How do the occurrence of recent disturbance, shoot density, and season affect branching activity (i.e., clonal reproduction)?

While this study has clear implications for the management of shellfish aquaculture practices on seagrass beds, it also contributes to the broader understanding of seagrass resilience by “experimentally” testing the effects of timing in a semi-controlled setting, at a much larger scale than past experimental work. In a world where seagrasses are threatened globally by anthropogenic disturbances, this work helps to fill an important knowledge gap in understanding seagrass resilience at a scale that is applicable to real-world disturbances.

Methods

Sampling Methods

Our study site, located in the northeastern portion of Willapa Bay, a coastal estuary of Washington state (USA), consists of a series of six contiguous intertidal Pacific oyster (*M. gigas*) culture beds, ranging 150–200 m in length (Fig. 1), that are maintained and harvested using mechanical techniques (i.e., dredging along the surface of the sediment by boat at high tide). The beds contain on-bottom cultured oysters that are harvested on a rotating schedule, meaning beds are at varying stages of the crop cycle at one given time. From spring 2021 to spring 2024, we measured vegetative shoot density, flowering shoot density, seedling density, and oyster shell percent

cover (visually estimated, including live oysters and remnant shell) in spring (late April/early May), summer (mid-June), and fall (late August/early September). All samples were taken using two parallel transects, for a total of twenty 0.25 m² quadrats per bed, with quadrats 15–20 m apart, depending on the bed width. Transects were set at approximately the same location for each sampling, about 20 m and 40 m from the lower edge of the bed (Fig. 1). Seedlings > 15 cm long were considered to be vegetative during summer sampling in terms of density counts, as this length of shoot cannot be identified as seedling or clonal source without excavation. During each sampling, we also collected shoots by excavating half of the quadrats to measure two variables: (1) branching rates (proportion branched of last four rhizome nodes), and (2) in the fall, the proportion of shoots that originated from seed that spring (including branches from seedling-source genets), versus clonal growth from an older plant. In 2021, we only excavated shoots in the fall, and no shoots were excavated in spring 2024. On beds with particularly sparse eelgrass (i.e., mostly empty quadrats), we collected the nearest shoots outside of the quadrats to have additional samples. Genets that originated from seed that year are typically still attached to their small coiled rhizome, showing where the seed germinated, whereas plants that are excavated with a thick broken rhizome were considered to be clones from plants ≥ 1 year old.

Periods of disturbance lasted from 1 to 5 months, encompassing a handful of acute disturbance events, that harvested oysters for sale and then leveled (“cleaned”) the bed for the next crop by dredging. Although the exact dates or number of disturbances within a disturbance period were not provided (Tables 1 and 2), the state of each oyster bed at the end of the disturbance period was comparable. We observed sparse clusters of adult shoots and rhizomes on each oyster bed, which would be the sole source for clonal expansion. The farms intentionally achieve flat and consolidated sediment by removing fines from the surface a few centimeters of sediment, which is accompanied by damage to or removal

Fig. 1 Schematic showing contiguous oyster culture beds with eelgrass that were sampled, as well as the sampling design

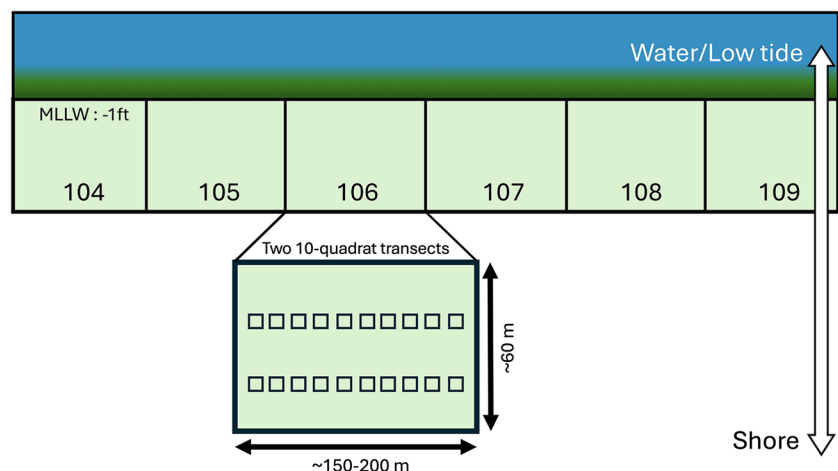


Table 1 Periods of mechanical harvest disturbance from 2020 to 2023 on the six bottom-culture oyster beds

