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Enhancing seagrass restoration success: Detecting and quantifying mechanisms of wave-induced dislodgement

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HIGHLIGHTS

- Understanding wave induced dislodgement of *Zostera marina* shoots after transplantation
- Replication of the restoration method with harvested shoots in a wave flume
- Evaluation of dislodgement factors across transplantation methods and shoot traits
- Not exceptional large waves but long-term cyclic loads drive seagrass dislodgement.
- Shoots with a rooting period < 12 days are especially vulnerable.

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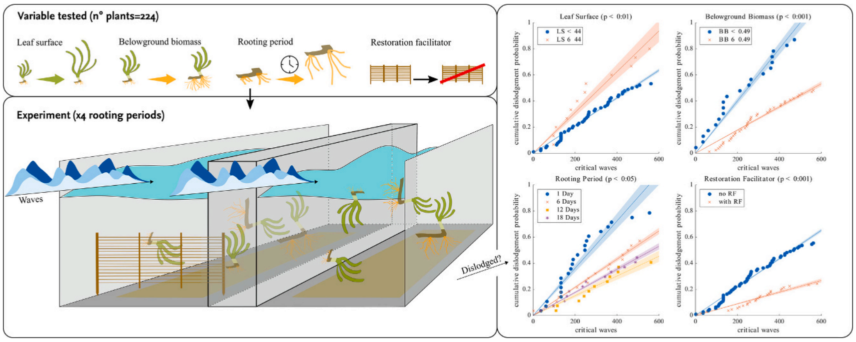
GRAPHICAL ABSTRACT



ABSTRACT

Seagrass meadows are one of the most productive ecosystems of the world. Seagrass enhances biodiversity, sequesters CO_2 and functions as a coastal protection measure by mitigating waves and enhancing sedimentation. However, populations are declining in many regions and natural recolonization of bare sediment beds is protracted and unlikely. The widely used single shoot transplantation method for seagrass restoration is time-consuming and expensive, thus it is important that chances of survival are high. Dislodgement due to wave action poses a particular high risk during the first days after transplantation. This study replicates the transplantation method with a total of 224 harvested shoots (*Zostera marina*) planted in a wave flume under real sea state conditions. After varying rooting periods in cultivation tanks with low hydrodynamic exposure, the shoots together with their surrounding soil were installed inside the flume and exposed to increasing sea state in intermediate water depth (near-bottom maximum orbital velocity MOV = 0.25–0.59 m/s) for 250 min (≈5000 waves). Half the plants were protected by a willow fence, serving as a restoration facilitator. Our results show that dislodgement is not driven by singular exceptional large waves, but by the wave-induced stress from long-term cyclic loads (fatigue). Furthermore, we found that shoots with a rooting period <12 days are especially vulnerable. We also detected that dislodgement is critically impacted by belowground biomass and leaf surface. The deployed restoration facilitator enhances shoot survival by 22.4 % and mitigates the effect of the rooting

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period. The findings indicate that wave exposure and shoot morphometrics are crucial to shoot survival in the first 12 days after transplantation. Considering morphometrics in shoot selection for transplantation may thus reduce the need for restoration facilitation. In conclusion, our research facilitates planning of seagrass restoration including the identification of suitable weather windows, restoration facilitator necessity, and shoot traits.

1. Introduction

As one of the most productive ecosystems of the world, seagrass meadows provide important ecosystem services (Costanza et al., 1997; Barbier et al., 2011), estimated to have a value of 29.000 USD2007/ha/year (Costanza et al., 2014). Seagrasses create commercial value to fisheries (Borum et al., 2004; Barbier et al., 2011) and through production of organic carbon it sequesters CO2 (Duarte et al., 2005; Orth et al., 2006; Fourqurean et al., 2012; Stevenson et al., 2023). Seagrass is also recognised as providing coastal protection (Ondiviela et al., 2014), where established meadows can reduce flow velocities induced by waves and currents (Hansen and Reidenbach, 2013; Gambi et al., 1990) as well as dampen waves (Barbier et al., 2008; Paul and Amos, 2011; Paul et al., 2012). Additionally, wave heights are mitigated by a reduction in relative water depth when seagrass-induced sedimentation (Hendriks et al., 2008) and substrate stabilization (Ward et al., 1984) result in a rising bathymetry (Christianen et al., 2013) of coastal waters.

Despite the fact that seagrass ecosystem services have been well established in the literature, the loss of seagrass habitat globally continuously to accelerated (Walker et al., 2006). While seagrass is also lost due to natural disturbances like diseases and storms, human activities have been identified as the main driver (Short and Wyllie-Echeverria, 1996). By expanding the meta-analysis of Waycott et al. (2009), Dunic et al. (2021) found a global net decline in seagrass coverage of 19.1 % since 1880, with the highest decline in the Temperate North Atlantic East (69 % since 1880).

Contrary to the global trend in seagrass distribution, following widespread losses, the Baltic Sea is currently experiencing a positive trend, due to improved habitat conditions (de Los Santos et al., 2019). Nevertheless, natural recolonization processes occur, if successful at all, at a slow pace due to several reasons: Established seagrass meadows improve water clarity and induce a positive seagrass sediment-light feedback (SSL) (Bouma et al., 2005; Adams et al., 2016; Maxwell et al., 2017). Thus, existing seagrass facilitates the growth of seagrass, while bare sediment beds prevent initial seagrass growth due to unfeasible hydrodynamic conditions (Carus et al., 2021). Additionally, the limited dispersal range hinders natural recolonization of areas with no seagrass nearby (Reusch, 2000; Hämmerli and Reusch, 2003). Therefore, seagrass recovery should be supported by restoration measures. Even with active restoration efforts, field trials in shallow water depth, high hydrodynamic exposure, or both showed low success (van Katwijk et al., 2016; Bos and Van Katwijk, 2007). The observed phenomenon may be attributed to prevalent transplantation techniques, as detailed by van Katwijk et al. (2016), which involve the physical methodologies of transplantation of individual seagrass shoots. These methods do not mitigate physical stressors (Temmink et al., 2020) and as a result are sensitive to hydrodynamic conditions. Especially the time shortly after restoration, when rooting of the shoots is not sufficient yet, is critical.

Hydrodynamic forces induced by either waves and/or currents act on the aboveground biomass of seagrass shoots, potentially dislodging the embedded plant from the sediment. Simultaneously, the anchoring forces, primarily produced by the belowground biomass (root system), function to maintain the shoot position. Therefore, newly transplanted shoots can be dislodged due to high hydrodynamic forces on the leaves (Christensen and Tackney, 1983) or due to erosion of the sand around the roots. Dislodgement can be triggered as an abrupt occurrence by an individual wave, by cyclic loading of waves that mimic a fatigue-like behaviour known from structural mechanics in engineering, or a combination of both. Little is known about which of the effects governs the dislodgement of seagrass, especially the underlying mechanics for newly transplanted shoots are not conclusively determined in the literature yet. In shallow waters, dense seagrass meadows that extend into the water column create higher flow resistance compared to deeper waters or to bare sediment. As newly restored sites have a lower flow resistance due to lower plant density, the hydrodynamic exposure on the few transplanted shoots is relatively higher than in established sites. This renders higher rates of erosion around the shoots and leads to higher hydrodynamic forces acting on the aboveground biomass (Christensen and Tackney, 1983).

A minimum wave or current induced flow velocity is necessary for seagrass survival, as with decreasing flow velocity the diffusive boundary layer forming around the leaves becomes too thick for carbon (needed for photosynthesis) to reach the inner-plant in a sufficient amount (Koch, 2001). Too intensive hydrodynamic exposure on the other hand can lead to dislodgement. Koch (2001) investigated thresholds for minimum (0.03–0.16 m/s) and maximum (0.5–1.8 m/s) current velocities suitable for *Z. marina*. Bobsien et al. (2021) investigated thresholds in the same range for *Z. marina* in the Baltic Sea, coupling a species distribution and a wave model. They found that maximum orbital velocities (MOV) < 0.4 m/s at a distance 0.5 m above the sea floor are indicative of *Z. marina* presence in the western part of the German Baltic Sea coast, while for $MOV > 0.7$ m/s the probability for seagrass occurrence is <10 %. In a similar approach Infantes et al. (2009) predicted the upper depth limit of *Posidonia oceanica* at 0.38–0.42 m/s near-bottom orbital velocity (induced by the mean wave height H_{mean}) at the Balearic Islands (Mediterranean Sea). To distinguish the upper depth limit of *P. oceanica* (mostly due to surf-related effects) Vacchi et al. (2014) developed an ecological model based on field measurements from Liguria (northwestern Italy). Erftemeijer et al. (2023) studied the hydrodynamic resilience of nine seagrass species growing in Adelaide's Coastal Waters (Australia). They found a MOV of 0–0.3 m/s (close to bottom) and currents of 0.05–1.5 m/s suitable for seagrass. The multitude of studies conducted for *Z. marina* and the geographic and methodological diversity while gaining similar outcomes, shows that these findings can be considered robust for established meadows. However, the scientific literature on newly restored seagrass is sparse. Conducting model tests with newly transplanted seagrass shoots in currents and waves Carus et al. (2020) found a steep increase in the dislodgement likelihood of the shoots around a bed shear stress of 0.4 N/m^2 (between $MOV = 0.16$–0.2 m/s).

