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RESEARCH ARTICLE

Storm resilience of subtidal soft-bottom mussel beds: Mechanistic insights, threshold quantification and management implications

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Abstract

1. With the projected escalation of extreme storm events, coastal ecosystems risk undergoing catastrophic shifts and losing essential ecosystem services. Subtidal soft-bottom mussel beds, vital components of these ecosystems, are particularly vulnerable to hydrodynamically-induced dislodgement (i.e., detachment of mussel clumps from the bed), especially during storms. However, the mechanisms underlying the resilience—comprising both resistance and recovery—of these beds to storms remain unclear, despite being essential for informed management.
2. This study addresses this knowledge gap regarding subtidal soft-bottom mussel beds by: (i) quantifying their dislodgement threshold (i.e., the hydrodynamics causing widespread dislodgement of mussel clumps) using novel in situ monitoring methodologies in a representative region, namely the Dutch Wadden Sea; (ii) unveiling the influence of prior life history (here, wave exposure extent) and storm durations on their dislodgement thresholds through a flume study; and (iii) assessing the impacts of repeated storms and prior life histories (here, wave exposure extent and substrate types) on their recovery (i.e. mussel re-aggregation) through mesocosm experiments.
3. Integrated experimental evidence indicates that: (i) hydrodynamic-induced dislodgement is a sudden process characterized by distinct near-bed orbital velocity thresholds, which were identified at our study site to be between 0.45 and 0.50 $m\,s^{-1}$; (ii) peak storm intensity, rather than storm duration, primarily drives the dislodgement of subtidal soft-bottom mussel beds, and prior wave exposure extent regulates the dislodgement threshold; (iii) repeated storms do not seem to affect the recovery of these beds following storm-related disturbances when the conditions between storms are conducive to mussel re-aggregation, whereas substrate type significantly impacts recovery.
4. *Synthesis and applications*. Overall, concerns regarding subtidal soft-bottom mussel beds degradation primarily stem from increasing storm intensity and their

limited resistance to such events. The methodology we developed enables low-cost quantification of mussel resistance thresholds across broad spatiotemporal scales, facilitating the pinpointing of vulnerable areas. Our findings inform strategic management by highlighting the influential role of prior life histories in shaping mussel bed resistance and the potential to accelerate mussel bed recovery through substrate modification (e.g., shell additions). Both our methodology and findings hold promise for application in comparable ecosystems, such as oyster and coral reefs.

KEYWORDS
mussel beds, resilience, soft-bottom system, storm, subtidal, threshold quantification, Wadden Sea

1 | INTRODUCTION

Anthropogenic climate change is reshaping global ecosystems, notably exemplified by the significant threat that extreme hydrodynamic events, such as storms, pose to coastal ecosystems (Hanley et al., 2020; Harley et al., 2006). These ecosystems may undergo catastrophic state shifts if disturbances surpass their critical tolerance thresholds (de Paoli et al., 2017; Reed et al., 2022). This is especially alarming due to the potential loss of essential ecosystem services such as carbon sequestration, sediment stabilization, biodiversity enhancement, and commercial food provision via aquaculture (Temmink et al., 2021; van der Schatte et al., 2020). Mussel beds are important ecological features of coastal ecosystems, typically found on soft sediments or hard substrates (like rocks) in intertidal and subtidal zones (Commito et al., 2014; Miner et al., 2021). For decades, increasing the survival rate and density of mussel beds to sustain their functionality has been the guiding principle in natural mussel bed conservation and commercial mussel bed management (Aldridge et al., 2023; Schotanus, Capelle, et al., 2020; Schotanus, Walles, et al., 2020). However, there remains a dearth of understanding regarding how extreme hydrodynamics influences the population dynamics of mussel beds (Capelle et al., 2019; Donker et al., 2013). This is especially evident for the subtidal zone, where mussel beds are consistently submerged underwater, posing challenges for both access and monitoring. With the anticipated escalation of extreme storm events (Hanley et al., 2020), it is foreseeable that there will be greater hydrodynamically-driven losses of mussel beds (Carrington et al., 2009; Schotanus, Capelle, et al., 2020). Therefore, there is an urgent necessity to understand how mussel beds respond to these events, including their resistance and recovery, in order to inform effective management strategies.

Natural and commercial mussel beds in Europe are typically situated on soft sediments and form distinctive spatial patterns by aggregating with conspecifics (de Paoli et al., 2017; van de Koppel et al., 2005). As mussels aggregate into patches, their resistance to hydrodynamic-induced dislodgement (i.e., detachment from the mussel bed) is initially robust (de Paoli et al., 2017). However, this also means that during storm events, mussels tend to be dislodged in clumps rather than individually, resulting in considerable loss of the mussel bed (Bertolini et al., 2019; Denny, 1995; Schotanus, Capelle, et al., 2020). Increased fragmentation within mussel beds would further erode their resistance to both storms and less severe hydrodynamic conditions. Studies concerning intertidal soft-bottom mussel beds have unveiled a significant correlation between mussel bed abundance and the peak (95th percentile) wave pressure, along with associated critical thresholds, beyond which mussel beds are at risk of sharp declines in abundance (Donker, 2015). This phenomenon may similarly apply to subtidal soft-bottom mussel beds, with storm impacts potentially even more pronounced. The intertidal zone can experience higher orbital velocities from relatively small waves due to its shallow depth, while storm waves are typically depth-limited (Karimpour et al., 2017). Conversely, in the subtidal zone, these smaller waves do not reach the seabed, but storm waves are able to induce higher orbital velocities as they are less constrained by depth (Weber, 1991). Surprisingly, our present comprehension of dislodgement thresholds and dynamics in subtidal soft-bottom mussel beds remains highly limited, particularly amidst storms.