	Bed 104	Bed 105	Bed 106	Bed 107	Bed 108	Bed 109
2020			Nov 2020– March 2021		Jan–Sept	
2021	Oct–Dec	March–June		January–April		
2022			March–April	Dec 2022 –April 2023	Nov 2022 –April 2023	Jan–Aug
2023	April–June	March–April				

Table 2 Categories of disturbance timing based on dates listed in Table 1

	Bed 104	Bed 105	Bed 106	Bed 107	Bed 108	Bed 109
2021	“Control”	LGS	EGS	EGS	“Control”	“Control”
2022	NGS	“Control”	EGS	“Control”	“Control”	LGS
2023	LGS	EGS	“Control”	EGS	EGS	“Control”

of most adult shoots. In the months following harvest, the beds were replanted with young oysters at a low (<20%) density; this replanting was not included in our analysis. We categorized the disturbance events as occurring during different approximate stages of growth for perennial *Z. marina* (Ruesink et al. 2022), where “Early Growing Season” (EGS) is January–April and “Late Growing Season” (LGS) is May–September (Tables 1 and 2, Fig. 2). Seed germination and branching disproportionately occur during EGS, whereas LGS is a period of rapid leaf turnover and increasing shoot size. Seeds typically mature and dehisce from shoots by late July (Ruesink et al. 2022). Thus seed germination occurred during a portion of EGS (estimated January through April per Boardman and Ruesink (2021)), and seed production during a portion of LGS (Fig. 2). Beds that had not been disturbed for over a year (from September), were considered controls (Table 2). We included a “Non-growing Season” (NGS, biologically, slow-growing), during October–December, but only had one bed during 1 year in which harvest and bed cleaning were completed during this time (excluding “controls”). In cases of long disturbance periods, the end of each period was used to determine the category of occurrence.

Data Analysis

Four analyses aligned with the four focal questions of the study and were performed in R (version 4.3.0; R core team 2023) using the glmmTMB package (Brooks et al. 2017) for linear mixed effects modeling and DHARMA package (Hartig 2016) for simulated residual analyses to test model fit. Relevant interactions were tested but not included in the final models, and the collinearity of variables was also tested; ultimately, models and distributions were selected based on residual analyses using DHARMA and AIC values from the model output. Eelgrass and shell variables, which were sampled in 20 quadrats per bed at each time point, were averaged within a bed per sampling event to

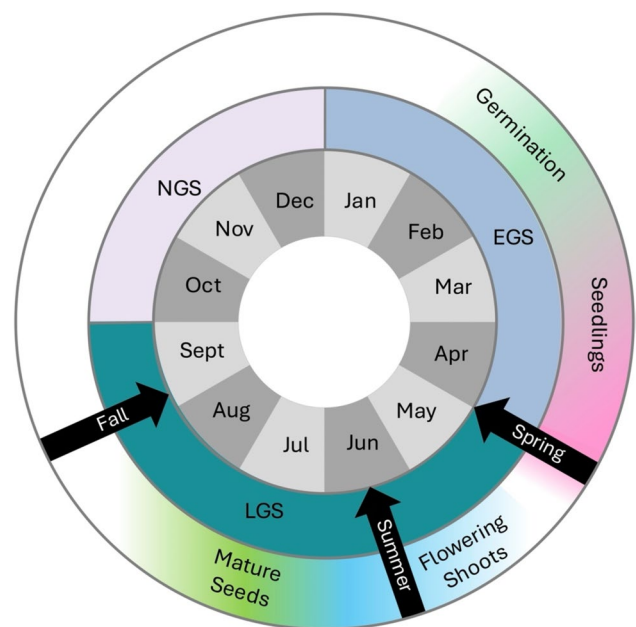


Fig. 2 Schematic showing timing of sampling (black arrows), as well as disturbance periods (EGS, early growing season; LGS, late growing season; NGS, non-growing season) and phenological stages of seedling development. Release of seeds occurs once maturation is reached followed by a period of dormancy, with germination occurring as early as January

avoid pseudoreplication and because quadrats were not positioned identically across sampling events (relevant to the latter three analyses). The bed was always used as a random effect to account for repeated sampling on the same beds over multiple years and across multiple seasons.

The first analysis examined the effect of disturbance timing on eelgrass density. We examined vegetative shoot count (average values from each bed, rounded to the nearest integer) as a function of “days since end of disturbance,” season disturbed, and year, including bed

as a random effect to account for repeated sampling; for this analysis, days since end of disturbance was a continuous variable that accommodated beds disturbed more than 12 months before, and there was no “control” category. Here, LGS and NGS disturbance were compared to EGS disturbance (since there was no “control” group), and a negative binomial distribution was used (link = log). The sample size was 54, as three seasonal samples in each of the 3 years for all six beds were included in this analysis.