Although it is well recognized that increased hydrodynamic conditions exert larger forces and impacts on seagrass shoots that may finally end up causing dislodgement, a gap remains in the comprehensive understanding of the factors that might mitigate uprooting and facilitate stability of restoration efforts. For instance, early post-transplantation periods are critical, as evidenced by shoot uprooting observed during restoration efforts (Cronau et al., 2023; van Katwijk et al., 2016). Yet, the precise timeframe and whether an individual wave, or the cumulative erosive effect of a multitude of waves trigger dislodgement remains only little investigated in the field and laboratory environments. Therefore, recommendations for best practices based on systematic research approaches are lacking. Additionally, research on the influence of plant traits, including their size and weight, on transplant survival is scarcely covered in existing literature (Carus et al., 2020). These series of knowledge gaps impede the identification of windows of opportunity (Balke et al., 2011) which in the scope of this study refer to periods during which hydrodynamic forces induced by waves are sufficiently low to allow transplanted seagrass shoots to remain rooted. They can be identified using historical metocean data and numerical models.

Additionally, knowledge gaps remain in the formulation of effective measures to improve shoot survival. In particular the role of restoration facilitators in shielding transplanted shoots and extending windows of opportunity needs to be explored. Restoration facilitators mimic the impact of seagrass meadows on hydrodynamic conditions to artificially create conditions suitable for the establishment of young seagrass shoots. Thus, they change the initial state of bare sediment to enhanced seagrass growth potential.

To address these gaps systematically, we transplanted harvested *Zostera marina* shoots into a laboratory wave flume to (1.) better understand the underlying causes and processes of shoot dislodgement in reference of individual and a series of waves. Further, we explored (2.) the influence of varying initial rooting periods on the dislodgement probability and (3.) quantified the naturally varying plant traits to evaluate their role in sensitivity on dislodgement. In addition (4.) we introduced a restoration facilitator (RF) and investigated its protective capabilities to enhance restoration efforts.

2. Methods

To investigate the seagrass' dislodgement behaviour, systematic laboratory experiments were conducted in a wave flume with controlled boundary conditions. The experiments were carried out over a period of 18 days with measurements being conducted on day 1, 6, 12 and 18. On each of the four measurement days, four sediment boxes with seagrass shoots were transferred into the wave flume.

2.1. Plant material

One day prior to the first measurement day (end of April 2023) *Zostera marina* plants were harvested by divers from the Kiel fjord, Baltic Sea in a water depth of 1–1.5 m (14.5 PSU, 9 °C). Adult seagrass shoots with attached roots and rhizomes were collected using shovels, in the same manner as that employed in Baltic Sea seagrass restoration (following methods of Orth et al., 1999). The shoots were kept wet for transport to the laboratory of the Ludwig Franzius Institute of Hydraulic, Estuarine and Coastal Engineering in Hannover-Marienwerder within a few hours in transport boxes filled with seawater. Seagrass shoots ($n = 224$) were picked in a random manner from the transport boxes, transplanted into 16 sediment boxes and stored in cultivation tanks. As reproductive shoots will die, they were neither used in the experiments, nor are they used for restoration.

In the laboratory, each seagrass shoot was individually identified and its baseline traits were recorded (cf. Table 1). This identification process involved a two-step marking technique. Initially, the tip of the third youngest leaf of each shoot was clipped to differentiate the leaf's sides. Subsequently, on the side corresponding to the lower vertex of the clip, we notched the row number, and on the opposite side, the column number indicating the shoot's position in the experimental box (cf. supplementary material Fig. S1). This clipping method was chosen to avoid the introduction of external markers on the plants, which could potentially create additional drag and introduce biases in the experiment.

In our study, we focused on seagrass shoot traits that are plausibly indicative of susceptibility to dislodgement. To this end, we counted the number of leaves and measured wet aboveground biomass and leaf surface area as typical indicators of each individual plant's potential drag force. Wet belowground biomass and planting depth (following Carus et al. (2020)) were measured, as a typical indicator of anchoring strength after the experiments. The wet biomass was precisely weighed using a precision balance with an accuracy of ±0.001 g after cutting the shoot at its most recent rhizome node, whereas the planting depth was measured with a calliper with an accuracy of ±0.5 mm. The planting depth measures the vertical growth on the rhizome in the sediment, as it is the distance between the most recent node and the point where the rhizome bends and starts growing horizontally below the seafloor. Leaf surface was determined by calculating the colour contrast of leaves placed on a white background, using the R Terra package (Version 1.7–65) within the R statistical framework (Version 4.2.1) after the experiments.

Table 1
Recorded variables and plant traits of the seagrass shoots. The sample size *n* differs as not for all shoots every variable or plant trait was measured.

Variable name	Acronym	Unit	Sample size *n*
Rooting period	*RP*	d	224
Restoration facilitator deployment	*RF*	–	224
Shoot density	*SD*	–	224
Dislodgement	*DSL*	–	224
Dislodgement time	t_{DSL}	min	79
Number of leaves	*NL*	–	96
Aboveground biomass	*AB*	g	217
Leaf surface	*LS*	cm^3	216
Belowground biomass	*BB*	g	209
Planting depth	*PD*	cm	96
Root-leaf ratio[a]	*RLR*	g/cm^2	208

[a] The root-leaf ratio is calculated from the root biomass and the leaf surface ($RLR = BB/LS$).

2.2. Sediment boxes and cultivation tanks

The sediment boxes with inner dimensions of 46.2 × 62.2 × 13.6 cm were filled with sand ($\rho = 2650$ kg/m^3, $d50 = 0.19$ mm). To limit turbidity during the experiment, the proportion of particles smaller than 0.063 mm did not exceed 1 % by mass. Around each shoot three fertilizer pellets ("Osmocote Exact Standard (5–6 M)"; $d = 2$–4 mm) were embedded, as the sand used to fill the sediment boxes did not contain any organic material or nutrients. For seagrass restoration in the field no fertilizers are used. Due to the limited size of the pellets, it is assumed that they have no significant effect on the local hydro- and morphodynamics.

The 16 sediment boxes were subdivided in four boxes for each of the four measurement days. In two of these four boxes, 22 shoots were transplanted with a high density (76.6 shoots/m^2), while the other two were planted with 6 seagrass shoots (low density = 20.9 shoots/m^2). Planting was conducted by hand using one finger to create a hole for the shoot's roots, imitating the divers planting method during restoration (Orth et al., 1999). The planting depth depended on the rhizome's length and morphology, as we aimed to completely embed it in the sand (Carus et al., 2020).

Sediment boxes were placed into eight connected cultivation tanks (depth ≈ 0.4 m; volume ≈ 400 l) filled with saltwater (12 PSU, 15 °C). The temperature was kept constant using a flow through aquarium radiator and monitored by two thermometers. The aligned cultivation tanks were set up as "communicating pipes", so that a pump (flow rate ≈ 8000 l/h) created constant water circulation through all tanks. In a height ≈ 1.2 m above each tank a plant grow lamp (by "ZEUSLIGHTNING"; 3500 K; >52.500 lm; >735 μMol/s) was installed and running time controlled for 16.5 h each day. Water temperature, salinity and light duration were chosen to mimic typical natural conditions at the German Baltic coast in May. The same timeframe is typically used for seagrass restoration (Moksnes et al., 2021) as it is before the month of greatest biomass growth (Boström et al., 2014).

2.3. Wave flume

The wave flume consisted of two identical but separate tanks using the same wave maker. Each tank of the wave flume was 30 m long, 2 m wide and 1.1 m deep. Artificial beaches (6.2 m long and 13.9 % slope) made of sand with a concrete surface layer and 5 cm thick foam mats acted as passive wave absorption at the back of the flume opposite of the wave generator. Two 1,5 m wide and 0.5 m long deepenings 3.6 m in direction of wave propagation in front of the wave paddle were used to place the sediment boxes flush with the flume's bottom. PVC sheets with holes the size of the sediment boxes were used to close the gaps between the deepenings and the boxes (Figs. 1 and 2).