Dislodgement within mussel beds on hard substrates typically arises from the failure of mussel byssal attachment (Miner et al., 2021). The related dislodgement threshold thus primarily hinges on the attachment strength of byssal threads and the frontal area of (i.e., drag forces experienced by) individual mussels (Denny, 1987). In contrast, dislodgement within mussel beds on soft sediment appears to be associated with mussel density and the resulting clump size, mass, and shape (Bertolini et al., 2019; Capelle et al., 2019). A flume study, targeting subtidal soft-bottom mussel beds, quantified the critical dislodgement threshold of such mussel clumps typically range between 0.3 and 0.4 $m s^{-1}$ of unidirectional flow (Capelle et al., 2019). However, these thresholds are remarkably low when compared to typical tidal flows and wave orbital velocities observed at the study site (i.e., the Wadden Sea; Donker, 2015). Empirical evidence further suggests that mussel beds in this region did not suffer significant losses at these velocities. This miss-match hints at two possibilities: (i) Mussel beds in the field may have a higher dislodgement threshold, potentially due to larger mussel patches and longer aggregation periods; or (ii) Mussel beds in the field experienced dislodgement as the threshold was surpassed but subsequently re-aggregated under calm hydrodynamics, undergoing repeated disturbance-recovery cycles. If the latter is the case, one can also anticipate that dislodgement thresholds of mussel beds may vary over time in response to their recent life history, as mussels have been proven to be highly adaptable to environmental conditions (Nicastro et al., 2010; Schotanus et al., 2019). To validate these hypotheses, it is imperative to quantify the critical dislodgement threshold of subtidal soft-bottom mussel beds in situ and delve deeper into their resilience mechanisms under (storm) wave impacts.

In this study, centred on subtidal soft-bottom mussel beds, our aims are: (i) to develop an effective methodology for continuously monitoring their dislodgement dynamics in situ under (storm) waves; (ii) to seek integrated experimental evidence for understanding the variability in their resistance and recovery under storm impacts and the associated driving mechanisms. *Firstly*, utilizing a novel method (i.e., Mussel Clump Accelerometer), we conducted continuous monitoring of mussel clump dislodgement throughout the storm season in a representative subtidal soft-bottom mussel habitat (i.e., the Dutch Wadden Sea) to quantify the associated dislodgement threshold. *Secondly*, employing a wave-generating flume, we investigated to what extent mussel clump dislodgement depends on recent life history and storm exposure duration. *Thirdly*, using wave-mimicked mesocosms, we conducted disturbance-recovery experiments to examine the effect of storm frequency on mussel bed recovery after dislodgement. *Finally*, we discussed the implications of our findings for advancing mussel bed resilience studies, as well as their relevance to mussel bed conservation and management.

2 | MATERIALS AND METHODS

2.1 | Novel method to quantify mussel movement

Small accelerometers (MSR-145B4) were used for continuous and high-frequency recording of mussel movements over the long term. With dimensions (62 × 20 × 14 mm) and a weight of 18 g comparable to those of individual mussels, these accelerometers were suitable for integration into mussel patches. To ensure natural aggregation within the existing mussel bed, approximately 10 live mussels (mean shell length = 4.8 cm and mean wet weight = 10.8 g) were glued onto each accelerometer, creating small clumps of mussels housing an embedded accelerometer (Mussel Clump Accelerometer [MCA], Figure 1a).

The accelerometers measure the acceleration ($m s^{-2}$) of mussel clumps in *x*, *y*, *z*-coordinates with a frequency of $25 s^{-1}$. As such, they do not measure acceleration by, for example, currents and individual waves, but instead measure orientation change in 25-s increments. The orientation change (δ_{ori}) between each measurement was calculated as follows:

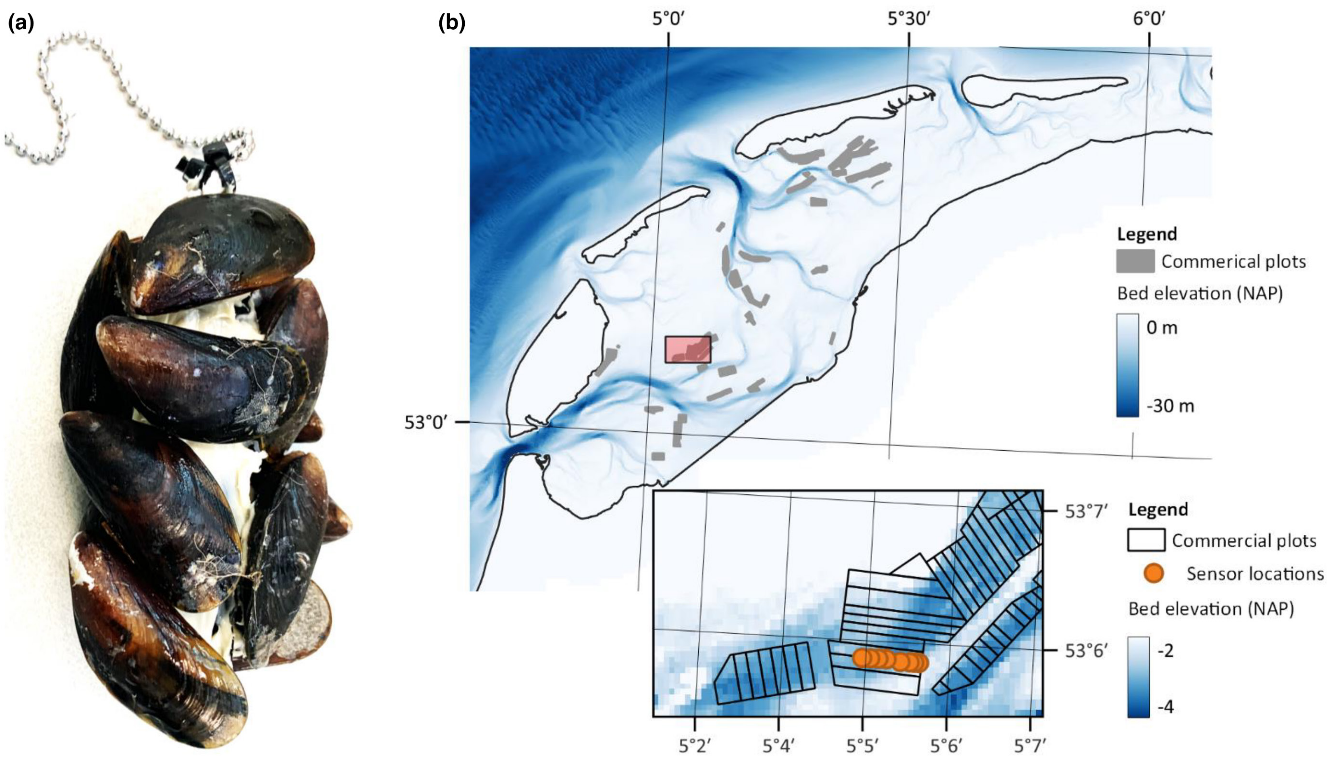

FIGURE 1 (a) Photograph showing the mussel clump containing an accelerometer, i.e., the Mussel Clump Accelerometer (MCA), which was developed to monitor the movement of mussel clumps in situ. (b) The geographical location of subtidal soft-bottom mussel beds selected for field monitoring in the Dutch Wadden Sea. The subplot depicts the layout of sensors deployment for in situ monitoring of mussel clumps movement and hydrodynamic regimes along an elevation gradient in a mussel bottom-culture plot.

