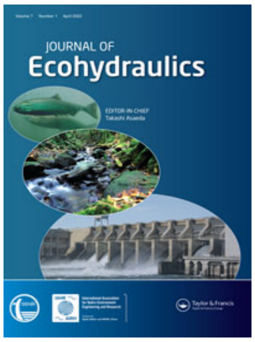

Journal of Ecohydraulics

ISSN: (Print) (Online) Journal homepage: https://www.tandfonline.com/loi/tjoe20

Effect of artificial seagrass on hydrodynamic thresholds for the early establishment of *Zostera marina*

J. Carus, C. Arndt, T. J. Bouma, B. Schröder & M. Paul

To cite this article: J. Carus, C. Arndt, T. J. Bouma, B. Schröder & M. Paul (2022) Effect of artificial seagrass on hydrodynamic thresholds for the early establishment of *Zostera marina*, Journal of Ecohydraulics, 7:1, 17-27, DOI: 10.1080/24705357.2020.1858197

To link to this article: https://doi.org/10.1080/24705357.2020.1858197

JOURNAL OF ECOHYDRAULICS
2022, VOL. 7, NO. 1, 17–27
https://doi.org/10.1080/24705357.2020.1858197

Effect of artificial seagrass on hydrodynamic thresholds for the early establishment of *Zostera marina*

J. Carus[a,b], C. Arndt[c], T. J. Bouma[d], B. Schröder[a,e] and M. Paul[f]

[a]Department Landscape Ecology and Environmental Systems Analysis, Institute of Geoecology, Technische Universität Braunschweig, Braunschweig, Germany; [b]Department Vegetation Studies, Landscape Management, Federal Institute of Hydrology, Koblenz, Germany; [c]Institute for Bioplastics and Biocomposites, University of Applied Sciences and Arts Hannover, Hannover, Germany; [d]Department of Estuarine and Delta Systems, Royal Netherlands Institute for Sea Research and Utrecht University, Yerseke, the Netherlands; [e]Berlin-Brandenburg Institute of Advanced Biodiversity Research, Berlin, Germany; [f]Ludwig-Franzius-Institut für Wasserbau, Ästuar- und Küsteningenieurwesen (LuFI), Leibniz University Hanover, Hannover, Germany

ABSTRACT

Seagrass meadows have disappeared on many coastal sections due to anthropogenic disturbances, diseases, and/or eutrophication. To facilitate informed seagrass restoration, we i) quantified the hydrodynamic dislodgement thresholds for newly transplanted *Z. marina* shoots, and ii) tested the effect of artificial seagrass (ASG) as a hydrodynamic protection measure. Experiments were carried out by planting *Z. marina* rhizomes with living shoots into a sediment bed and exposing them to a range of wave and current conditions in a flume. The use of ASG significantly reduced wave height, as well as current velocity. The applied waves led to the development of ripples whereas currents led to erosion of the sediment bed. The number of shoots that were uprooted and dislodged increased with increasing bed shear stress and erosion. By reducing bed shear stress, the ASG raised the input current velocity threshold, which the transplanted shoots were able to withstand. The present study offers insight into the effect of artificial seagrass (ASG) on wave and current attenuation, as well as sediment erosion and shoot dislodgement. Our results help to inform the setting of hydrodynamic thresholds for the early establishment of *Z. marina* and to define the improvement of hydrodynamic conditions by ASG.

ARTICLE HISTORY
Received 22 June 2020
Accepted 27 November 2020

KEYWORDS
Current velocity; wave energy; seagrass restoration; erosion; ripple formation; bed shear stress

Introduction

Seagrass meadows modify hydrodynamic conditions by attenuating currents and waves (Fonseca and Cahalan 1992; Newell and Koch 2004; Koch et al. 2007; Fonseca et al. 2019). They stabilise the sediment, may prevent the need for beach nourishments and thereby provide valuable coastal protection (Barbier et al. 2011; Christianen et al. 2013). Field experiments acknowledge a 40% reduction in near-bed flow to a *Zostera noltii* bed (Widdows et al. 2008) and a reduction in wave height by 25–49% (Reidenbach and Thomas 2018) to a *Zostera marina* meadow. Reidenbach and Thomas (2018) also found that bed shear stress at the sediment - water interface was significantly lower at a vegetated, compared to an unvegetated site. Moreover, recent field-flume studies revealed that critical erosion thresholds to resuspend sediment increases with the density of a seagrass meadow (James et al. 2019; James et al. 2020). Overall, this results in the so-called seagrass-sediment-light (SSL) feedback, where seagrass reduces turbidity, causing more light and hence better growing conditions for seagrass (Bower 2007).

The strength of the seagrass-sediment-light (SSL) feedback depends on both the environmental characteristics (e.g., wave and current speed, sediment properties) and the properties of the seagrass meadow (e.g., meadow length and shoot height, canopy density, leaf morphology). For example, the impact of seagrass on hydrodynamics and thus sediment erosion and resuspension is greater under higher input flow velocities (Adams et al. 2016). Higher shoot densities for instance lead to higher reductions in near-bed velocity (Wilkie et al. 2012), wave height (Paul and Amos 2011) and sediment resuspension (Widdows et al. 2008). The seagrass-sediment-light (SSL) feedback is dependent on plant functional traits, like being adapted to hydrodynamically stressful environments (Carus et al. 2016). By investing in belowground biomass, seagrass also improve their anchorage system, and thereby its critical capacity to withstand dislodgement during sediment erosion (Widdows et al. 2008; Infantes et al. 2011).