In order to protect the seagrass shoots from the propagating waves, a fence-type restoration facilitator made of willow branches (Fig. 3) was placed in one of the two tanks. Its position was between wave maker and seagrass with 2.5 m distance to the sediment boxes' centre. The position of the fence was derived from pre trials (not shown here) investigating the wave induced orbital velocities behind the restoration facilitator. Highest reduction of orbital velocities in the restoration facilitator's wake was found 3/8 wavelength (L) behind it, with a steep recovery subsequently. Thus, it was chosen as the maximum distance between the fence and the seagrass to generate effective protection. The restoration facilitator stretched the whole width of the wave tank and protruded 0.32 m into the water column. It consisted of two parts, each 1 m wide, which can be purchased as horticultural elements. Vertical wooden poles ($\varnothing = 2$ cm) on each side and in the centre of the elements held the horizontal willow branches. Thinner vertical poles ($\varnothing = 1$ cm) provided additional stiffness. The crest width was 3 cm at the widest points. The permeability which is here defined as light transmissibility in direction of wave propagation, was measured by taking a picture of the prototypes in front of a green screen. The permeability $\left(\phi = P_{green}/P_{total}\right)$ is defined as the ratio of the number of green pixels (P_{green}) to the total number of pixels (P_{total}) resulting in $\phi \approx 0.15$.

2.4. Waves

Both sides of the wave flume were filled to a level of $d = 0.65$ m with water with a salinity of 10.6 PSU. The salinity of the ca. 78 m^3 water in the flume was slightly lower than in the cultivation tanks. Since the difference was within the limits of the natural salinity fluctuations seagrass experiences in the Baltic Sea and the seagrass's duration in the flume is brief ($\sim$ 10 h), this was not considered relevant. To investigate the dislodgement of seagrass shoots under natural wave conditions a JONSWAP-TMA spectrum was used, as seagrass typically grows in shallow to intermediate water depth at the German coast of the Baltic Sea. A 10-min-long time series (Fig. 4) with a significant wave height $H_{m0} = 0.094$ m and a peak period of $T_p = 3.06$ s was generated using MATLAB. Using linear wave theory, the wave length derived from peak period and water depth is $L_p = 7.35$ m, resulting in an intermediate water depth ($d/L_p \approx 0.09$). The time series was then scaled to create five identical series of increasing magnitudes. The significant wave heights were between $H_{m0} = 0.094$ and 0.216 m inducing MOVs of 0.247 to 0.589 m/s measured at a height above the bed of 0.17 m. Using linear wave theory (Dean and Dalrymple, 1991) the theoretically expected MOVs can be calculated using the maximum wave height H_{max} and the corresponding period T_{Hmax}:

$$MOV_{calc} = \pi \frac{H_{max}}{T_{Hmax}} \frac{\cosh(k(z+d))}{\sinh(kd)}$$

The wave number k is defined as $k = 2\pi/L$ and z is the vertical coordinate ($z = 0.17 \text{ m} - d = -0.48 \text{ m}$). The measured MOVs approximately fit the MOVs calculated ($MOV_{calc}/MOV_{meas} \approx 1.0$–$1.1$, Table 2). Each of the five 10 min long time series was repeated five times creating a total of 250 min increasing sea state.

2.5. Measurements

Four ultrasonic sensors (USS, by General Acoustics) used as wave gauges were placed 1 m in front and 1 m behind the restoration facilitator and at the respective position in the other tank (noRF) of the wave flume. The wave gauges were mounted 0.45 m above the still water level measuring with a frequency of 300 Hz, a vertical resolution of <1 mm and an accuracy of ±1 mm. In each tank of the flume one Acoustic Doppler Velocimeter (ADV, vectrino by Nortek) was placed propagating from the top at the centreline between the two sediment boxes (Fig. 1). It measured at a height of 0.17 m above the bed with a frequency of 200 Hz. During data processing the obtained time series of the ADVs and the USSs were despiked using the true 3D Phase-Space Thresholding method (Wahl, 2003) established by Goring and Nikora (2002) using MATLAB functions from Mori et al. (2007). Identification of individual waves for the calculation of wave parameters (wave height H, period T and maximum orbital velocity MOV) was accomplished using the zero-up-crossing-method.

To monitor seagrass dislodgement three observers watched the seagrass during the whole experiment. Dislodged plants were taken out of the water with a landing net and the time of dislodgement and the plants initial position were recorded. After each 10 min long time series the wave machine was stopped and it was double checked that all dislodged shoots were recorded. Additionally the observed shoot's position was confirmed with the marking system of the shoots (cf. Fig. S1).

2.6. Data analysis

The presence of the restoration facilitator influences the measured wave parameters (MOV, H, T) behind it. To have a comparable measure of the restoration facilitator's influence on the shoot dislodgement the uninfluenced wave parameters measured in the tank without restoration

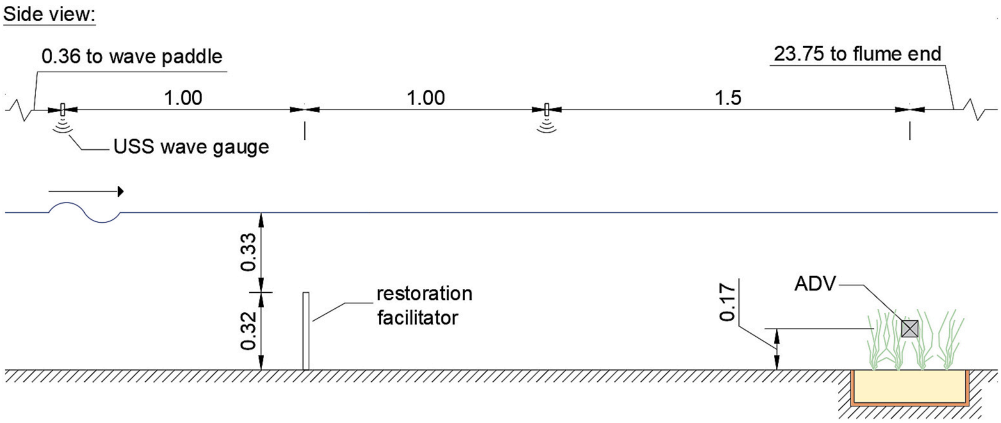

Fig. 1. Side view of the experimental setup in the wave tanks: The restoration facilitator is only installed in one of the two tanks with same setup. Dimensions in meter.

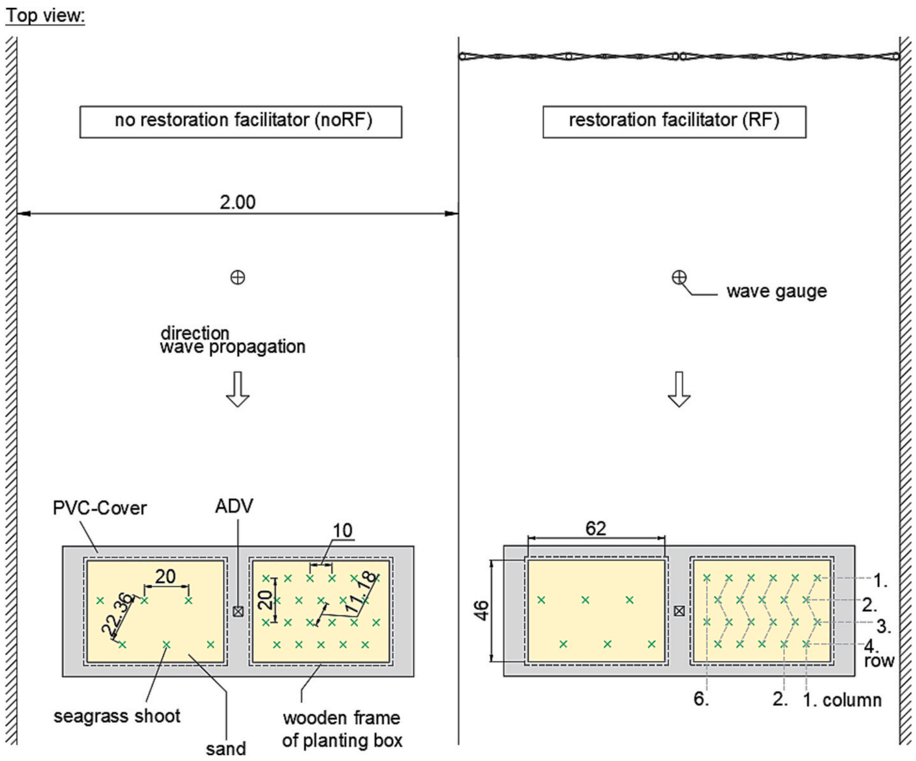

Fig. 2. Top view of the experimental setup in the two wave tanks: With restoration facilitator (right) and without restoration facilitator (left). Sediment boxes (yellow) with low density (left) and high density (right), respectively. Dimensions in meter.