$$\delta_{ori} = \sqrt{\partial_{a,x}^2 + \partial_{a,y}^2 + \partial_{a,z}^2}$$

where $\partial_{a,x}^2$, $\partial_{a,y}^2$, and $\partial_{a,z}^2$ are the changes in acceleration in *x*, *y*, and *z* direction. As the measurement frequency of accelerometers is relatively low compared to wave period, it is not possible to directly distinguish dislodgement from other movements via δ_{ori} from a single measurement, so the movement intensity was defined as the sum of δ_{ori} over a 30-min rolling window.

To find out whether dislodgement could be accurately distinguished from other movements (such as swaying under mild waves) from accelerometer readings, validation tests were conducted in a racetrack flume (see Zhao et al., 2022 for flume details). Loose mussels were placed within the straight test section of the flume to establish a mussel bed (1.6×0.6 m) with a density of 10 kg m^{-2}. Four MCAs were introduced, along with mild waves (near-bed orbital velocity = 0.21 m s^{-1}), to facilitate their aggregation into the mussel bed for 3 days. Thereafter, the flume was operated at its maximum attainable wave setting (near-bed orbital velocity = 0.47 m s^{-1}) for 1 day to induce the dislodgement of MCAs. The experiment was replicated twice, with one run using loose MCAs, and one run where MCAs were attached to ball chains and secured to the beam above the flume, to assess whether attachment to MCAs by ball chains (as done for field deployment, details below) influences the measured movement intensity. Tukey-HSD tests were performed to assess statistical differences in movement intensity between treatments (i.e., loose MCAs vs. chained MCAs) and mussel state (i.e., stable under mild waves vs. dislodgement under strong waves). For this we used the mean movement intensity of each MCA during the period where we observed either stable MCAs or dislodged MCAs. Mean movement intensity was log-transformed to obtain normality, assessed with Shapiro–Wilks tests, and homogeneity of variance, assessed with Bartlett's test.

2.2 | Field monitoring: Quantifying mussel bed dislodgement threshold in situ

The field monitoring was conducted in the Dutch Wadden Sea, with the bottom-cultivated mussel beds in Scheurrak tidal inlet selected as the optimal site for deploying MCAs (Figure 1b). These beds characterized by similarly sized juvenile mussels and management measures were in place to minimize predation pressure from starfish. As mussel losses by hydrodynamic-induced dislodgement in this region have been observed anecdotally by mussel farmers to correlate with depth, a total of 30 MCAs were deployed during the storm season of 2021–2022 at eight locations along a depth transect, with water depths ranging between −4 and −2 m NAP (Dutch ordinance level). To be able to retrieve them, the MCAs were attached with 2-mm thick ball chains to poles that the mussel farmers use to indicate the boundaries of their plot.

To link MCAs movement to hydrodynamic forces, waves were measured using pressure sensors (OSSI-010-003C). While the study area is also subject to tidal currents, wave-induced bed shear stresses on shallow-water mussel beds are significantly higher during both calm and stormy conditions (Donker et al., 2013). These sensors were deployed along the same transect, measuring water depth at a frequency of 10 Hz during 7.5-min burst with 15-min intervals between bursts. Two sets of MCAs did not have an adjacent pressure sensor due to practical limitations, thus the data from the nearest pressure sensor, deployed at a similar water depth, was used. Wave height was calculated from the pressure signal via spectral analysis. A depth correction was applied to the spectral amplitude to account for pressure attenuation:

$$d_c = \frac{\cosh(kz)}{\cosh(kd)}$$

where d_c is depth correction (−), *k* is wave number (−), *z* is installation height above bottom (0.5 m), and *d* is water depth (m). The wave number was calculated empirically (Guo, 2002):

$$k = \frac{y}{d}$$

where

$$y = x^2\left(1 - \left[\!\left[\exp\left(-x^{2.4908}\right)\right]\!\right]\right)^{\frac{1}{2.4908}}$$

and

$$x = \frac{d\omega}{\sqrt{gd}}$$

where *g* is gravitational acceleration (9.81 m s^{-2}) and ω is orbital speed (rad s^{-1}). The significant wave height (H_s, m) was calculated from the depth-corrected spectral amplitude:

$$H_s = 4\sqrt{\int E(f)df}$$

where *E* is spectral amplitude (m^2 Hz^{-1}), and *f* is frequency (Hz). The lower frequency limit was set to 0.05 Hz for removing infragravity waves, and the upper limit was set to 2 Hz to remove turbulence.

We used the near-bed orbital velocity as an indicator for the hydrodynamic forces experienced by mussel beds, because determining the shear stress experienced by them requires an estimation of roughness, which would add a factor of uncertainty. The near-bed orbital velocity (*u*; m s^{-1}) was calculated from water depth and significant wave height via linear wave theory:

$$u = \frac{\omega H_s}{2\sinh(kd)}$$

The water depth was corrected by adding or subtracting the difference in local bed elevation between the MCAs and pressure sensor for those MCAs that did not have an adjacent pressure sensor. All fieldwork was conducted with the support of the local management agency and did not require any special permits.