CONTACT Jana Carus ✉ Carus@bafg.de Department Vegetation Studies, Landscape Management, Federal Institute of Hydrology, Mainzer Tor 1, 56068 Koblenz, Germany

Unfortunately, seagrass meadows have disappeared on many coastal sections due to anthropogenic disturbances, diseases, and/or eutrophication (Orth et al. 2006). After a seagrass meadow is lost, the SSL feedback is destroyed so that turbidity increases and regrowth is hampered (van der Heide et al. 2007). Natural re-establishment of seagrass is hence only possible under very specific conditions (Ganassin and Gibbs 2008). Restoration is often the only way to enable re-establishment of seagrass meadows and hence promote natural coastal protection at exposed locations. Different restoration techniques have been developed (van Katwijk et al. 2016) involving the use of seeds (Pickerell et al. 2005) or pre-reared seedlings (Paling et al. 2009), as well as the transplantation of seagrass fragments from a donor bed (Davis and Short 1997; van Katwijk et al. 2009). In the so called bare-root technique, seagrass shoots are transplanted along with a small length of rhizome (2-20 cm) with or without anchor (Davis and Short 1997). Because the roots of seedlings or transplanted shoots penetrate less deeply into the sediment, it is to be expected that they are more vulnerable to sediment movement than adult seagrasses within established meadows (Infantes et al. 2011).

The success of the bare-root method is indeed highly depended on hydrodynamic energy at the transplanting location (Campbell 2002; Bos and van Katwijk. 2007) and the resulting sediment movement. Restoration experiments in the Wadden Sea showed that hydrodynamic exposure is unfavourable for transplant survival: only 28% of transplanted shoots survived the first three weeks at a location with high wave and current exposure (compared to 76% at the locations with low exposure) (Bos and van Katwijk 2007), and prevalent water dynamics, particularly wave action, were too high for the establishment and sustainment of *Z. marina* at depths below − 0.20 m mean sea level (van Katwijk and Hermus 2000). In a laboratory experiment, *Thalassia testudinum* seedlings developed best under medium current velocities of 0.3 cm s^{-1} (Koch 1999).

One possibility to make use of positive feedback mechanisms for seagrass restoration is planning restoration sites near existing vegetation or mussel beds (Bos and van Katwijk 2007; van Katwijk et al. 2009; Hengst et al. 2010). If such natural protection structures are not present at the selected restoration site, another possibility is the use of artificial structures as protection against hydrodynamic energy (van Keulen et al. 2003) to anchor the transplants (Davis and Short 1997; Park and Lee 2010; Unsworth et al. 2019) or to stabilise the sediment by mimicking a rhizome mat (Temmink et al. 2020). A promising application of these concepts would be to create a seagrass-like artificial structure, mimicking the natural facilitation effect of a real seagrass meadow by providing suitable hydrodynamic and light conditions as well as sediment stabilisation. The utilization of artificial seagrass (ASG) mats can lead to significant increase in transplant survival (Campbell and Paling 2003), but data on their functioning and requirements for their design are scarce. We aim to provide insight in the hydrodynamic design criteria that need to be realised when using ASG for seagrass restoration.

While established seagrass beds can tolerate current velocities of up to 1.2–1.5 m s^{-1} (*Z. marina*) (Fonseca et al. 1983), hydrodynamic threshold values for the establishment of transplants remain unknown. In order to assess whether a transplantation project at a certain location will be successful, and to assess if the installation of ASG can be used to create such conditions, it is of major importance to know these hydrodynamic thresholds. We hence conducted racetrack flume experiments to quantify the hydrodynamic thresholds that allow early establishment of *Z. marina* and to evaluate how functional traits such as rhizome length influence the capacity of transplanted shoots to remain anchored. In these experiments, we furthermore evaluated the effect of different current and wave conditions on sediment dynamics affecting seagrass transplant survival. Additional measurements were performed with artificial seagrass as a protection measure against hydrodynamic forcing in order to quantify the improvement of hydrodynamic conditions by ASG and to define the minimum requirements on the eco-engineering capacity of ASG for the restoration of *Z. marina*.

Methods

Living seagrass shoots

Z. marina shoots used in the experiments were obtained from Kiel Fjord, Baltic Sea, Germany (54°23’16.4"N 10°12’27.9"E) at the beginning of June 2018. Terminal rhizomes with one to two shoots were harvested manually by diving. The plants were transported in boxes containing seawater to NIOZ, Yerseke, Netherlands within 48 hours and stored in an aerated water basin with conditions matching the ones at the sampling site (17 PSU, 20 °C) until being used in the experiment.

For analysing the effect of plant characteristics, we measured the following parameters before the experiment: Length of shoot (148 ± 44 mm), length of rhizome fragment (24 ± 7 mm), maximum root length (64 ± 28 mm), fresh biomass (0.78 ± 0.4 g).

Artificial seagrass (ASG)

To analyse the protective effect of an artificial structure on newly transplanted seagrass plants, an ASG mat was constructed. It consisted of a PVC plate (60 × 100 cm) with ribbon stripes arranged at points in alternating rows with an interval of 5 cm between points and rows. Six ribbon stripes (PP, 30 cm long, 0.5 cm wide) were attached at each point/shoot (Figure 1), resulting in a density of 390 shoots or 2340 leaves m^{-2}.