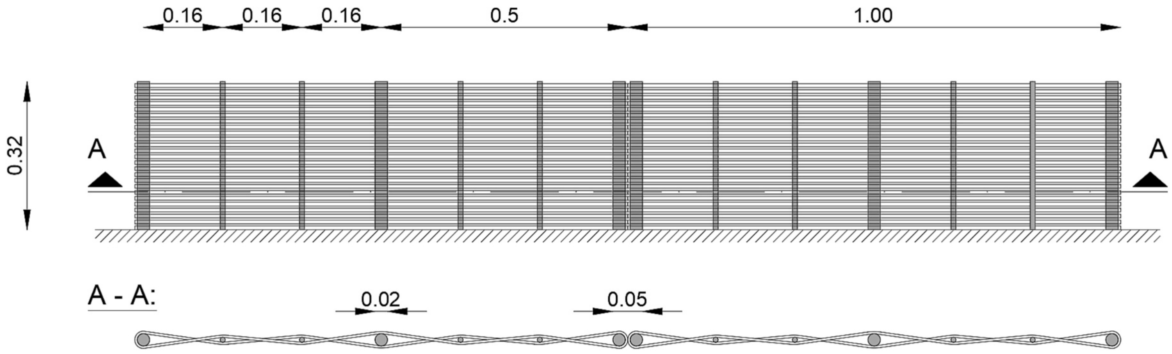

Fig. 3. Technical drawing of the restoration facilitator: Front view (top) and top view (bottom). Dimensions in meter.

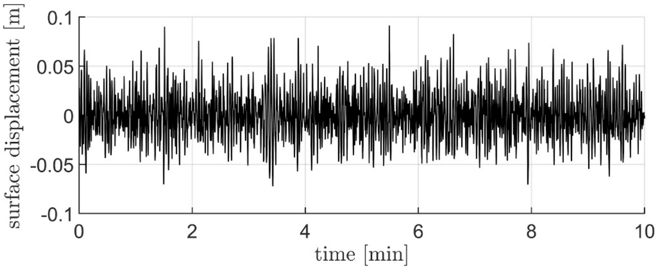

Fig. 4. Time series of water surface displacement: 10 min wave record (H_{m0} = 0.094 m; T_p = 3.1 s) measured in the wave tank without restoration facilitator at the wave gauge closest to the wave paddle.

Table 2

Measured wave parameters (H_{m0}, T_p, H_{max}, T_{Hmax} and MOV_{meas}) and calculated maximum orbital velocities (MOV_{calc}) of the five sea state intensities. The time refers to the respective sea states application time during the 250 min long experiment.

No.	Time [min]	H_{m0} [m]	T_p [s]	H_{max} [m]	T_{Hmax} [s]	MOV_{meas} [m/s]	MOV_{calc} [m/s]
1	0–49	0.094	3.06	0.151	3.13	0.247	0.269
2	50–99	0.126	3.06	0.202	3.17	0.328	0.361
3	100–149	0.160	3.06	0.257	3.15	0.439	0.459
4	150–199	0.187	3.06	0.305	3.20	0.528	0.547
5	200–249	0.216	3.06	0.328	3.76	0.589	0.602

facilitator were used to calculate the dislodgement probability for all shoots.

To determine whether individual waves with a high orbital velocity or long-term cyclic loads within the complete wave record predominantly drive dislodgement, two statistical tests were conducted:

2.6.1. *Dislodgement due to individual waves*

In order to assess the potential influence of the short-term wave-induced velocity on the shoot dislodgement, an analysis of variance (one-way ANOVA) was conducted. An analysis of variance (ANOVA) tests if there are statistically significant differences between two (or more) samples. Thus, it was statistically possible to determine whether the shoot's time of dislodgement (t_{DSL}) was randomly distributed within the wave records or was forced by higher orbital velocities (induced by higher waves). The purpose of the one-way ANOVA is to compare the *MOV*s measured shortly before each dislodged seagrass shoot to *MOV*s randomly picked from the ADV-record. If individual waves had a noteworthy effect on the seagrass' dislodgement, the distribution of the measured *MOV*s varies significantly from the distribution of the random *MOV*s. In order to do that, the *MOV*s were determined in the interval $[(t_{DSL} - \Delta t); t_{DSL}]$ for each dislodged seagrass shoot and, as negative control, before random points in the interval $[(t_{RND} - \Delta t); t_{RND}]$. t_{RND} mirrors the same distribution as t_{DSL}, meaning that the number of points in time across the five intensity steps is consistent between t_{RND} and t_{DSL} and RF and noRF. To increase statistical significance this process was repeated with 1000 different random distributions (t_{RND}). As t_{DSL} is not the real time of dislodgement but the "time of discovery", Δt represents the time it takes from plant dislodgement to discovery. It was estimated by the observers to be 0–30 s. Therefore, for all $\Delta t \in [1; 30]$ s a one-way ANOVA was conducted, comparing the measured *MOV*s to the random *MOV*s.

2.6.2. Dislodgement due to long-term cyclic loads

To assess the influence of long-term cyclic loads on seagrass dislodgement, the number of critical waves until shoot dislodgement (N_{DSL}) was determined. Various options to define a critical wave exist, such as relative wave height (H/d) and maximum orbital velocity (*MOV*). relative wave height is derived from wave height and water depth, while *MOV* additionally incorporates the wave period (T). Other dimensionless numbers like the Froude and Cauchy numbers were considered, but these did not yield better results. Consequently, MOV_{crit} was used as the threshold to identify critical waves. To find the value of MOV_{crit} that most accurately predicts N_{DSL}, the linear correlation was calculated for varying values of MOV_{crit} within the range $[0.01; 0.45]$ m/s. Using N_{DSL}, data acquired during different sea state intensities were merged to calculate the cumulative dislodgement probability ($CDP(N)$).

Using the number of waves as a parameter to calculate damage is a common procedure, for example, for the dimensioning of rubble mound breakwaters in coastal engineering (Van der Meer, 1998).

The cumulative dislodgement probability is defined as:

$$CDP(N) = S_{DSL}(N)/S_{total}$$

With $S_{DSL}(N)$ being the number of dislodged shoots after N critical waves and S_{total} being the total number of shoots. Additionally, CDP_{total} provides the cumulative dislodgement probability after the completion of the 250 min long experiment.

To draw conclusions from the experiments for field-based restoration, the influence of the recorded variables (Table 1) on the cumulative dislodgement probability is examined by calculating ($CDP(N)$) for subsets of the dislodged seagrass shoots derived from recorded variables.

Lines of linear regression were fitted to the respective $CDP(N)$s. Due to the nature of the experiment (limited amount of seagrass shoots and increasing sea state intensity) $CDP(N)$ tends to describe a sigmoid function. Nevertheless, a homogeneous linear function ($f = ax$) is used for three reasons: During a restoration measure, significantly more shoots are transplanted than in our experiments. The decreasing slope of the sigmoid function is therefore attributable to the model conditions and is not realistic for a real restoration. Assuming that the dislodgement behaviour depends solely on the number of critical waves, it makes sense that $CDP(N) = 0$ when $N = 0$. Additionally, the effect of the recorded variables can be compared solely by examining the slope of the fit (a), which is an advantage for decision taking and application in the field. Besides, the linear fit has a high correlation with the data ($r^2 =$ 0.88–0.98, cf. Figs. 6 and 7).

Restoration works in the German Baltic conducted with single shoots are known to be successful despite initial losses of up to 25 % in the first 14 days. Thus, for this study $CDP = 25$ % is deemed as the threshold for successful restoration. $N_{25\%} = 0.25/a$ is the number of critical waves needed to reach this threshold.

3. Results

Across all four measurement days 93 shoots were dislodged. One of the total 224 shoots was lost in the cultivation tank. For 77 shoots the exact time of dislodgement was recorded. 10 shoots were recognized as dislodged after the corresponding 10 min long series of waves ended ($t_{DSL} \pm 5$ min). The remaining 6 dislodged shoots were only recognized as dislodged after the experiment ended. As *CDP* is dependent on the dislodgement time, only the 87 shoots for which t_{DSL} is known were used as its numerator and $217(= 224 - 1 - 6)$ as its denominator, creating $CDP_{total} = 40.1$ %. Thus, 59.9 % of the shoots did not dislodge under the influence of the five sea state intensities. The sea state intensity was not increased any further as the fifth intensity already marked the limit of the wave machine's capability under the used water depth (d) and peak period (T_p).

No shoots dislodged under the influence of the first two sea state intensities ($H_{m0} = 0.094$ and 0.126 m). 8 Shoots (9.2 % of dislodged shoots) dislodged during the third intensity, 39 (44.8 %) during the fourth and 40 Shoots (46.0 %) during the highest sea state intensity. All shoots either dislodged or persisted except one which broke between above- and belowground biomass.