2.3 | Flume study: Identifying the effect of storm duration on mussel bed dislodgement threshold

Mussel beds were pre-constructed in the racetrack flume to evaluate the effects of storm duration on mussel bed dislodgement. This involved evenly distributing individual juvenile mussels over a 1.6×0.6 m test section containing a sediment-shell mixture (sand:shell = 7:3; thereafter referred to as mixed substrate), resulting in a bed density of 10 kg m^{-2}. The mixed substrate represents a typical bottom feature in the Dutch Wadden Sea (Capelle et al., 2019). The sediment, with a grain size range of 365–405 μm, positioned on the coarser side of the spectrum found in this region, was chosen to minimize the impact of scouring. These mussels (mean shell length = 4.8 cm and mean wet weight = 10.8 g) were collected from the commercial mussel bed where the field study was conducted in the same year. A total of 16 mussel beds were constructed for the following four treatments, with four replicates each.

1. *Calm*: Mussel beds developed in still water for 3 days.
2. *Calm-Storm*: Mussel beds developed in still water for 3 days and then were exposed to stronger but non-mussel-dislodging waves (u = 0.28 m s^{-1}) for 3 days.
3. *Wavy*: Mussel beds developed under mild waves (u = 0.21 m s^{-1}) for 3 days.
4. *Wavy-Storm*: Mussel beds developed under mild waves (u = 0.21 m s^{-1}) for 3 days and then were exposed to stronger but non-mussel-dislodging waves (u = 0.28 m s^{-1}) for 3 days.

After each treatment, the mussel bed was subjected to dislodgement threshold quantification. That is, waves were increased stepwise with u increments of approximately 0.05 m s^{-1} until dislodgement was observed. The u was measured with an Acoustic Doppler Velocimeter (Nortek Vectrino) with a sampling frequency of 200 Hz. The dislodgement threshold was calculated as the average of all orbital velocity peaks over a 60-s period during which dislodgement was observed. The Tukey-HSD test, following the Shapiro–Wilk test on data distribution, was adopted to evaluate the statistical differences in dislodgement thresholds of mussel beds among different treatments.

2.4 | Mesocosm experiment: Revealing the effect of storm frequency on mussel bed recovery

Disturbance-recovery experiments were conducted to examine the effect of storm frequency on mussel bed recovery after dislodgement. Mussel plots with a density of 10 kg m^{-1} were pre-assembled in metal containers (0.6×0.3×0.15 m), using juvenile mussels from the same source as for the flume study. A total of 16 mussel plots were prepared and distributed across eight aquariums housed in a climate chamber. These aquariums were filled with 400 L of filtered seawater, maintaining a constant water temperature of 12°C. Mussels were fed daily with 10 mL of highly concentrated algae solution, resulting in a peak concentration of approximately 2 billion cells mL^{-1} within the aquariums. Four of the eight aquariums were characterized by still water, while the other four were equipped with a pneumatic wave-paddle to create wave-mimicked oscillatory flow (period = 4.5 s, u = 0.13 m s^{-1}). The two mussel plots in each aquarium were configured with different sediment types, namely soft sediment or mixed substrate. Overall, this resulted in the following four treatments, each with four replicates.

1. *Calm-Soft*: Mussel plots developed in still water on soft sediment.
2. *Calm-Mixed*: Mussel plots developed in still water on mixed substrate.
3. *Wavy-Soft*: Mussel plots developed under mild waves on soft sediment.
4. *Wavy-Mixed*: Mussel plots developed under mild waves on mixed substrate.

For each treatment, the recovery after dislodgement was assessed by experimentally breaking up mussel clumps within each mussel plot by hand and measuring their re-aggregation thereafter. This mimicked the dislodgement caused by storms and subsequent recovery during hydrodynamical-calm periods. The breaking up of mussel clumps was carried out twice a week for 2 weeks, resulting in a total of four disturbance-recovery events that is representative of an extreme sequence of repeating storms.

The re-aggregation of mussel clumps was measured using time lapse cameras set to an interval of 20 min. Images were processed by removing the optical distortion and increasing the contrast, so mussels could be clearly distinguished from the substrate (see Figure S1a). The fraction of the substrate which was covered by mussels was used as an indicator for aggregation. When mussels are spread out evenly, the initial cover fraction is high. The more the mussels aggregate, the lower the cover fraction. The mussel cover fraction was determined by separating mussels from substrate using a threshold in the red colour band, yielding a binary image (Figure S1b). To remove noise, patches identified as mussels within the binary image but smaller than half the size of a single mussel were rejected. Additionally, small gaps between mussels within a patch, identified as bare substrate in the binary image, were removed by filling patches smaller than 1.5 times the size of a single mussel (Figure S1c). Shapiro-Wilks tests were employed to examine the normality of the data distribution, followed by three-way analysis of variance (ANOVA) to assess the effects of different treatments and disturbance counts on the recovery of the mussel plots post-disturbance.

All mussels used in this study were sourced from local mussel farmers, and no ethical approval was required.

3 | RESULTS

3.1 | Effectiveness of new method to quantify mussel movement

The flume validation tests revealed significant differences in the movement intensity between stable and dislodged MCAs, regardless of whether they were loose or chained ($p < 0.001$; Figure 2). This confirms the effectiveness of MCAs in monitoring the hydrodynamic-induced dislodgement of mussel clumps. Notably, the movement intensity after dislodgement of chained MCAs was significantly higher than that of loose MCAs ($p<0.01$; Figure 2), whereas the movement intensity of stable chained MCAs was nearly identical to that of stable loose MCAs ($p=1.0$; Figure 2). The chains prevented dislodged MCAs from sliding away over the substrate, which does not necessarily result in a change in orientation of the accelerometer. Instead, chains were observed to tug on the MCAs, which prevented them from moving larger distances but increased the measured movement intensity as tugging increases δ_{ori}.