Experimental set-up

The experiments were conducted in a racetrack shaped flume (Figure 2 + 3) at the Royal Netherlands Institute for Sea Research (NIOZ) (Size, see Figure 2). The flume was filled to a height of 30 cm with a mix of sea and tap water to adjust the salinity to 17 PSU.

Determining threshold values of dislodgement under waves and currents

We evaluated the effects of two different wave heights (58 and 78 mm significant wave height) and three different current velocities (0.25, 0.45 and 0.60 m s^{-1} mean current velocity) on the persistence of transplanted seagrass shoots. For this purpose, ten rhizome fragments of *Z. marina* with one to two living shoots were transplanted into the sediment bed of the racetrack flume. Depending on size and form of the rhizome, shoots had to be plugged differently deep into the sediment to cover the whole rhizome and the first millimetres of the shoot by sand. The resulting planting depth was between 6 and 40 mm and was recorded for each shoot.

Figure1. Utilized artificial seagrass (ASG) made out of a PVC plate and 30 cm long PP-ribbon stripes and one transplanted seagrass shoot in the flume.

The pattern and distance between the shoots are demonstrated in Figure 3. The sediment had a grain size median D50 of 249 ± 11 µm. A conveyor belt in the racetrack flume (Figure 2) generated the currents. Waves were created by a vertical wave paddle and attenuated by a porous slope at the end of the test section (Figure 2). For each hydrodynamic setting, new shoots were transplanted. After setting up the intended hydrodynamic forcing, it was maintained for 30 minutes. To define the threshold for shoot dislodgement, the experiment was started with the highest of the three hydrodynamic settings and lower currents and waves were set in subsequent runs until no dislodgement of shoots was observed. The sediment bed was smoothened after each run.

To test the effect of artificial seagrass (ASG) as protection measure for transplanted seagrass shoots, the experiment was repeated with the same settings as before, but an ASG mat was positioned in front of the natural shoots (Figure 3).

For both parts of the experiment with and without the ASG, we recorded the following parameters:

(1) experimentally imposed wave height and current velocity (input)
(2) wave height and current velocity at the transplanting location (output)
(3) sediment erosion and ripple formation in the transplanting location
(4) bending and dislodgement of transplants

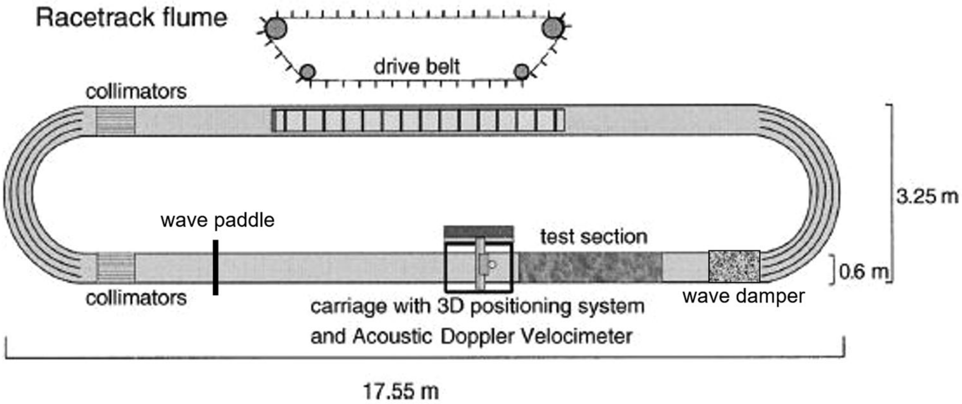

Figure 2. Schematic representation of the racetrack flume. In the case of the wave experiments, a wave paddle was installed between the collimators and the test section and a wave damper after the test section (changed after Bouma et al. 2005).

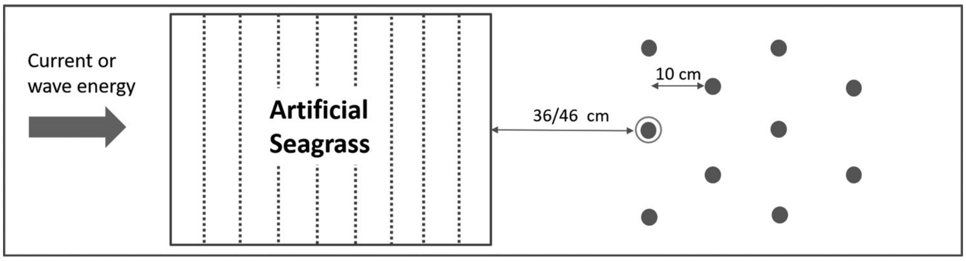

Figure 3. Test section of the racetrack flume (see Figure 2) with *Z. marina* shoots (grey dots) and a section either with or without artificial seagrass. The grey ring marks the point of velocity measurements.

Wave height and period was calculated from pressure data recorded by a Level Sensor (PTX 1830), which was located in the middle of the test section. The sampling rate was 25 Hz and measurements were taken for 60 seconds prior to seagrass planting.