Next, to test if the timing of disturbance affects the contribution of seedlings towards recovery, we examined the proportion of shoots from seedling origin (excavated in the fall) as a function of season of disturbance and year, with bed as a random effect. This model used a Tweedie (link = log) distribution, which accommodates data with zero values and wide variation in the proportion from seedlings when present. The sample size was 18 (six beds sampled in fall over 3 years).

For the third analysis, to determine which factors influence the density of seedlings in the spring, we modeled spring seedling density as a function of the previous summer's flowering shoot density, as well as current oyster coverage per bed, and year, with bed as a random effect. Due to the study period of 2021–2024, this analysis only examines seedling densities from 2022, 2023, and 2024 (using flowering shoot densities from 2021, 2022, and 2023), resulting in a sample size of 18. We were unable to reliably test the effect of disturbance during important seed stages (i.e., post-seed settlement, germination), although a higher summer flowering shoot density results from beds being undisturbed in the months leading up to summer sampling (Fig. 1). This model used a Tweedie (link = log) distribution family.

Lastly, we tested how branching was related to recent disturbance, shoot density, and season. We determined the average branching activity for each excavated quadrat containing vegetative shoots, and up to 10 quadrats per bed were averaged to calculate the proportion of the latest four nodes branched. We only examined plants that had gone through at least one winter season (i.e., seedlings were excluded), due to potential differences in phenology. The proportion of nodes branched was analyzed as a function of season, the occurrence of disturbance within the last 4 months, vegetative shoot density, and year, with the bed as a random effect, and used a Tweedie distribution (link = log). The sample size was 54 (six beds with three seasonal samples for 3 years).

Results

Eelgrass in six large areas with different disturbance histories showed a general pattern of lowest vegetative shoot densities at the conclusion of a period of disturbance

(Fig. 3). Phenological changes were indicated by the relatively high densities of seedlings in spring, which transitioned to vegetative shoots by the summer sampling time. Some beds returned to about 40 shoots/m² in between disturbance events, which is within the range of observed eelgrass bed densities for the large morphotype present in Willapa Bay (Thom et al. 2003), while others failed to recover within the study timeframe (Fig. 3).

Our first analysis determined that days since disturbance had a strong positive effect on vegetative shoot density, while LGS disturbance had a significant negative effect on shoot density relative to EGS disturbance (Table 3). The model estimates that for 200 and 400 days post-disturbance, shoot density following EGS disturbance is more than double that of LGS disturbance (Fig. 4, Table 3). Shoot densities were generally higher in 2021 (6.47 per 0.25 m²) than in 2022 or 2023 (4.05 and 3.67, respectively), as indicated by the positive estimate statistically (Fig. 4, Table 3).

In the second analysis, relative to controls without disturbance for at least a year, seedling-origin shoots contributed significantly more to beds that were disturbed during EGS and NGS, whereas LGS disturbance (i.e., within the past 4 months before September sampling) had no effect. Up to 71% of the shoots present on beds at the end of the growing season were only present due to successful seedling establishment earlier in the year (a mean of 20% from seedling contribution). The year also had significant effects, with 2022 having 0.37 contributions from seedling-origin shoots, while lower contributions from seedlings occurred in 2021 and 2023 (0.14 and 0.11 proportion seedling contribution, respectively, Table 4).

The third analysis, testing factors that influence the density of seedlings in the spring, revealed that flowering shoot density from the previous summer is a strong predictor of spring seedling density. Percent oyster shell, ranging from 0 to 30% on average, showed a trend of a positive effect on spring seedling density, but this was not statistically significant (Fig. 5). Year was again a significant predictor, with 2023 having a greater spring seedling density, averaging 2.98 per 0.25 m², while 2022 and 2024 averaged 1.06 and 1.14 seedlings per 0.25 m², respectively (Fig. 5, Table 5).