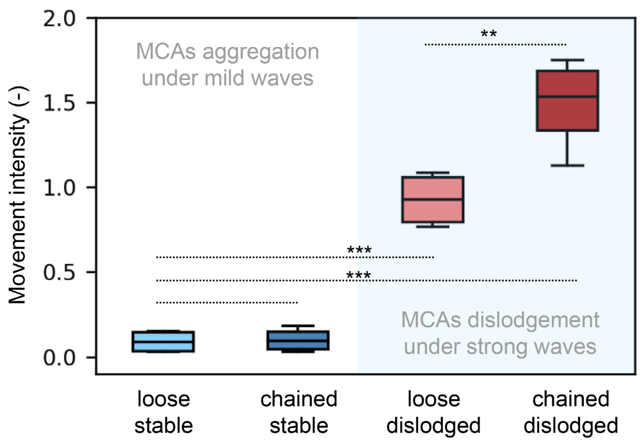

FIGURE 2 Results from flume validation tests on the effectiveness of MCAs (Mussel Clump Accelerometer; developed to quantify mussel clump movement). MCAs were deployed in pre-constructed mussel beds in two configurations, loose and chained, and allowed to aggregate for 3 days. During aggregation, both loose and chained MCAs remained stable, after which they were exposed to strong wave to induce dislodgement. The *x*-axis labels indicate the four resulting treatments, while the *y*-axis labels depict the movement intensity (i.e., accelerometer readings, logarithmically transformed) of MCAs under treatments. Asterisks indicate the significance levels between treatments (***0.001; **0.01; *0.05).

3.2 | Dislodgement threshold of subtidal soft-bottom mussel bed

Due to unanticipated strong storms during deployment and resulting technical malfunctions during retrieval, only 12 out of the 30 deployed MCAs were recovered, of which 9 had aggregated into the existing mussel bed and 3 remained loose clumps. Data from wave sensors indicated that the monitoring period included both calm and stormy conditions. This corresponded to the multiple cycles of stable and movement recorded by MCAs for mussel clumps, consistently showing intense movement during stormy conditions (Figure 3a). The movement intensity (>30; Figure 3b) of MCAs under stormy conditions closely matched that (>$10^{1.5}$; Figure 2) of dislodged chained MCAs observed in the flume validation tests, confirming that mussels were indeed dislodged. Notably, there were four large storms, of which three occurred over a 6-day timespan (Figure 3b). The largest storm (named *Eunice*) was among the three heaviest storms recorded in the last 50 years, resulting in a peak H_s of 1.26 m at the study area.

Loose MCAs exhibited higher movement intensity compared to aggregated MCAs under lower near-bed orbital velocities (*u*; Figure 4). Movement of loose MCAs was observed from $u = 0.05$ m s^{-1} and increases exponentially until peaking at $u = 0.3$ m s^{-1} (Figure 4). Movement of aggregated MCAs remained stable at $u < 0.1$ m s^{-1} and then increased exponentially between $u = 0.1$ and $u = 0.3$ m s^{-1}, but only peaked at a lower value (Figure 4), indicating that the MCAs experienced slight movement due to waves but were not dislodged. The difference in movement intensity between loose and aggregated

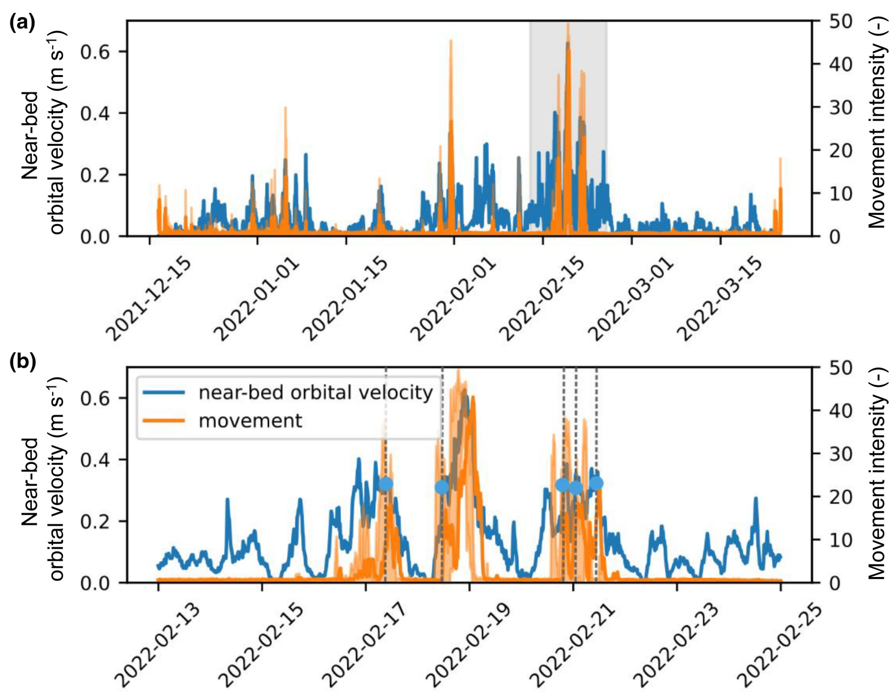

FIGURE 3 (a) Near-bed orbital velocity and mean movement intensity of the aggregated MCAs (Mussel Clump Accelerometer; developed to quantify mussel clump movement) during field monitoring period, with the storm period outlined in grey. (b) Near-bed orbital velocity and mean MCAs movement intensity during the storm period. Vertical dashed lines and blue markers indicate MCAs dislodgement events.

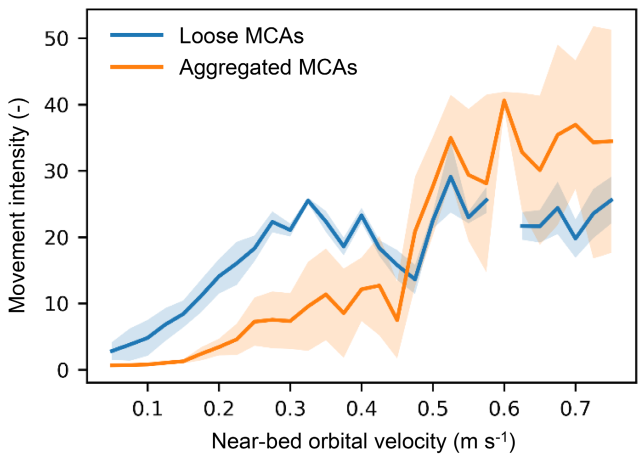

FIGURE 4 Movement intensity of loose and aggregated MCAs (Mussel Clump Accelerometer; developed to quantify mussel clump movement) at various near-bed orbital velocities as measured in the field. Loose MCAs refer to those that failed to aggregate onto existing mussel beds after deployment, while aggregated MCAs refer to those that successfully aggregated onto existing mussel beds post-deployment. The orbital velocity interval at which the movement intensity of aggregated MCAs exceeded that of loose MCAs was recognized as the dislodgement threshold for the mussel bed, that is between 0.45 and 0.50 m s^{-1}.