Flow was characterized by measuring current velocity 5 cm above the sediment bed in the middle of the flume at the first planting row (Figure 3) using an Acoustic Doppler Velocimeter (ADV Vectrino, Nortek, Norway). The ADV sampling rate was 25 Hz and measurements were taken for 40 seconds in a sampling volume of 7 mm and with a nominal velocity range of 2.5 m s^{-1}. Sediment erosion and ripple formation was measured by scanning the sediment bed before and after the respective setting via the distance scan mode of the ADV. The spatial grid had a mean resolution of 10 mm in the longitudinal (parallel to the flow) and 5 mm in the transversal (cross-stream) direction. Data was interpolated by inverse distance with the R package gstat (Pebesma 2004). For the investigation of the sediment erosion, only negative elevation changes were regarded.

Calculation of bed shear stress

Bed shear stress of waves ($\tau_{b,max}$) was calculated according to the following equations, elaborated from Malcherek (2018):

$$\tau_{b,max} = f_W \cdot \rho \cdot \frac{A^2 \cdot g \cdot k}{\sin\,h(2kh)} \tag{1}$$

where f_W represents the wave friction factor:

$$f_W = 0.00251 \cdot e^{(5.21 \cdot A_b / K_S{}^{-0.19})} \tag{2}$$

where A_b represents the amplitude of orbital excursion above the bed:

$$A_b = A/\sin\,h(kh) \tag{3}$$

with L = wavelength (m), h = water depth (m), ρ = water density (kg/m^3), A = wave amplitude (m) and K_S = d90 (m) = 0.386×10^{-3} m, which is the equivalent sand roughness.

Bed shear stress of currents ($\tau_{b,c}$) was calculated based on Balke et al. (2011):

$$\tau_{b,c} = 0.125 \rho f_c v^2 \tag{4}$$

$$f_c = 8\frac{g}{C^2} \tag{5}$$

$$C = 18 \log \frac{12h}{K_s} \tag{6}$$

with f_c = friction coefficient (m), υ = flow velocity (ms^{-1}) and C = Chézy coefficient.

Data analysis

The effect of ASG on wave height ($n = 1500$), current velocity ($n = 1000$) and on erosion ($n = 7059$) was tested using a Student's t-test. Since we have a large number of measured data points resulting from the fine-scaled distance scans of the ADV, we used a random sample of 500 data points to test the effect of ASG on erosion. To analyze the relationship between bed shear stress and erosion, we used a linear regression with log transformed erosion values. We applied generalised linear models (McCullough and Nelder, 1989) with binomial error distribution and the logit-link function (i.e., logistic regression) to test the effect of bed shear stress on the number of transplants that were uprooted and dislodged after 30 minutes. The erosion at the position of the shoots was tested by the nonparametric Wilcoxon rank-sum statistic (Wilcoxon 1945). All data pre-processing, processing, and statistical analysis were conducted within the free software environment R 3.5.3 (R Core Team 2019) as well as MATLAB® (R2017b).

Results

Effect of artificial seagrass on waves and currents

The input wave heights of 58 and 78 mm as obtained by the two imposed wave frequencies (0.53 and 0.76 Hz), were significantly reduced by adding transplant protection in the form of 1 m long ASG (Table 1). The three input flow velocities (0.25 m s^{-1}, 0.45 m s^{-1} and 0.60 m s^{-1}) have also been significantly reduced by ASG (Table 2, Figure A2). This reduction ranged from 10 to 28%, with the

Table 1. Results of the racetrack flume experiment with two different input wave heights, with and without artificial seagrass (ASG) as protection measure. Standard deviations are given in brackets. Stars specify the results of t-tests on the reduction of the respective parameter by ASG as protection measure. Level of significance: ***P <= 0.001, **P <= 0.01, *P >= 0.05, n.s. = not significant.

Protection measure	Mean wave height (mm)	Wave frequency (Hz)	Bed shear stress (N m^{-2})	Mean ripple height (mm)	Dislodged shoots
none	57 (1.1)	0.53	0.23	7 (7)	0
ASG	56 (0.9) ***	0.53	0.23	7 (6) n.s.	0
none	74 (1.4)	0.76	0.33	6 (7)	4
ASG	73 (1.8) *	0.76	0.32	6 (11) n.s.	1

Table 2. Results of the racetrack flume experiment with three different input current velocities, with and without artificial seagrass (ASG) as protection measure. Standard deviations are given in brackets. Stars specify the results of t-tests on the reduction of the respective parameter by ASG as protection measure. Level of significance: ***P <= 0.001, **P <= 0.01, *P >= 0.05, n.s. = not significant.

Protection measure	Mean current velocity (m s^{-1})	Bed shear stress (N m^{-2})	Mean erosion (mm)	Dislodged shoots
none	0.25 (0.04)	0.12	2 (2)	0
ASG	0.18 (0.05) ***	0.06	2 (2) n.s.	0
none	0.45 (0.08)	0.39	10 (5)	4
ASG	0.38 (0.11) ***	0.28	4 (4) ***	0
none	0.6 (0.06)	0.69	28 (5)	10
ASG	0.48 (0.13) ***	0.44	13 (7) ***	6

highest reduction at high input current velocities (0.6 m s^{-1}) (Table 2).

Ripple formation and erosion

The applied waves led to the development of ripples in the sediment bed that ran perpendicular to the wave direction (Figure 4). However, the height of these ripples was very small and not correlated to bed shear stress or reduced by ASG (Table 1).