Lastly, analyzing the effects of recent disturbance (within 4 months), season, vegetative shoot density, and year on branching (proportion of last four nodes branched), we found that branching changed seasonally, with the highest rates in spring (significantly greater than in fall) that declined in summer and fall. Additionally, the year was a significant predictor, with 2022 having lower branching rates overall. The lowest average branching rate was 0.10 during fall 2022, and the highest was 0.40 during spring 2023. There was a negative effect of vegetative shoot

Fig. 3 Vegetative shoot and seedling density shown over the 3-year sampling period (excluding spring 2024). Gray blocks indicate periods of disturbance. Color strips along the top and bottom edges indicate disturbance time categories (EGS, early growing season; LGS, late growing season; NGS, non-growing season). For density counts, shoots were considered vegetative once they were > 15 cm long, even if they originated as seedlings that spring

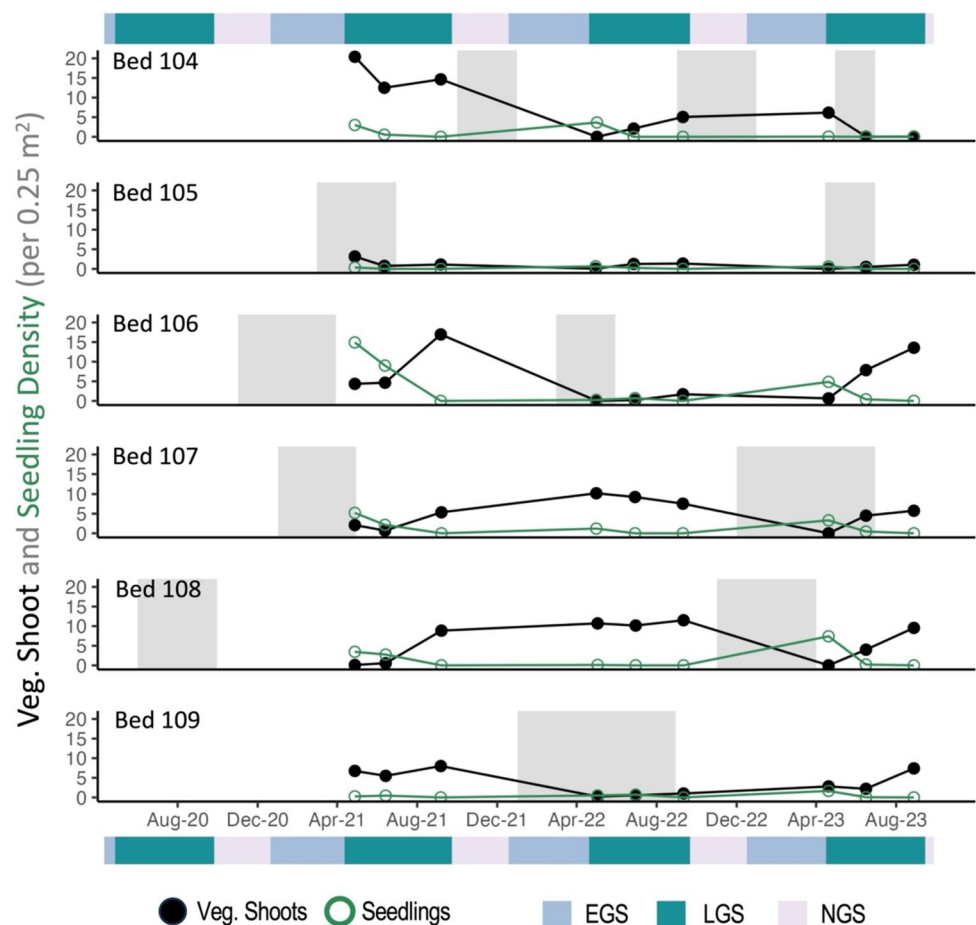


Table 3 Results of linear mixed effects model testing shoot density as a function of days since disturbance, season of disturbance, and year, with bed as a random effect

	Estimate	Std. error	Z value	Pr (> z)
(Intercept)	0.8280	0.2627	3.152	0.0016
Days since disturbance	0.0033	0.0005	6.598	<0.0001
LGS disturbance	-0.7710	0.3319	-2.323	0.0202
NGS disturbance	-0.2357	0.2549	-0.924	0.3553
Year 2022	-0.3600	0.2300	-1.565	0.1175
Year 2023	-0.1018	0.2753	-0.370	0.7115

density as well as a negative effect of disturbance within the past 4 months on the proportion branched (Fig. 6, Table 6).