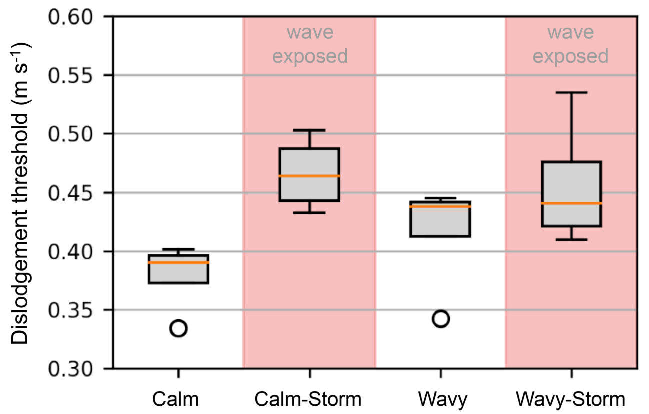

FIGURE 5 Dislodgement thresholds (i.e., the near-bed orbital velocity causing the dislodgement of mussel clumps) of mussel beds developed under four treatments (*x*-axis labels) quantified by flume studies. Calm: Mussel beds developed in still water for 3 days. Calm-Storm: Mussel beds developed in still water for 3 days and then were exposed to stronger but non-mussel-dislodging waves for 3 days. Wavy: Mussel beds developed under mild waves for 3 days. Wavy-Storm: Mussel beds developed under mild waves for 3 days and then were exposed to stronger but non-mussel-dislodging waves for 3 days.

MCAs diminished between $u = 0.45$ and $u = 0.50$ m s^{-1}, where there was a rapid increase in movement intensity of aggregated MCAs which exceeded that of loose MCAs (Figure 4). This rapid increase in movement intensity is indicative for the dislodgement threshold.

3.3 | Effects of storm duration on mussel bed dislodgement threshold

Flume measurements showed little overall variation in mussel bed dislodgement threshold between the different treatments (Figure 5). Mussel beds developed in still water (i.e., *Calm*) had a lower dislodgement threshold (0.38 ± 0.02 m s^{-1}) compared to the other treatments (Figure 5). The threshold increased after exposure to strong waves (i.e., *Calm-Storm*) to 0.47 ± 0.03 m s^{-1}, albeit not significantly ($p = 0.06$; Figure 5). There was no significant difference in dislodgement threshold between mussel beds developed in still water and under mild waves (i.e., *Calm* vs. *Wavy*; $p = 0.57$; Figure 5). Moreover, exposure to strong waves did not affect the dislodgement threshold when mussel beds were developed under mild waves (i.e., *Wavy* vs. *Wavy-Storm*; $p = 0.99$; Figure 5). This indicates that storm duration does not affect the dislodgement threshold of mussel beds; instead, this is determined by the peak storm intensity.

3.4 | Effect of storm frequency on mussel bed recovery

In the mesocosm experiment, mussels were observed to aggregate more strongly on soft sediment compared to mixed substrate, resulting in smaller final coverage (i.e., *Calm-Soft* and *Wavy-Soft* vs. *Calm-Mixed* and *Wavy-Mixed*; $p < 0.001$; Figure 6a; Table 1). Wave exposure did not influence mussel aggregation after disturbance (i.e., storm-related dislodgement) on the same substrate (i.e., *Calm-Soft* vs. *Wavy-Soft* and *Calm-Mixed* vs. *Wavy-Mixed*; $p = 0.549$; Figure 6a; Table 1). There was little effect of repeated disturbances on mussel aggregation rate, as mussels were observed to reach an equilibrium pattern (i.e., cover) within 20–40 h in all cases (Figure 6a; Figure S2). On mixed substrate (i.e., *Calm-Mixed* and *Wavy-Mixed*), repeated disturbances did not influence the equilibrium mussel cover irrespective of wave exposure (Figure 6a,b). On soft substrate and exposed to waves (i.e., *Wavy-Soft*), mussels were observed to aggregate stronger after the first disturbance ($p = 0.05$; Figure 6b), but the equilibrium mussel cover remained similar to the initial cover following subsequent disturbances ($p = 0.73$ and $p = 0.61$ for disturbance-2 and disturbance-3, respectively). No significant increase in mussel cover, indicating a decrease in aggregation, was observed in any of the treatments for any number of disturbances. This indicates that mussels demonstrate resilience to frequent storm-related disturbance when post-storm conditions support recovery.

4 | DISCUSSION

Discrete high-energy hydrodynamic events, such as storms, are changing in both frequency and intensity (Donat et al., 2011; Hanley et al., 2020), potentially exacerbating the collapse risk of vital ecosystems such as subtidal soft-bottom mussel beds. Our results suggest that the increasing frequency of storms does not necessarily undermine the long-term stability of subtidal mussel beds by