In the current velocity settings, elevation change was mainly negative (i.e., eroding) and no scouring was observed around the transplanted seagrass shoots (Figure 5). The erosion of the sediment bed (E in mm) in the test section increased with increasing bed shear stress ($\tau_{b,c}$ in N m^{-2}) (log-lm: $E = e^{4.8 \times \tau_{b,c} + 0.02}$, $R^2 = 0.65$, p-value < 0.001, $n = 500$) (Figure 6, Table 2). By reducing bed shear stress, the use of ASG significantly reduced the erosion of the sediment bed for input current velocities of 0.45 m s^{-1} and 0.6 m s^{-1} (Figure 4 & A3, Table 2). While the erosion was distributed evenly over the sediment bed without protection measures, the erosion reduction of the ASG with intermediate and high input current velocities (0.45 and 0.6 m s^{-1}) was even higher in the first 46 cm behind the ASG.

Dislodgement of transplanted seagrass shoots

All transplanted shoots were strongly bent by waves and currents; however, no tensile breaking occurred. The proportion P of shoots that were uprooted and dislodged after 30 minutes under waves as well as currents increased with increasing bed shear stress (τ_b) (Figure 7) (binominal GLM: explained deviance = 0.91, Table A1). The proportion of dislodged shoots depending on bed shear stress can be calculated by $P = \frac{e^{-8.73+21.52\ \tau_b}}{1+e^{-8.73+21.52\ \tau_b}}$ which is equivalent to a formulation using the steepness of the logistic curve and τ_{b0} (N m^{-2}), which has the physical interpretation of being the bed shear stress at which half the shoots are dislodged, i.e., $P = \frac{1}{1+e^{-21.52(\tau_b-\tau_{b0})}}$ with $\tau_{b0} = 8.73/21.52$. Shoots started to rip out at a bed shear stress threshold of 0.3 N m^{-2} and all shoots were dislodged above 0.6 N m^{-2}.

Under waves, the transplanted shoots were mainly dislodged in ripple valleys but erosion did not significantly affect their dislodgement (Wilcoxon rank sum test: p-value = 0.28, $n = 40$). Under currents, however, the erosion at the position of the transplants differed between persistent and dislodged shoots and could explain whether a shoot was dislodged or not (Wilcoxon rank sum test: p-value < 0.001, $n = 60$). Dislodgement started when $^1/_4$ of the rhizome was exposed, however most shoots were only dislodged when erosion exceeded planting depths, showing that the shoots are able to persist in the sediment, until the whole rhizome is exposed (Figure 8). Neither the position of the shoots in the test section nor any of the measured plant characteristics affected their dislodgement under waves or currents.

Discussion

Effect of artificial seagrass on waves and currents

Hydrodynamic energy is one of the major reasons for the failure of seagrass restoration schemes (van Katwijk and Hermus 2000). It is therefore

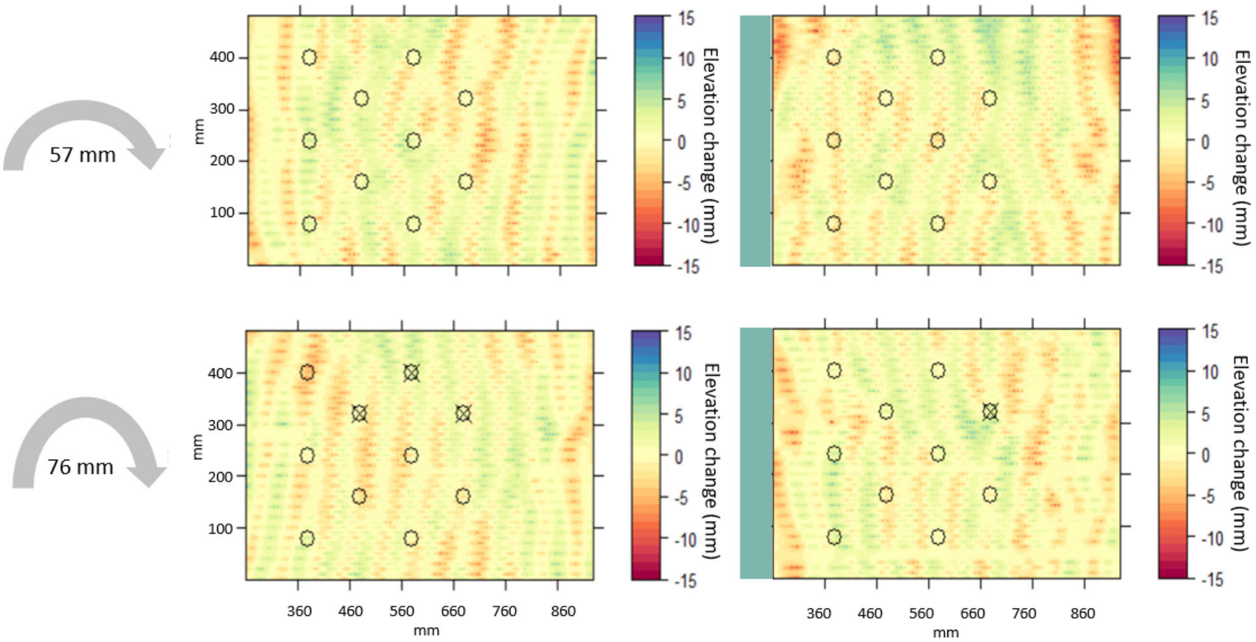

Figure 4. Scan of sediment bed after runs with two different input waves (wave direction was from left to right as indicated by grey arrows) with and without artificial seagrass (ASG) (positioned on the left-hand side of the plots as indicated by the green bars). Position of the transplanted *Z. marina* shoots are marked with a circle, the crosses mark shoots that were dislodged within 30 min.