Discussion

Our results indicate that timing is a key factor when determining the extent to which an eelgrass bed will recover and by which mechanism. If beds are disturbed at high intensity that removes most shoots and rhizomes, recovery depends

on seedlings. Because seeds last only a few months (Jarvis et al. 2014), the eelgrass bed must have been allowed to flower undisturbed the previous year. Furthermore, only beds disturbed during the non/slow-growing season or early-growing season will experience the appropriate timing for seedlings to emerge at a higher rate and be able to grow to adult shoots. Beds disturbed during the late growing season risk removal of seedlings that germinated that spring, as well as damage to adult shoots before they have flowered and produced seeds. Our findings support and help to explain the inconsistency of dominant recovery mechanisms and recovery success that are reported in the literature from small-scale experimental work or opportunistic studies of natural disturbances. When comparing the recovery of *Z. marina* beds following climatic events in Chesapeake Bay during 2005 and 2018, Johnson et al. (2021) report different recovery dynamics, with one case dominated by seedlings while the other was largely recovered via clonal expansion. A collection of other work also documents variability in the recovery potential of *Zostera* species, with some reporting seedling contribution as the dominant recovery mechanism (Olesen and Sand-Jensen 1994; Plus et al. 2003; Jarvis and Moore 2010; Johnson et al. 2021), while other cases are

Fig. 4 Eelgrass (*Zostera marina*) shoot density as a function of days since disturbance, with color indicating disturbance time category. Best fit lines with a y-intercept at 0 included for visual purposes; see Table 2 for results from the generalized mixed model

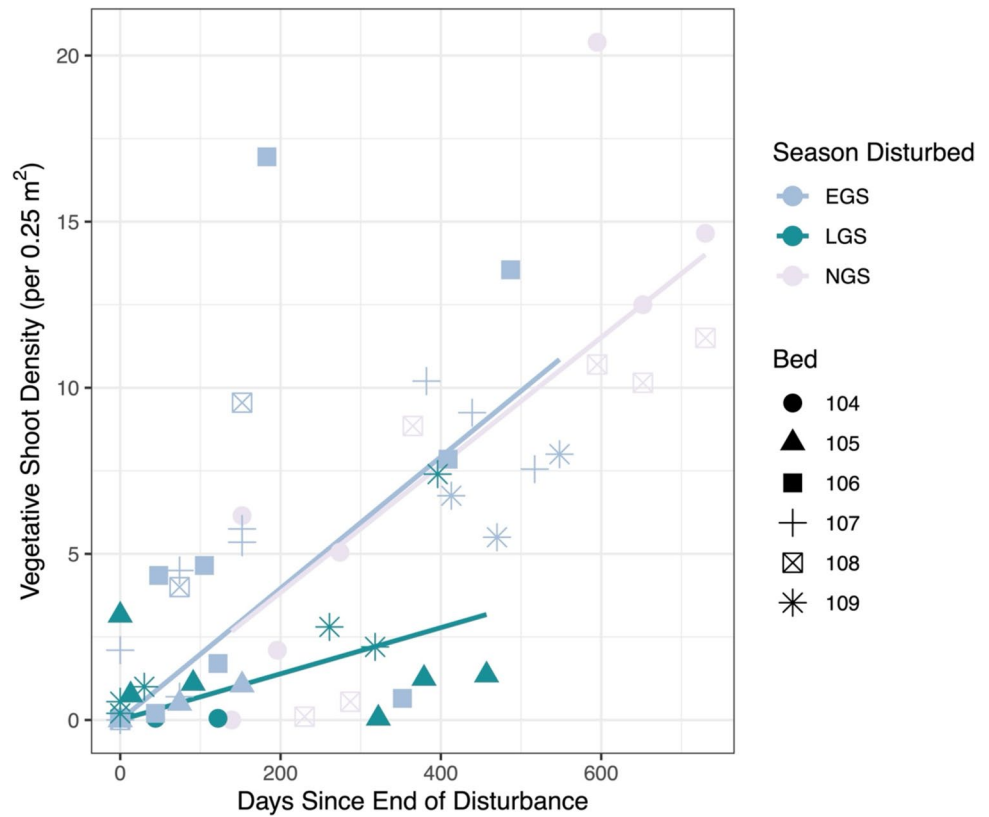


Table 4 Results of linear mixed effects model testing factors that influence the contribution of seedling-origin shoots towards eelgrass (*Zostera marina*) recovery, as the proportion of seedling-origin shoots at the end of the growing season (September) relative to undisturbed control beds

	Estimate	Std. error	Z value	Pr ($> z $)
(Intercept)	-3.1739	0.3774	-8.411	<0.0001
Disturbed EGS	1.8652	0.3707	5.032	<0.0001
Disturbed LGS	0.6672	0.4715	1.415	0.1570
Disturbed NGS	1.7759	0.5744	3.092	0.0020
Year 2022	1.2215	0.3296	3.706	0.0002
Year 2023	-0.6491	0.3678	-1.765	0.0776

reliant on clonal reproduction (Boese et al. 2009; Macreadie et al. 2014).