3.1. Understanding dislodgement

An ANOVA (one way) comparing the short-term *MOV* at measured and random times of dislodgement was conducted to investigate the influence of individual waves on the dislodgement. For $\Delta t \in [1; 30]$ the most significant difference ($p \approx 0.032 \pm 0.01$ due to randomness of t_{RND}) between the measured (t_{DSL}) and random (t_{RND}) distribution of *MOV* is reached for $\Delta t = 17$ s. Nevertheless, a clear effect of the *MOV* on the short-term dislodgement cannot be recognized.

However, the correlation between the number of critical waves propagating until shoot dislodgement (N_{DSL}) and the cumulative dislodgement probability ($CDP(N)$) is high. To find the value for MOV_{crit} for which N_{DSL} predicts $CDP(N)$ best, the linear correlation ($r^2 \approx 0.98$) was calculated for varying values of MOV_{crit} ($\in [0.01; 0.45]$ m/s). For all shoots (RF and noRF) N_{DSL} predicts $CDP(N)$ best with $MOV_{crit} = 0.33$ m/s (Fig. 5). It should be noted, that N_{DSL} refers to the undisturbed orbital velocities (noRF) for the unprotected and the shoots protected by the restoration facilitator. For the used peak period T_p and water depth d,

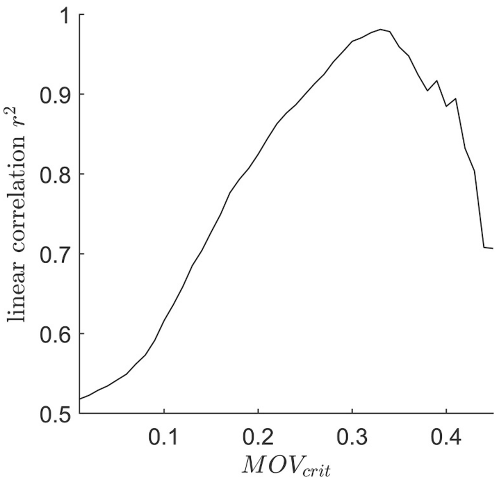

Fig. 5. Linear correlation (r^2) between $CDP(N)$ and N_{DSL} as a function of MOV_{crit}: Highest correlation of 'all' plants at $MOV_{crit} = 0.33$ m/s.

MOV_{crit} corresponds to a critical relative wave height of $H_{crit}/d \approx 0.29$. A similar value ($H_{crit}/d = 0.26$) is derived when using the same method as for determining MOV_{crit}. Using the Bayesian Information Criterion, we identified the most relevant predictors for shoot dislodgement from the measured variables (Table 1): Application of the restoration facilitator, the rooting period, belowground biomass, leaf surface and the ratio of the latter two, i.e. the root-leaf ratio. Additionally, the aboveground biomass was a relevant predictor. As it essentially measures the same aspect of plant growth as leaf surface, it is highly correlated to it and therefore not further discussed.

For both shoots protected with the RF and those without protection, a slightly lower cumulative dislodgement probability was observed for the shoots planted with a high density compared to the shoots planted with low density. However, the results were not significant (one-way ANOVA; $p > 0.05$).

Since the influence of the restoration facilitator was highly significant ($p < 0.001$, one-way ANOVA) and its use or non-use are mutually exclusive scenarios, only a separate analysis of the above-mentioned predictors' effects is valid. Therefore, the following results refer only to the seagrass shoots tested without the protection of the restoration facilitator and the effect of the RF is presented thereafter.

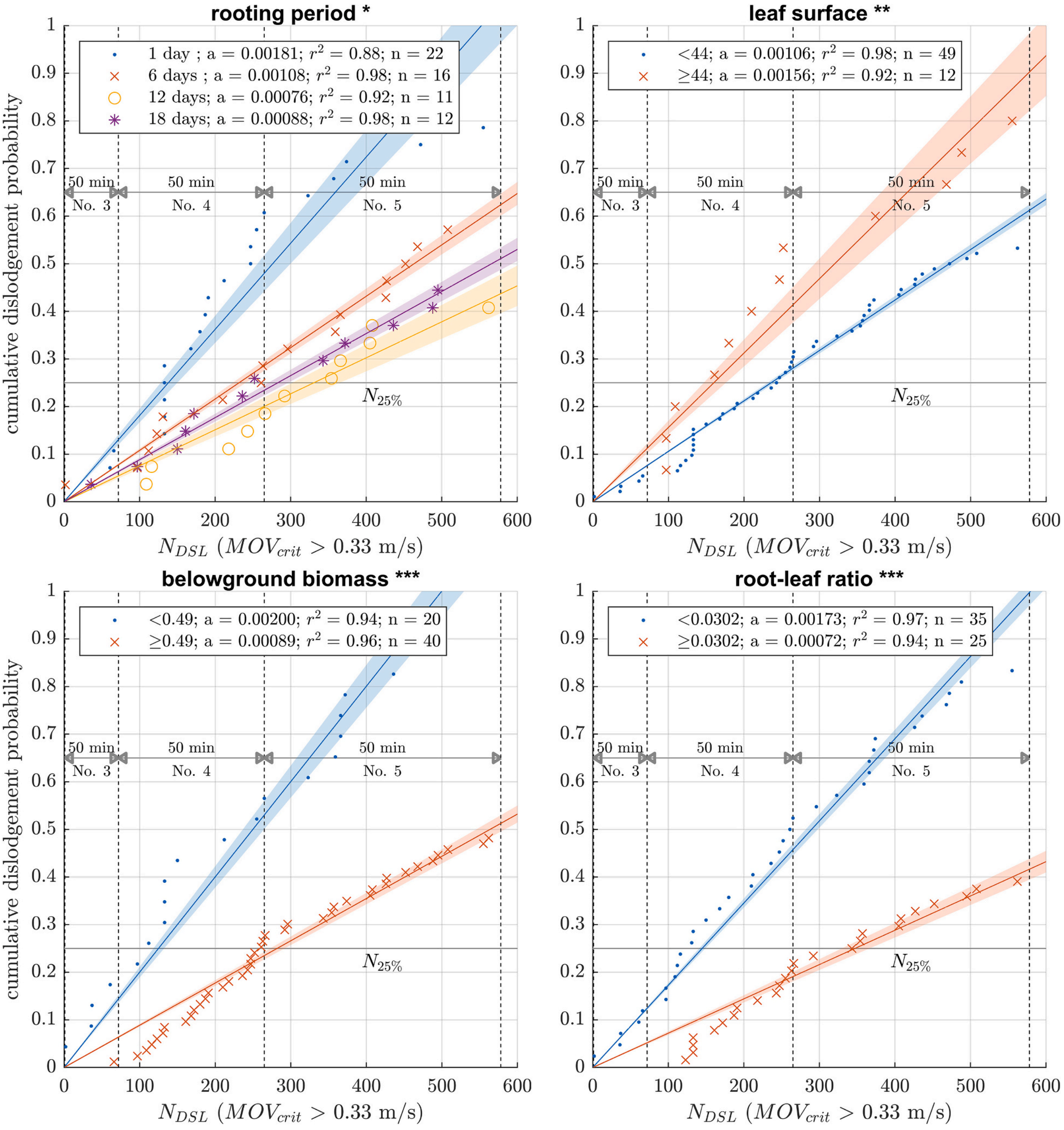

Fig. 6. Influence of the rooting period, leaf surface, belowground biomass and root-leaf ratio on the cumulative dislodgement probability ($CDP(N)$) in relation to the number of critical waves until shoot dislodgement N_{DSL}: Markers represent the recorded data and solid lines the best linear fit ($f = ax$) with the 95 % confidence bounds as shaded areas. Dashed vertical lines represent changes of the sea state intensities (No.). Only data of shoots without protection of the restoration facilitator was used. Level of significance (α): *** < 0.001; ** < 0.01; * < 0.05.