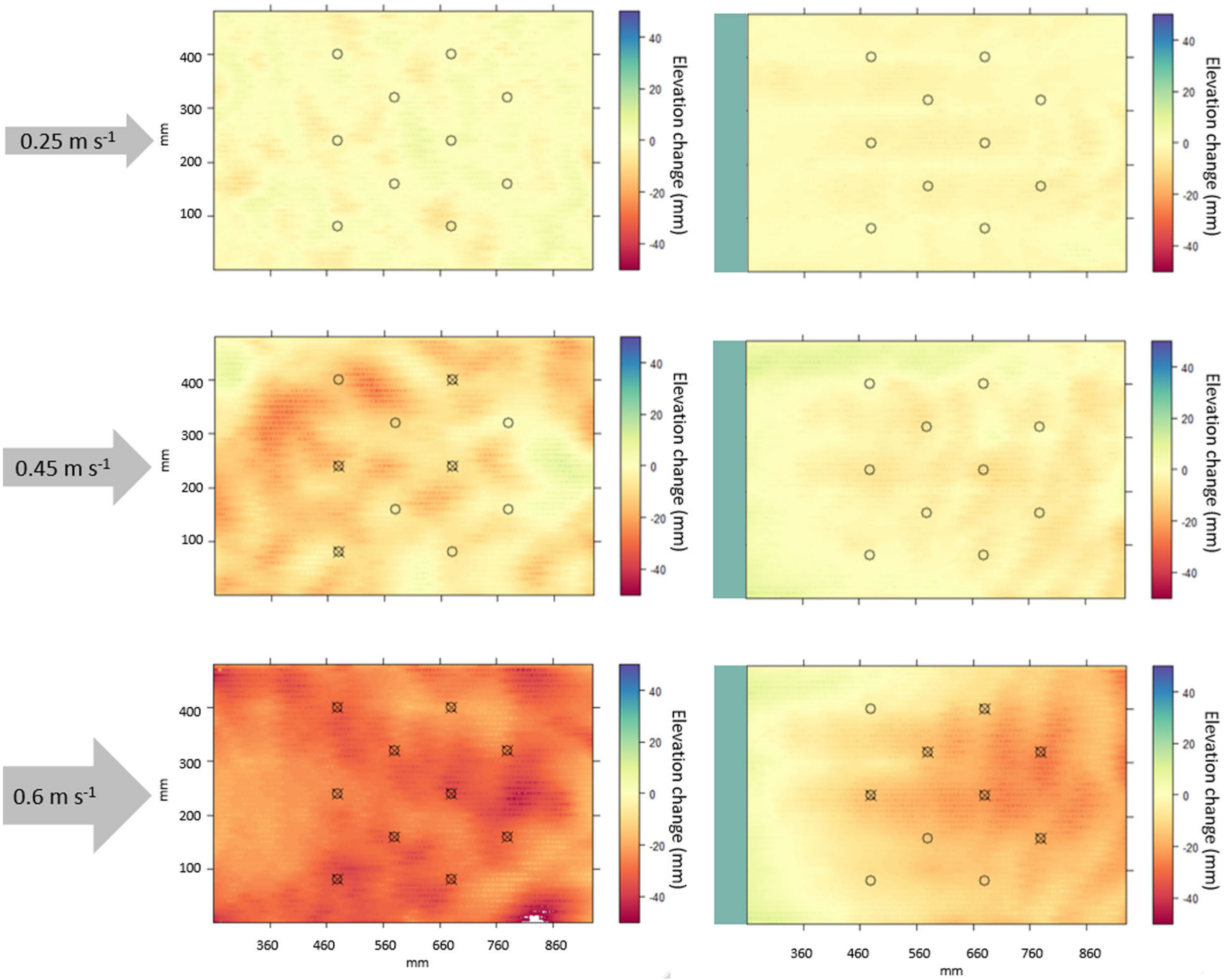

Figure 5. Erosion scan of sediment bed after runs with three different input current velocities (current direction was from left to right as indicated by grey arrows) with and without artificial seagrass (ASG) (positioned on the left-hand side of the plots as indicated by the green bars). Position of the transplanted *Z. marina* shoots are marked with a circle, the crosses mark shoots that were dislodged within 30 min.

particularly important to investigate new techniques that allow seagrass restoration in areas of high hydrodynamic energy. The present study offers insight into the effect of artificial seagrass (ASG) on wave and current attenuation. Although we found a significant effect of ASG on waves, the mean reduction of wave height accounted for just 1 mm and was thus very small. The wave attenuation capacity of seagrass, no matter whether real or artificial, depends on a range of parameters. For one thing, wave attenuation increases with distance into the vegetation (Chen et al. 2007; Bouma et al. 2010); the short length of the ASG meadow used in our experiment (1 m) could thus be one reason for its low wave attenuation capacity. Furthermore, since wave attenuation increases with increasing stem density (Lei and Nepf 2019), the wave height and thus wave energy could probably be further reduced with a denser ASG-meadow.