As disturbance intensity increases, two constraints for resilience are (1) fewer shoots for clonal reproduction and (2) reduced flowering shoot density (Unsworth et al. 2015; O'Brien et al. 2018). At the extreme severity of disturbance, where no adult shoots nor rhizome remain, all recovery must occur from the seed bank produced prior to shoot removal. If disturbance frequency is high, where disturbance reoccurs within 2 years, then any seedlings in the population will not have sufficient time to produce their own seeds (Setchell 1929), and this timing particularly erodes

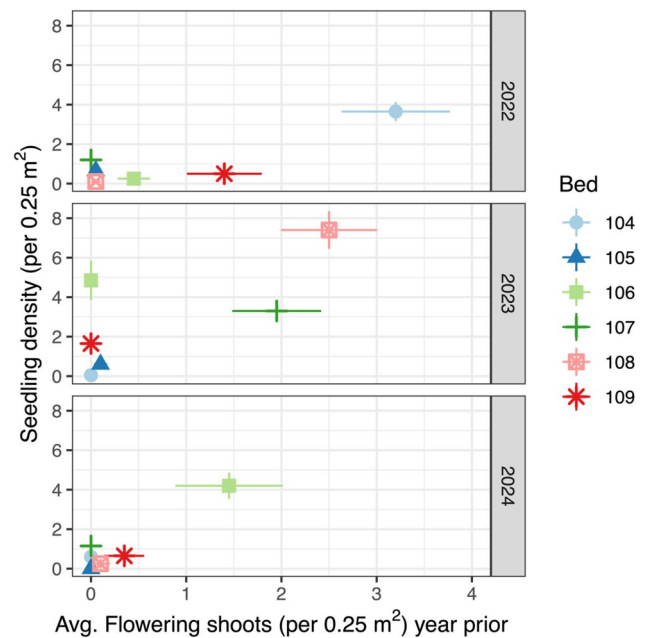


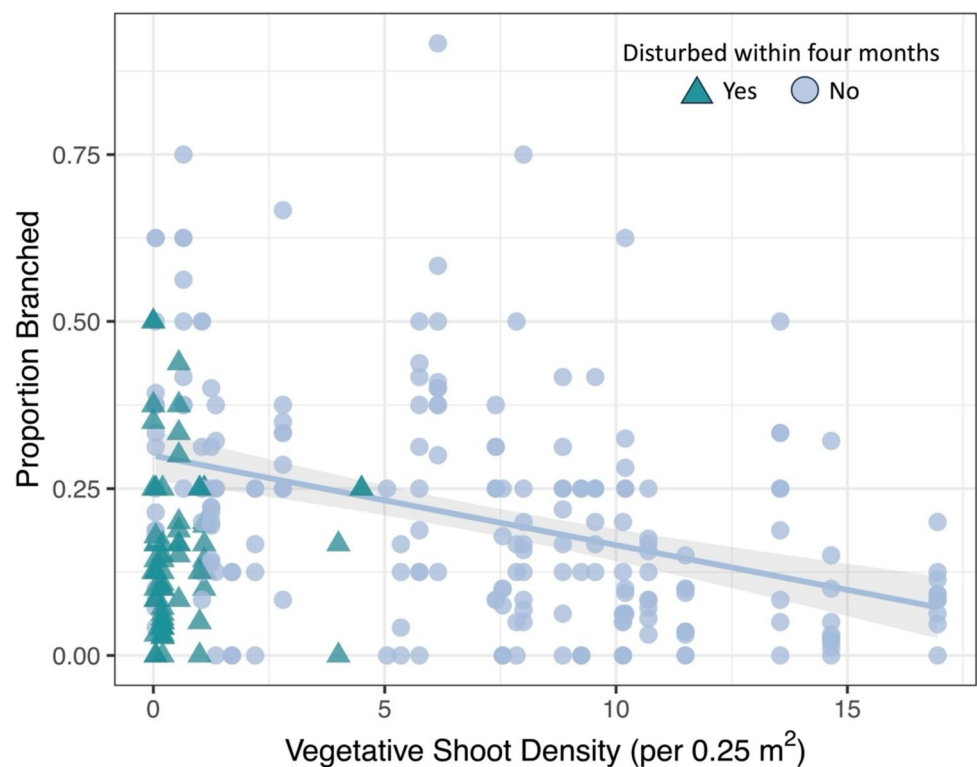
Fig. 5 Average seedling density per bed and year as a function of average flowering shoot density from the prior summer. Graph shows the mean values used in the analysis with standard error. See Table 4 for results from the generalized mixed model