3.2. *Rooting period*

Increasing the rooting period up to 12 days decreased the cumulative dislodgement probability (Fig. 6), as it provides the seagrass shoots with more time to grow roots and therefore anchor themselves. However, the belowground biomass measured after the experiments did not show a statistically significant ($p = 0.208$, one-way ANOVA) increase for samples with longer rooting period ($RP = 12$ and 18 days). While the main source for anchorage are the small roots instead of the thick rhizomes (Li et al., 2023), they barely have an influence on the belowground biomass. Additionally, it could not be guaranteed that no small roots were torn from the plant during dislodgement. As a result, these may not have been noted during the measurement of biomass. For the seagrass shoots tested following a rooting period of 18 days, the cumulative dislodgement probability slightly increased compared to $RP = 12$ days. While there was a significant difference of means between $CDP(N)$ for $RP = 1$ day compared to $RP = 12$ and 18 days ($p = 0.007$ and 0.012, post-hoc analysis using least difference procedure), there was no such statistically significant differences between $RP = 1$ and 6 days ($p = 0.080$), $RP = 6$ and 12 days ($p = 0.261$), $RP = 6$ and 18 days ($p = 0.373$), and $RP = 12$ and 18 days ($p = 0.809$). Thus, it could not be determined, whether the increase of the cumulative dislodgement probability from $RP = 12$ to 18 days was due to coincidence or due to unsuitable conditions in the cultivation tanks. Yet, this finding may also suggest that a rooting period of 12 days is sufficient to create a meaningful robustness of individual shoots against being dislodged ($p = 0.008$, one-way ANOVA). In summary, $N_{25\%}$ increased from 138 waves ($RP = 1$ day) and 232 waves ($RP = 6$ days) to 331 waves after a rooting period of 12 days. For 18 rooting days, it reduced to $N_{25\%} = 283$ waves.

3.3. *Plant traits*

The plant size played a decisive role for the cumulative dislodgement probability. It is quantified by the belowground biomass, the leaf surface and its ratio which provides the belowground biomass per leaf surface. As belowground biomass anchors the seagrass shoots it is negatively correlated with $CDP(N)$, while a larger leaf surface creates a larger area for the wave force to attack and therefore increases the dislodgement likelihood (Fig. 6). With increasing root-leaf ratio, the cumulative dislodgement probability decreases.

To split the continuous variables into a sample with high CDP and one with low CDP, the threshold values were derived using one-way ANOVA to create samples with the highest significant difference (Table 3). Using this method it is possible to quantify the effect the plant traits had on dislodgement. For example, using only shoots with high root-leaf ratio compared to transplanting only shoots with low root-leaf ratio increases $N_{25\%}$ 139 % from 145 to 347 waves (Fig. 6).

3.4. *Restoration facilitator*

The restoration facilitator is the most relevant indicator for the dislodgement of seagrass shoots. 61 unprotected shoots ($n_{noRF} = 110$) dislodged leading to a cumulative dislodgement probability of $CDP_{total} = 55.5$ %, while 26 of the protected seagrass shoots ($n_{RF} = 107$) were dislodged ($CDP_{total} = 24.3$ %, Fig. 7). Considering 25 % dislodgement as the threshold for a successful restoration, an unprotected restored seagrass meadow withstands $N_{25\%} = 230$ critical waves. With protection of the restoration facilitator the number of waves increased to $N_{25\%} = 560$ (+143 %). In this context it should be noted that N (and thus N_{DSL} and $N_{25\%}$) is based on the velocity measurements without restoration facilitator also for the seagrass shoots protected by it.

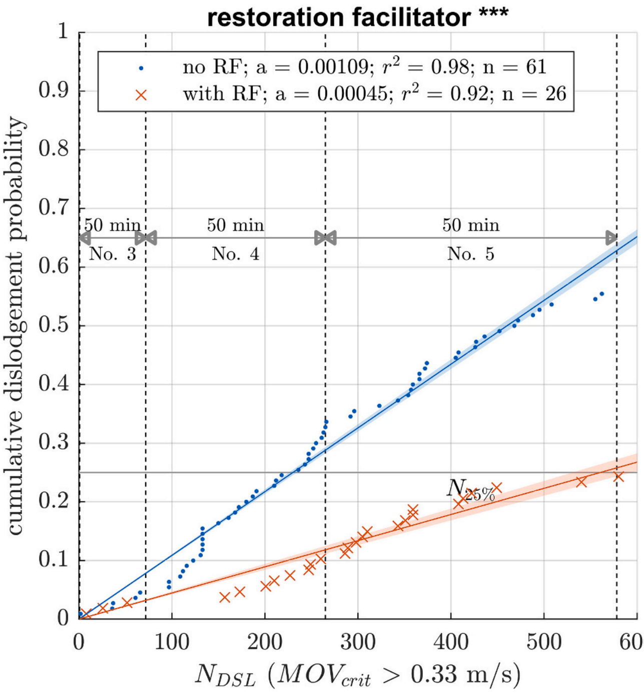

Fig. 7. Influence of the restoration facilitator on the cumulative dislodgement probability ($CDP(N)$) in relation to the number of critical waves until shoot dislodgement N_{DSL}: Markers represent the recorded data and solid lines the best linear fit ($f = ax$) with the 95 % confidence bounds as shaded areas. Dashed vertical lines represent changes of the sea state intensities (No.). Level of significance (α): *** < 0.001.

The restoration facilitator's capability to protect shoots from dislodgement is attributed to its wave damping properties. A similar effect can be reached for example by bamboo fences (Mai Van et al., 2021) or natural reefs (Narayan et al., 2016). Comparing the measured MOVs behind the restoration facilitator with the MOVs at the corresponding position in the wave flume's tank without restoration facilitator showed a mitigation of approx. 17.6 % (linear fit: $MOV_{RF} = 0.824 MOV_{noRF}$, $r^2 = 0.896$).

To provide an understanding that the magnitude of the restoration facilitator's impact is not independent of the above-mentioned predictor variables (rooting period, belowground biomass, leaf surface and root-leaf ratio), a logistic regression was fitted to CDP_{total} as a function of these variables (for the rooting period: $CDP_{total}(RP) = 1/(1+$

Table 3
Threshold values to split continues variables into two categories. One category with properties favourable for seagrass restoration and one with less favourable properties.

	Without restoration facilitator	With restoration facilitator
Belowground biomass [g]	0.49***	0.36***,[a]
Leaf surface [cm^2]	44**	12***
Root-leaf-ratio [g/cm^2]	0.0302***	0.023**

** Level of significance $\alpha < 0.01$.

*** Level of significance $\alpha < 0.001$.

[a] Threshold with highest significance would be 0.3, But would create a category with only $n = 6$ shoots. Using a threshold of 0.36 has a similar significance but creates a category with $n = 12$ shoots.