The effect of ASG on current velocity was more pronounced than on wave height. The impact of seagrass on hydrodynamics is greater under high input flow velocities (Adams et al. 2016). We found that this is also true for artificial seagrass: Although all input current velocities were significantly reduced by ASG, the slower input current velocities of 0.3 m

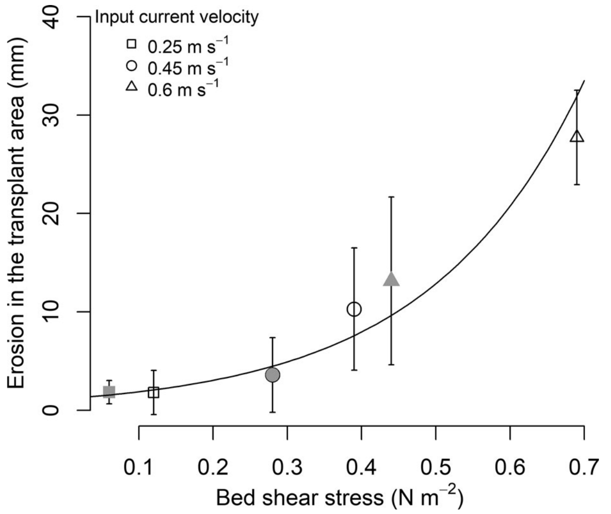

Figure 6. Effect of bed shear stress imposed by currents on sediment erosion (only negative elevation changes were included) in the transplant area. Error bars on mean erosion represent ± standard deviation. Grey data points represent results from experiments with artificial seagrass (ASG) as protection measure. The black line indicates the function fitted to the data.

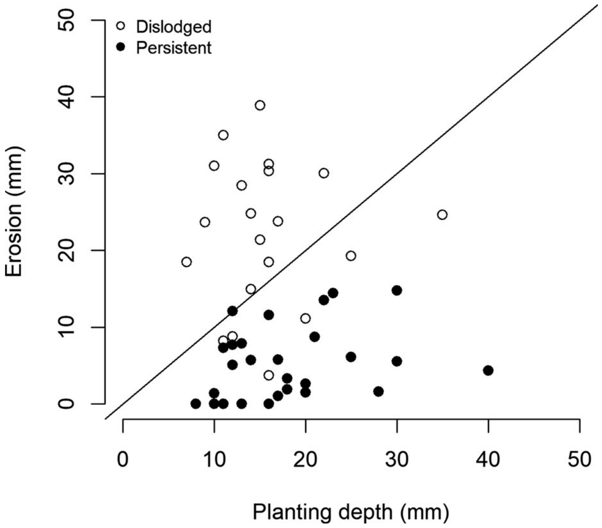

Figure 8. Relation between planting depth and erosion at the position of the shoots for dislodged and persistent shoots.

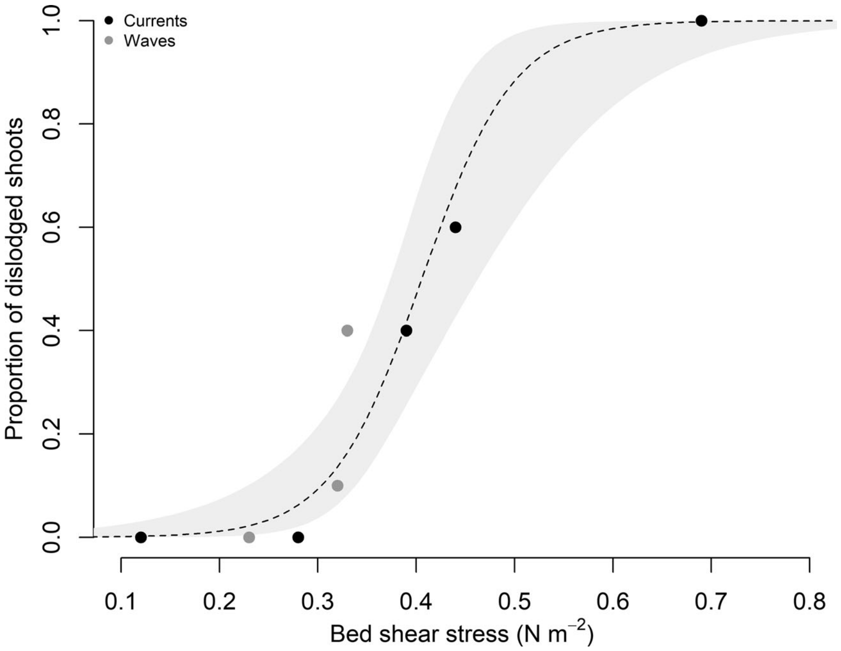

Figure 7. Effect of bed shear stress on the proportion of transplanted *Z. marina* shoots that were dislodged within 30 min. Grey data points represent results from wave experiments, black points from experiments under currents. The line represents the function fitted to the data and the shaded area the 95% confidence interval.

s^{-1} were only reduced by 10%, while the input current velocities of 0.6 m s^{-1} were reduced by 28%.

Ripple formation and erosion

Newly establishing plants in coastal vegetation, being either naturally establishing seedling or transplanted shoots, have to cope with hydrodynamically imposed sediment dynamics resulting from alternating erosion and deposition. These sediment dynamics have proven to be a key limitation for the establishment of mangroves, salt marshes and seagrasses alike (Balke et al. 2011; Infantes et al. 2011; Balke et al. 2013; Balke et al. 2014; Bouma et al. 2014; Cao et al. 2018).