Table 5 Results from linear mixed effects model testing spring seedling density as a function of flowering shoot count from the previous summer, percent shell cover, and year, with bed as a random effect

	Estimate	Std. error	Z value	Pr ($> z $)
(Intercept)	-1.3196	0.5909	-2.233	0.0255
Flowering shoot count (prev. summer)	0.8272	0.2126	3.891	<0.0001
Percent shell cover	0.0258	0.0212	1.215	0.2243
Year 2023	1.1492	0.4101	2.802	0.0051
Year 2024	0.2995	0.4889	0.613	0.5401

population resilience if disturbance interferes with seed production or removes young seedlings post-germination. That is, the period after seed production and before the end of the seedling germination window (i.e., NGS and EGS)

is when eelgrass beds show the highest resilience to disturbance. This effect of frequent disturbance is evident in Fig. 2, where beds with more frequent disturbance (e.g., 104, 106) show a reduction in seedling counts and overall slower recovery of shoot density. Furthermore, consistently poor recovery in bed 105 may reflect low seed densities from repeated and poorly timed disturbances predating the study (Fig. 2). Lower intensity disturbance, where some adult shoots remain, offers multiple methods by which eelgrass can recover and is less likely to result in long-term change. More research is needed to understand the extent to which disturbances directly affect seagrass seed banks. For example, here, it is presumable that some seeds would be removed or displaced by the dredging process. However, our findings suggest that in this scenario, the largest threat to the seed bank is a disturbance that prevents seeds from developing and settling in the sediment, as opposed to a disturbance of

Fig. 6 Proportion of the last four nodes branched as a function of vegetative shoot density (per 0.25 m²), with disturbance in the last 4 months indicated by color and shape. Quadrat values averaged across beds in the analysis are shown as individual points; linear best-fit lines of samples *not* recently disturbed included for visualizing the relationship of branching and vegetative shoot density**Table 6** Results from linear mixed effects model testing proportion of last four shoots branching as a function of season, vegetative shoot density, year, and whether or not there was disturbance within the last four months, with bed as a random effect

	Estimate	Std. error	Z value	Pr ($> z $)
(Intercept)	-1.4269	0.1525	-9.359	<0.0001
Spring	0.2900	0.1001	2.898	0.0038
Summer	-0.0279	0.1252	-0.223	0.8235
Vegetative shoot density	-0.0490	0.0106	-4.641	<0.0001
Year 2022	-0.3853	0.1496	-2.576	0.0100
Year 2023	0.3707	0.1405	2.638	0.0083
Disturbed within past four months	-0.3576	0.1214	-2.945	0.0032

the sediment during the NGS or EGS period (post-seed settlement). In other types of disturbance, or different methods of dredging, direct damage to the seed bank during NGS or EGS disturbance could be problematic. It is possible that following seed settlement, organic material from decaying large late-summer seagrass shoots, and/or other sources of sedimentation, could result in a layer of soft sediment that is then removed by dredging without harming or removing seeds buried below. Alternatively, seeds may act as large dense particles and return to the sediment while fines are moved off the bed. While we only measured seed production (flowering shoot density) and emergence of seedlings, the seed bank would be an extremely valuable metric to further understand the impact of various disturbances, and also as a management tool to gauge the potential resilience of particular seagrass beds.

Having two methods of recovery, clonal and via seeds, is a feature that makes *Z. marina*, among other grasses, naturally quite resilient (Unsworth et al. 2015). In the case that adult shoots are removed in a large disturbance event, the seed bank exists as a backup that can still allow recovery. And in fact, an intermediate level of disturbance can cause increased genetic diversity, further contributing to the resilience of that eelgrass population (Hughes and Stachowicz 2011; Foster et al. 2021). It is well established that prescribed disturbance can be used in terrestrial grassland management to promote biodiversity (Edwards et al. 2007; Valko et al. 2014). In these cases, timing and method of disturbance—and how they promote clonal growth versus seed bank contribution—must be considered to achieve desired species composition and not facilitate undesired or invasive taxa that could grow to dominate the landscape (Lewis et al. 2010; Larios et al. 2013; Merou et al. 2013). Unlike most terrestrial grasslands, *Z. marina* regularly exists in monoculture and has short-lived seeds, so cases of high-severity disturbances repeated at high frequency that push eelgrass past the “tipping point” may cause a permanent shift to an unvegetated state, or only gradually be repopulated by nearby *Z. marina* propagules. However, in cases where *Z. marina* coexists with or occurs near other seagrass species, ruderal, and in some cases non-native, species may be established after the removal of *Z. marina* (Moore et al. 2014; Bando 2006).