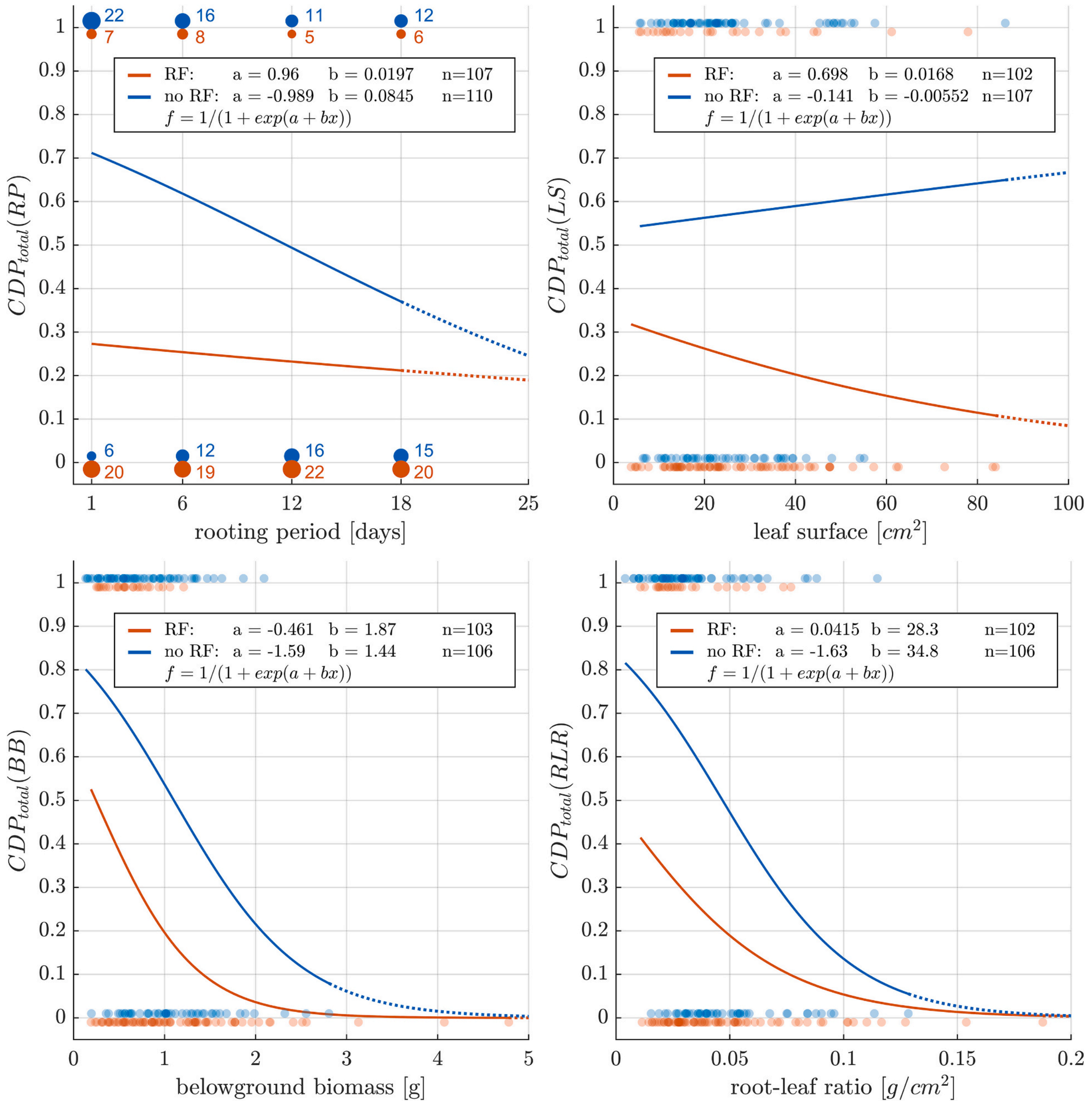

Fig. 8. Binary logistic regression of the influence of the restoration facilitator (RF) on the dislodgement (CDP_{total}) as a function of rooting period, leaf surface (LS), the root-leaf ratio ($RLR = BB/LS$) and belowground biomass (BB); Circles indicate binary dislodgement data for each seagrass shoot (0 = not dislodged; 1 = dislodged). Size of Circles in top left plot indicate number of seagrass shoots. Solid lines are the best fit of the function $CDP_{total}(RP) = 1/(1 + exp(a + b(RP)))$; Dotted lines represent the extrapolation of the best fit.

$exp(a + b(RP)))$. A comparison of the logistic regressions of $CDP_{total,noRF}$ and $CDP_{total,RF}$ (Fig. 8) shows that with increasing rooting period, belowground biomass and root-leaf ratio the effect of the restoration facilitator distinguishes. Increasing leaf surface enhances the impact of the restoration facilitator.

3.4.1. *Rooting period*

While the rooting period has a strong influence on the dislodgement behaviour of the shoots without restoration facilitator, the effect is much less pronounced for the shoots protected with the RF (Fig. 9). Nevertheless, the logistic regression ($CDP_{total,noRF}(RP)$) shows the same trend (Fig. 8). Due to the small sample size of dislodged plants protected by the restoration facilitator, however, the results are not significant.

As a longer rooting period provides the seagrass shoots with extra time to take root, making them less vulnerable to wave attack, the logistic regression $CDP_{total,noRF}(RP)$ approaches the respective logistic regression for the restoration facilitator. Thus, at a rooting period of 1 day the difference is approx. 45 %-points and declines until it is reaches 16 %-points at a rooting period of 18 days (Fig. 8).

3.4.2. *Plant traits*

For plants with a belowground biomasses >2.8 g the difference between implementing the RF and restoration without RF is <10 %-points while it is >30 %-points for seagrass shoots with a belowground biomass of 1 g (Fig. 8). It should be noted that the logistic function loses its validity for belowground biomass values near zero, as seagrass shoots without roots are incomplete and cannot be transplanted. The leaf surface is the only measured variable that, as it increases, induces an

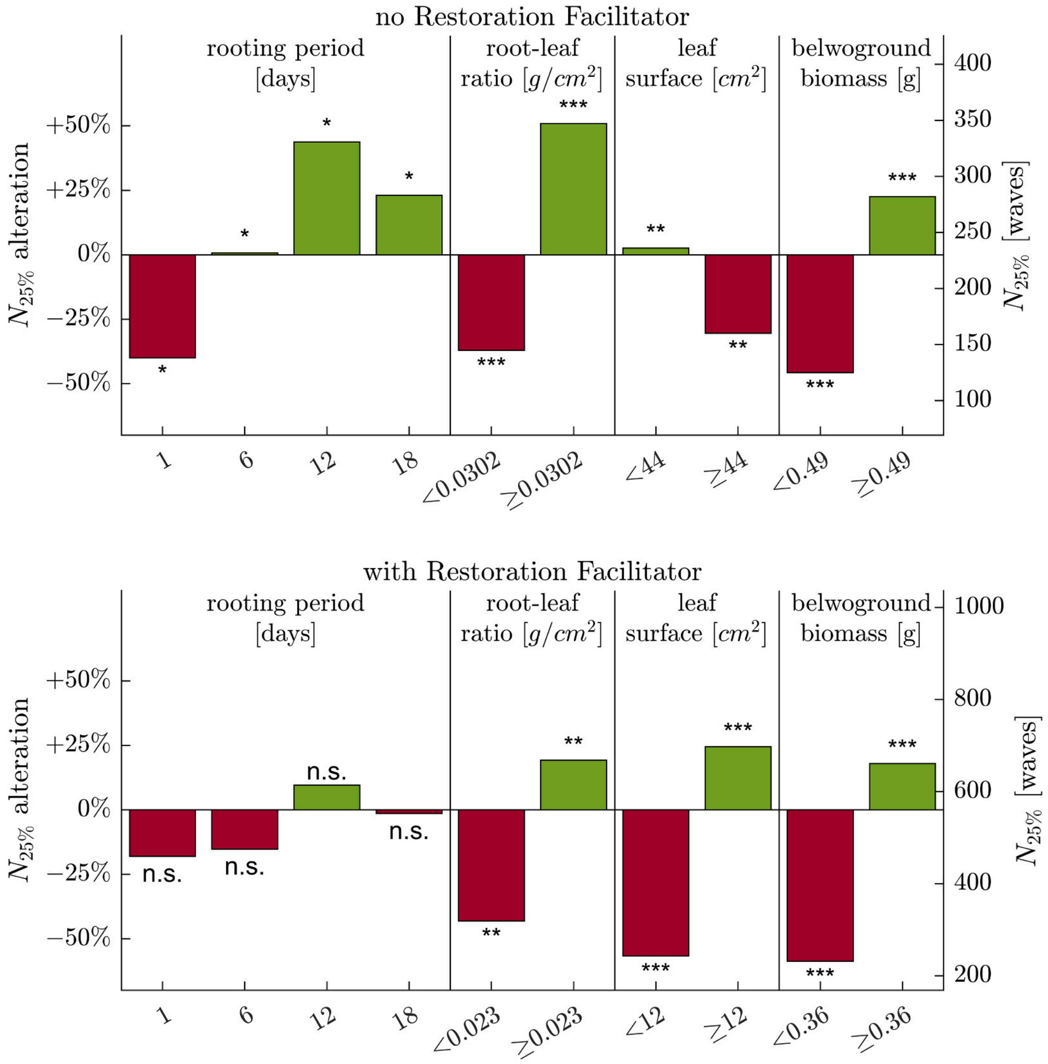

Fig. 9. Effect of the predictor variables (rooting period, root-leaf ratio, belowground biomass and leaf surface) on the number of waves the seagrass shoots can withstand for a successful restoration ($N_{25\%}$). Top: Without restoration facilitator. Bottom: With restoration facilitator. Left y-axis: Alteration of $N_{25\%}$ for varying values of the predictor variables (for example: $\left(N_{25\%,noRF,RP=1} - N_{25\%,noRF}\right)/N_{25\%,noRF}$). Right y-axis: Absolute $N_{25\%}$-values. Level of significance (α): *** = 0.001; ** = 0.01; * = 0.05; n.s. = not significant.

increase of the effect of the restoration facilitator. In this context it is important to note, that the facilitator has a dampening effect on the hydrodynamic exposure of the leaves. This dampening has a greater effect with a larger leaf surface. Thus, for $LS = 80$ cm^2 the difference of CDP_{total} is >50 %-points. Since the reciprocal of the leaf surface is incorporated into the root-leaf ratio ($RLR = BB/LS$), the ratio of root biomass to leaf surface has a similar effect on the influence of RF as the root biomass alone. Like for belowground biomass, the logistic regression loses validity close to zero for leaf surface and root-leaf ratio.