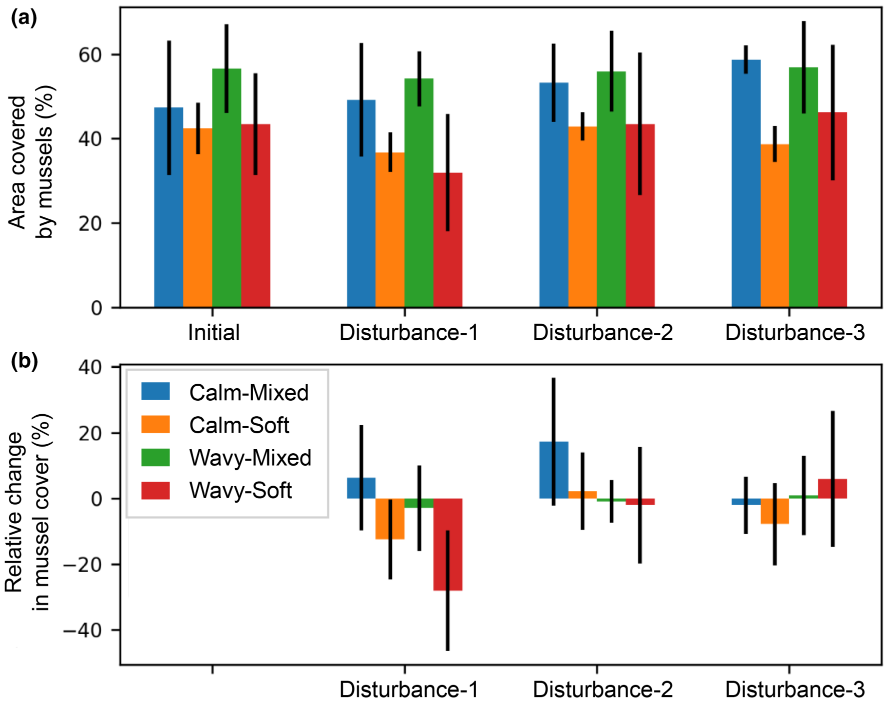

FIGURE 6 Recovery after repeated storm-related disturbances of mussel beds developed under different treatments (displayed with different coloured bars) in the mesocosm experiment. Calm-Mixed: Mussel plots developed in still water on mixed substrate (i.e., sediment-shell mixture). Calm-Soft: Mussel plots developed in still water on soft sediment. Wavy-Mixed: Mussel plots developed under mild waves on mixed substrate. Wavy-Soft: Mussel plots developed under mild waves on soft sediment. (a) Area where mussels re-aggregated (i.e. re-covered) after each disturbance, shown as the mean area covered 24–28 h after the disturbance. (b) Percentage change in mussel cover generated by recovery after each disturbance compared to the initial cover.

TABLE 1 Results from the three-way ANOVA assessing the effect of different treatments on recovery after disturbance of mussel beds in the mesocosm experiment.

	sum_sq	df	*F*	*p*(>*F*)
Substrate	0.401	1.0	39.957	<0.001
Wave exposure	0.004	1.0	0.364	0.549
Disturbance count	0.032	3.0	1.055	0.377
Substrate:wave exposure.	3.7×10^{-5}	1.0	0.037	0.952
Substrate:disturbance count	0.004	3.0	0.140	0.938
Wave exposure:disturbance count	0.002	3.0	0.069	0.976
Substrate:wave exposure:disturbance count	0.007	3.0	0.221	0.881
Residual	0.461	46		

Note: These treatments include substrate (i.e., soft sediment vs. mixed substrate), wave exposure (i.e., still water vs. mild waves), and disturbance count.

reducing their recovery ability, as mussels were able to rapidly re-aggregate after repeated dislodgement, provided that the conditions during recovery are suitable. Concerns about their degradation of subtidal mussel beds should primarily stem from increasing storm intensity and their limited resistance to these extreme events. Mussel dislodgement typically occurred because of a single peak event where the critical dislodgement threshold is exceeded. The value of this dislodgement threshold was found to be primarily shaped by the prior life history of mussel beds rather than the storm duration.

4.1 | Mechanisms driving resilience of subtidal mussel beds

Non-linear responses to changing abiotic stresses are prevalent in coastal ecosystems (Harley et al., 2006). Such responses are typically caused by discrete thresholds, where variation in stress levels can trigger disproportionately substantial ecological responses, culminating in abrupt states shift when critical thresholds are surpassed (Reed et al., 2022; Stagg et al., 2020). Our study marks the first in situ exploration of the non-linear response of subtidal soft-bottom mussel beds to hydrodynamic disturbances, during which the dislodgement threshold range between 0.45 and 0.5 $\mathrm{m\,s^{-1}}$ were identified. Our flume experiment further suggested that these dislodgement thresholds may be context-dependent. Specifically, mussels in wave-exposed areas tend to allocate more energy toward producing stronger byssal threads or forming larger patches (Nicastro et al., 2010; Schotanus et al., 2019), resulting in higher dislodgement thresholds compared to those in wave-sheltered areas. Essentially, mussel (clump) dislodgement depends on the balance between the mussels' tolerance to hydrodynamic stress and the instantaneous hydrodynamic intensity (Carrington et al., 2009). Other environmental conditions, such as pH, emersion time, heatwaves, and predator pressure, as well as mussel bed characteristics, such as size, density, spacing, and mussel age, could further modulate these dislodgement thresholds by potentially influencing byssal thread strength and patch complexity (Capelle et al., 2016; Dickey et al., 2018; Li et al., 2020; Schotanus et al., 2019).

During our field monitoring, several storms occurred over a short time span, all of which produced near-bottom orbital velocities that far surpassed the identified dislodgement threshold of target mussel beds. Aligned with our initial hypothesis, the dislodged mussel clumps managed to re-aggregate into the mussel bed and were dislodged again at similar thresholds during subsequent storms, resulting in a repetitive disturbance-recovery cycle. This finding underscores the impressive recovery capability of subtidal mussel beds, with a short window of opportunity (e.g., 2–3 days) being sufficient for the dislodged mussel clumps to re-aggregate after storms. This is consistent with previous findings, which have shown that mussels can complete patterned aggregation behaviour and produce byssal threads to anchor themselves within few days (de Paoli et al., 2017; van de Koppel et al., 2008). Notably, our field setup using ball chain secured MCAs ensured that mussel clumps would be dislodged but not lost as the threshold was surpassed, allowing them to settle and aggregate in proximity during subsequent hydrodynamic-calm periods. While this scenario might manifest in reality, we cannot disregard other possibilities, such as dislodged mussel clumps being expelled by storms (especially the resulting strong currents) from their original beds and ending up in unsuitable habitats. This would undoubtedly lead to fragmentation of the mussel bed, and its recovery would necessitate the recruitment of external mussels or clumps, such as those expelled by storms from nearby or distant mussel beds. Extensive experimental research is still necessary to rigorously validate these possibilities. Nevertheless, the use of ball chains is essential for recovering MCAs, and they can effectively amplify the movement intensity of mussel clumps after dislodgement. This enables the distinction between stable and moving states of the mussel clumps and facilitates the quantification of the critical dislodgement threshold. To prevent the loss of MCAs due to long ball chains becoming entangled or breaking during strong storms, strategic adjustments to current deployment methods are recommended, such as using shorter (e.g., 20 cm) ball chains to attach MCAs to a custom metal frame with multiple branches.