Just as different aspects of disturbance may have positive or negative relationships to recovery via seeds, so too does disturbance affect the ability of adult shoots to produce clonal branches. The pattern of branching due to disturbance was overlain on a typical seasonal pattern, in which densities are lowest in winter, and clonal branching rapidly increases shoot densities as day length increases (Olesen and Sand-Jensen 1994; Ruesink et al. 2022). Branching rates can increase as a phenotypically plastic response to shoot thinning or

transplant at low density (Ruesink et al. 2012; Ruesink 2018), and the current results involving large-scale disturbances also demonstrated negative density dependence in which branching declined at higher adult shoot density. However, if disturbance had occurred within the last 4 months, branching activity declined (Fig. 6), likely because physical damage to leaves and stress can inhibit branching (Ruesink et al. 2012). While the survival of adult shoots following disturbance still certainly boosts resilience potential in a bed, it is important to consider that their ability to contribute to clonal repopulation may be hindered following physical damage.

From a management perspective, for aquaculture or otherwise, these findings have straightforward applications for supporting resilience in *Z. marina* beds. If beds are to be disturbed at levels that leave few remnant shoots, ideally, it would (1) be during a slow or early growing stage for the local *Z. marina* population (this varies regionally), (2) leave adults shoots with rhizome in place and only disturb a subset of the meadow extent to contribute to clonal expansion, and (3) not be repeated annually in the same location, with breaks of > 1 year for beds to recover and for shoots to mature to resupply seed banks. Handpicking of shellfish is also a lower-disturbance (albeit less efficient) harvest method that can be used to limit disturbance while allowing for harvest during critical time periods. Furthermore, although planting seagrass is not a typical step in shellfish aquaculture, beds with low shoot and seed densities could be restored by spreading *Z. marina* seeds from nearby beds at the end of the summer, supplementing a seed bank if flowering shoots are rare (Marion and Orth 2010). Although not a significant finding here, further research is needed to understand the direct effects of on-bottom oyster culture on seedlings to inform the best timing for oyster planting. Low densities of shells or oysters may protect delicate seedlings from wave action or desiccation simply by providing structure. Similarly, there is the potential for low densities of oysters to support the growth of seedlings by providing biodeposits that improve conditions for germination or growth (Unsworth et al. 2022).

Findings from this work can also be applied to other types of disturbances that contribute to seagrass loss around the globe. Acute, large-scale disturbances to seagrass have been caused by wasting disease, storms, anoxia, macroalgal blooms, turbidity, and extreme temperature or salinity, as well as human activities (den Hartog and Jacobs 1980; Plus et al. 2003; Short and Wyllie-Echeverria 1996; Waycott et al. 2009; Arias-Ortiz et al. 2018). Some of these disturbances have characteristic timing, for example, a summer heatwave could cause mortality before or after the seed set. If damage occurs to flowering shoots before they have had a chance to drop mature seeds, then sourcing seeds from a nearby population to outplant may help support resilience in that meadow. Large-scale disturbances may also differ in intensity, particularly in the

degree of thinning and whether meristems are removed. Events that allow for the persistence of rhizome and meristem have the potential to recover via clonal growth in many seagrasses (Campbell 2003, Di Carlo et al. 2011, Lai et al. 2018). Overall, the timing of disturbance relative to the phenology of seagrass, as well as impacts on clonal or sexual reproduction (or both), shape the available recovery mechanisms of seagrass, allowing biologists to predict which meadows are most “at-risk,” versus seagrass beds that are more likely to recover without intervention.

In a world witnessing global seagrass declines, while simultaneously leveraging the ocean for sustainable food production (Costello et al. 2020; Gentry et al. 2017), it is critical to understand how long-term damage to seagrass beds can be mitigated. While the disturbance documented here on eelgrass is a product of shellfish aquaculture, disturbances generally are becoming increasingly common and widespread due to continued shoreline development and extreme weather events (Orth et al. 2006; Short et al. 2014). Where there is a direct anthropogenic cause, management decisions around the timing and intensity of disturbance can support the long-term resilience of eelgrass beds. In conclusion, the findings from this work contribute to a path forward to support eelgrass resilience during an era of global seagrass declines with increasing nearshore development and climatic extremes. *Z. marina* and other seagrass species have evolved to use resilience mechanisms, which can be leveraged by considering disturbance timing, intensity, and seagrass life histories.

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Author Contribution Both authors contributed to data collection and study design. F. Boardman performed the data analyses and composed the manuscript. J. Ruesink advised analyses and contributed edits to the manuscript.

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