4. Discussion

In an effort to define the necessary conditions for identifying and creating windows of opportunity for seagrass restoration, this study confirms that early post-transplantation periods are critical for seagrass restoration. In accordance with Carus et al. (2020), we quantified the effect of wave-induced orbital velocities on the shoots. Furthermore, the identification and quantification of the most important plant traits affecting the dislodgement process (Fig. 9) is a novel contribution of this study. In general rooting periods ≥12 days and high belowground biomass (ideally ≥0.49 g) increased survival chances of the individual seagrass shoots, while high leaf surface area (≥ 44 cm^2) increased dislodgement likelihood. For practical reasons, i.e. sorting shoots in the field, the leaf surface can be substituted by the number of leaves a seagrass shoot has. For the seagrass sample we used, the number of leaves was recorded for 91 shoots. A number of ≤10 leaves predicted with high accuracy (> 92 %) that the leaf surface was <44 cm^2. Additionally, it was shown that introducing a restoration facilitator increases restoration success significantly by limiting dislodgement during the first days following transplantation and, in the case of greater leaf surface, through mitigation of wave induced orbital velocities.

Individual waves shortly before dislodgement did not differ significantly from the rest of the waves. Hence, dislodgement could not be attributed to individual waves. The number of critical waves, however, showed high correlation with the cumulative dislodgement probability. The statistically derived threshold of $MOV_{crit} = 0.33$ m/s as critical for newly transplanted seagrass seems realistic in the context of known thresholds for established seagrass meadows (Koch, 2001; Infantes et al., 2009; Erftemeijer et al., 2023). Investigating natural seagrass occurrence in the same regional context (German Baltic Sea) but with completely different methodology (coupling species distribution and wave models) Bobsien et al. (2021) found $MOV < 0.4$ m/s indicative for presence of established seagrass meadows.

Carus et al. (2020) conducted similar experiments with regular waves with a setup comparable to shoots tested after one day rooting period. From the given wave parameters, water depth and experiment duration induced orbital velocities and total number of waves can be calculated using linear wave theory. They found no dislodgement of unprotected seagrass shoots for approximately 950 regular waves ($\approx 1800s \cdot 0.53Hz$) inducing a $MOV = 0.16$ m/s (linear wave theory) and 40 % dislodgement for ~1370 waves ($\approx 1800s \cdot 0.76Hz$) with $MOV = 0.2$ m/s. Recalculating our results using a threshold of $MOV_{crit} = 0.2$ m/s for critical waves, $CDP = 40$ % is reached after 1146 waves. Thus, the studies show good agreement for the dislodgement of unprotected shoots. Using artificial seagrass as a facilitator Carus et al. (2020) decreased the dislodgement probability from 40 % to 10 %. Under the same conditions the fence type restoration facilitator reduced the *CDP* from 40 % to 12.7 % (± 2.5 %, 95 % confidence bounds).

While the restoration facilitator only provided up to 17.6 % damping of the *MOV* under the given conditions, it increased the number of waves the seagrass withstands until 25 % of the shoots are dislodged ($N_{25\%}$) by 143 %. A similar effect of wave damping was observed for artificial seagrass, the damping effect on wave height was only 1 mm but shoot persistence increased significantly (Carus et al., 2020). Additionally, the presence of the restoration facilitator statistically alters the dislodgement probability in the dimensions of rooting period, leaf surface, belowground biomass and root-leaf ratio. While the rooting period has a major effect on the dislodgement when no restoration facilitator is deployed, its effect is not any longer statistically significant for seagrass shoots protected by the restoration facilitator. The influence of belowground biomass and root-leaf ratio stays in a similar order of magnitude with and without restoration facilitator (Fig. 9). However, the impact of leaf surface area changes when a restoration facilitator is introduced. In the absence of a restoration facilitator, a leaf surface of <44 cm^2 is beneficial. Which is not found to be true when the restoration facilitator is present. The restoration facilitator reduces wave pressure on the leaves, making it plausible that the leaf becomes less significant for dislodgement. Nevertheless, our results do not reflect this reduced significance. This discrepancy may be attributed to the correlation between leaf surface and belowground biomass, which could obscure the direct influence of leaf surface (Fig. 9). Therefore, the restoration facilitators may enable the use of shoots with larger, more photosynthetically efficient leaves. As the latter is likely to lead to faster root growth, it could potentially shorten the rooting period, decreasing the chances of dislodgment due to adverse weather.

The shoot density showed no significant effect in our trials. This is also confirmed by restoration measures in and around Kiel with shoot densities of 8 and 16 shoots/m^2. (T. Ó Corcora, personal communication, 3rd May 2024). For densities between 246 and 1246 shoots/m^2 Fonseca et al. (2019) did not find any significant influence of the shoot density on drag force exerted on the shoots by currents, neither.

The dislodgement of the seagrass shoots was strongly affected by their position in the sediment boxes. Without restoration facilitator plants in the first row of the high density boxes (closest to wave paddle) dislodged with a probability of ca. 90 % while the seagrass shoots planted furthest away only dislodged with a probability of ca. 21 %. This effect was less pronounced with restoration facilitator (45 % and 17 %, respectively). Studies show that erosion of sand beds in the vicinity of seagrass plants has a strong influence on their probability of uprooting. Cabaço et al. (2008) found 50 % dislodgement for an erosion depth of 4.5 cm (*S. filiforme*) and 2 cm (*Z. noltii*). Carus et al. (2020) found that seagrass shoots started to dislodge when 25 % of the rhizome was set free, but most of the shoots dislodged when the erosion depth exceeded the planting depth. Based purely on visual observations, this effect can be confirmed for these experiments, too, as scouring at the sediment boxes' edge closest to the wave paddle was observed during the experiments. Studies show that a similar scour pattern is observed when a bed changes from stone to sand material (Petersen et al., 2015). Therefore, the first row is most likely biased by the experiment setup, which causes the erosion at the front edge of the sediment box. Thus, the higher dislodgement probability closer to the wave paddle is not considered as a natural edge effect. However, due to time constraints it was not possible to measure the bathymetry in the sediment boxes and thus quantify the effect.

It is evident, that the prevailing conditions in the cultivation tanks had an influence on the results regarding the rooting period. For instance, the decrease in *CDP* found after a rooting period of 18 days compared with that after 12 days was unexpected and might be caused by unfavourable conditions in the cultivation tanks weakening the seagrass over time. Light availability and water temperature were considered suitable as they reproduced natural conditions. The suitability of the flow velocity and, depending on this, the nutrient supply are more difficult to assess. For nutrients sufficiently reaching the seagrass' leaves through the diffusive boundary layer Koch (2001) investigated thresholds of 0.03–0.16 m/s current. These velocities could not be reached in the cultivation tanks. To compensate for this and the nutrient free sediment, fertilizer pellets were added to the sediment. Peralta et al. (2006) showed that the magnitude of the flow velocity significantly influences root growth of *Z. noltii* shoots within four weeks. To rule this out for the *Z. marine* shoots in our cultivation tanks, pretrials (not published) investigating this behaviour were conducted. No correlation between the current velocity (0–0.35 m/s) and root growth was observed over a period of 17 days. Both, in the preliminary trials and in the trials described in this study, the seagrass plants appeared healthy over the entire duration of the trial, regardless of the flow velocity. Post-hoc analysis (using least difference procedure) reveals that the decrease of the cumulative dislodgement probability after a rooting period of 18 days (compared to $RP = 12$ days) is not significant ($p = 0.815$). Therefore, this does not indicate unsuitable conditions in the cultivation tanks, as the difference lies within the margin of error.

5. Conclusion

By conducting physical experiments in a wave flume, it was possible to facilitate site-specific optimization of the restoration method, involving suitable weather window identification, restoration facilitator necessity, and shoot traits. The wave conditions in the flume mirror coastal wave conditions in intermediate water depth which is the typical habitat for seagrass.

If restoration is carried out without a restoration facilitator, a rooting period of 12 days should be ensured during which the exposure to critical waves ($MOV_{crit} \geq 0.33$ m/s) is as low as possible. In our experiment, orbital velocities $\geq$0.33 m/s were indicative for dislodgement of the transplanted shoots. It is also important to ensure that the plants have well-developed roots (belowground biomass $\geq$0.49 g) and leaves that are not too large in proportion (leaf surface <44 cm^2).

The purpose of the restoration facilitator is versatile. On the one hand, it can be used in areas where high hydrodynamic exposure makes natural resettlement unfeasible. It can also be deployed if the prospects of long enough weather windows with low wave impact and therefore long enough rooting periods are low. The decision-making process, however, should be based on sound knowledge of the local wave climate and bathymetry. It might be more feasible to identify long enough (rooting period $\geq$12 days) 'windows of opportunity' (Balke et al., 2011) with suitable wave conditions for the restoration using historic metocean data and numerical models, than deploying a cost and time intensive restoration facilitator.

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CRediT authorship contribution statement

Lars Kamperdicks: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation. **Matteo Lattuada:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Data curation, Conceptualization. **Tadhg O**

Corcora: Writing – review & editing, Resources. **Torsten Schlurmann:** Writing – review & editing, Supervision, Resources. **Maike Paul:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Used data is available at the following link: https://doi.org/10.25835/nbs95s4o

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