Surprisingly, the repeated storms (four times within 2 weeks) in our mesocosm experiments did not have a notable impact on the recovery of subtidal soft-bottom mussel beds after dislodgement. With future climate scenarios expected to bring more frequent and irregular storm events (Donat et al., 2011; Hanley et al., 2020), it is possible that mussel beds may not fully recover before facing another storm, leading to a slowdown in their recovery rate due to the mussels becoming exhausted during re-aggregation. Follow-up studies should consider the rising frequency and irregularity of storm events (Hanley et al., 2020). Nevertheless, our mesocosm studies revealed that substrate type plays a crucial role in determining mussel bed recovery. Mussels residing on mixed substrates exhibited a faster aggregation rate following repeated storm events compared to those on soft sediment, albeit resulting in weaker final aggregation. Mixed substrates like sediment-shell mixture have also been demonstrated to effectively shorten the window of opportunity for mussels to develop resistance against hydrodynamic-induced dislodgement (Capelle et al., 2019). This may be attributed to the shells providing mussels with a solid attachment surface, eliminating the need for conspecific aggregation movements and thus conserving more energy to produce more byssal threads (Christensen et al., 2015; Commito et al., 2014). Other factors that influence mussel byssal thread strength or aggregation behaviour, such as habitat conditions and body size (Babarro & Carrington, 2013; Dickey et al., 2018; Li et al., 2020), may also hold the potential to further regulate the recovery ability of subtidal mussel beds.

4.2 | Implications for subtidal mussel bed management

To achieve strategic management with the goal of maintaining ecosystem integrity, predicting the locations, timing, and extent of potential mussel dislodgement and recovery under intensified hydrodynamic disturbance is a challenging but indispensable mission, with in situ observations of target mussel beds being a fundamental cornerstone (Hanley et al., 2020; Schotanus, Capelle, et al., 2020; Schotanus, Walles, et al., 2020). This study established for the first time a cost-effective and feasible monitoring system (i.e., MCAs), incorporating accelerometers and pressure sensors, tailored to this purpose. This system is capable of long-term, high-frequency recording of the fine-scale behaviours of mussel beds in response to hydrodynamic disturbances, even during storms, while allowing for mass deployment at a comparatively low unit cost. Cheap unit cost facilitates simultaneous investigation at various locations to assess ecosystem resilience on a large scale, which is imperative given that our findings point toward the existence of spatial variability in dislodgement threshold and recovery potential of subtidal mussel beds.

Multiple-site monitoring using our developed method would enable the identification of critical factors (which may include depth, wave intensity, pH, substrate type, etc.) driving spatial variations in dislodgement thresholds and the establishment of relevant response relationships (Carrington et al., 2009; Dickey et al., 2018; Schotanus et al., 2019). This makes broadly identifying site-specific dislodgement threshold through spatial interpolation possible, offering a solution for technical and workload difficulties in this context (Beguería & Vicente-Serrano, 2006; Greene & Daniels, 2017). By integrating monitoring or modelling of regional hydrodynamic regime, it becomes feasible to undertake large-scale and long-term predictions of mussel bed dislodgement risk. Moreover, continuous monitoring and large-scale predictions also allow for tracking the frequency and irregularity of threshold being surpassed (i.e., dislodgement events), thereby potentially identifying site-specific windows of opportunity for mussel bed recovery (see Hu et al., 2015 for a relevant example). This approach also holds promise for broader implementation in other regions or analogous underwater ecosystems (such as intertidal and freshwater mussel beds, offshore, subtidal, and intertidal oyster reefs, as well as coral reefs) to make organism resilience under hydrodynamics more predictive.

The resulting large-scale risk assessment can help pinpoint vulnerable areas where targeted management interventions are needed to strengthen mussel resilience against hydrodynamic disturbances. Our study revealed that subtidal mussel beds exhibit higher critical dislodgement thresholds under relatively harsh conditions, suggesting the possibility of enhancing mussel bed resistance by manipulating prior life history factors, such as the degree of wave exposure, when selecting source populations. Relevant pioneering practices are emerging in the Netherlands and New Zealand, where juvenile mussels collected by suspended seed collectors deployed in wave-exposed areas are relocated to wave-sheltered areas for bottom cultivation or ecological restoration (Benjamin et al., 2023; Schotanus, Capelle, et al., 2020). These juvenile mussels, conditioned by high-energy environments, exhibit higher dislodgement thresholds that are less likely to be exceeded in the relocated sites, ensuring stable presence during the early establishment phase. Additionally, our study highlights the influential role of substrate composition, particularly the presence of shell material, in shaping mussel bed recovery. This finding underscores the potential benefits of substrate modification, such as the addition of bivalve shells to sediments, at target sites to maximize the success of cultivation or restoration efforts by further enhancing ecosystem resilience (see Schotanus, Walles, et al., 2020; Temmink et al., 2021 for inspirational examples).

AUTHOR CONTRIBUTIONS

Jaco C. de Smit, Zhiyuan Zhao, Jacob J. Capelle and Tjeerd J. Bouma conceived the ideas and designed methodology; Jaco C. de Smit and Zhiyuan Zhao collected and analysed the datasets; Jaco C. de Smit, Zhiyuan Zhao, Jacob J. Capelle, Theo Gerkema, Johan van de Koppel and Tjeerd J. Bouma led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available via the 4TU. Research data Repository https://doi.org/10.4121/ce413614-1c82-4e81-90c0-323aa7d2fabd (de Smit et al., 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Image filtering process. The original image is filtered by setting a threshold on the red colour band. This threshold is selected manually for each set of images due to variation in lighting between experimental runs. The filtered image is processed by removing 'mussel' patches smaller than half the area of a single mussel, and filling 'bare' patches within the mussel bed smaller than 1.5 times the area of a single mussel.

Figure S2. Development of mussel cover over time for each experiment and replicates. On hard substrate, mussel cover hardly changes after a very brief initial settlement (i.e., mussels attach to the substrate). On soft substrate, there is an aggregation phase of approximately 20–40h. There is no clear change in aggregation visible as a result of repeated disturbances, as the differences between replicates are larger.

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