The wave experiments showed that a higher wave frequency and height resulted in increased bed shear stress, but this did not cause higher ripples or significantly more erosion (Table 1). This may be due to the fact that the applied waves stirred up the sediment, but without a simultaneously acting current, the sediment was not transported off. Furthermore, the difference in wave height is quite small, which might lead to negligible differences in ripple height. Under currents, artificial structures can mimic the facilitation effect of seagrass in reducing the sediment dynamics from erosion. Villanueva et al. (2020) observed a sheltering effect of ASG by a reduction in current velocity up to 80%. Our study confirms, that ASG provides shelter under flow conditions by reducing current velocity and consequently bed shear stress. The fact that the reduction in bed shear stress by the ASG was higher at higher input currents (Figure 6) is consistent with our analyses of the sediment erosion behind the ASG. Whereas almost no erosion occurred between a bed shear stress of 0.06 – 0.28 N m^{-2}, the erosion increased significantly at 0.39 N m^{-2}. Thus, the erosion threshold for the used sediment (grain size median (D50) of 249 ± 11 µm) lays between 0.28 and 0.39 N m^{-2} and was thus higher than the theoretical critical bed shear stress based on the grain size median (D50) used in this study which is 0.19 N m^{-2}. In our current velocity experiment, the difference in erosion between no protection and protection with ASG was highest at the highest input current velocity of 0.6 m s^{-1}. Hu et al. (2018) did experiments with a current velocity of 0.09 m s^{-1} and observed a zone with reduced velocity and turbulent kinetic energy behind an artificial meadow, which led to an increase in sediment deposition. With a leaf length similar to water depth, as in our case, this zone had a length of 24 cm. Our current velocity experiment was conducted at higher velocities and we did not observe sedimentation, but less erosion for a length of 46 cm behind the ASG (Figure 5).

Dislodgement of transplanted seagrass shoots

To realise seagrass restoration with ASG as protection measure against hydrodynamic energy, it is important to learn more about the hydrodynamic conditions that transplanted shoots can withstand and to illuminate the mechanisms that lead to their dislodgement. In our experiment, the threshold bed shear stress for plant dislodgement was 0.3 N m^{-2}, well matching the bed shear stress of 0.27 N m^{-2} applied by Balke et al. (2011).

The use of ASG led in our experiment to a flow reduction of 15% with an input flow velocity of 0.45 m s^{-1} as well as a reduction in bed shear stress of 28%, and by this prevented the dislodgement of plants (Table 2).

This is associated with an erosion of 4 mm, compared to 10 mm without ASG. We furthermore detected a threshold for the dislodgement of the transplanted shoots: they started to dislodge when 25% of the rhizome was set free, but most of the seedlings dislodged when the erosion depth exceeded the planting depth (Figure 8). Infantes et al. (2011) analysed the critical threshold for dislodgement of transplanted seedlings under waves for two seagrass species (*Posidonia oceanica* and *Cymodocea nodosa*). They determined that 50 – 60% and 80% of root length could be set free until seedlings are dislodged, respectively. Balke et al. (2011) reported a linear relationship between critical erosion depth and root length in mangrove seedlings, but 4 cm need to remain covered. They suggest that the erosion depth leading to dislodgement is a highly plant-specific parameter.

Although the depth of rhizome planting positively affected the resistance of the transplanted shoots, it should be noted that seagrass health can be negatively affected by being buried too deep (e.g., Cabaço and Santos 2007; Mills and Fonseca. 2003).

In contrast to other studies (e.g., Wicks et al. 2009; Infantes et al. 2011), the influence of the aboveground characteristics such as leaf length on dislodgement could not be confirmed with our results: The dislodgement seems to depend only on the excavation by erosion and not on the drag on the aboveground biomass.

While erosion explains the dislodgement of shoots under currents, this is not true for the dislodgement of shoots under waves. The main difference between the two wave treatments is the wave frequency and the resulting wave velocity and height. The plants swayed back and forth more often at the higher frequency during the tested time interval of 30 minutes, thus potentially loosening the rhizomes' position in the sediment. The higher drag forces induced by the higher wave velocity may have subsequently led to dislodgement. Dislodgement of *P. oceanica* seedlings increased at flow velocities between 0.07 and 0.18 m s^{-1} (Infantes et al. 2011), showing a similar threshold to the *Z. marina* shoots in this study, where dislodgement started between 0.16 and 0.23 m s^{-1}.

Implications for seagrass restoration

Before starting any restoration efforts, the restoration site needs to be characterised in terms of waves, currents, sediment type and nutrient concentration, because these characteristics play an important role for identifying suitable sites for restoration (van Katwijk et al. 2016). Our results suggest that due to a reduction in bed shear stress and erosion under the influence of currents, ASG can improve hydrodynamic site characteristics in restoration trials when the bare-root technique is used.

However, an ASG cannot support restoration efforts, when the main obstacle for seagrass growth is eutrophication and thus increased growth of algae, which impede the photosynthesis of seagrass. Furthermore, the effect of ASG depends on the sediment composition. Carr et al. (2016) emphasised that the positive feedback of vegetation (in our case ASG) for light availability is more important at sites with sediment consisting mainly of silt and clay and not of coarse sand. The bed shear stress needs to be reduced by a canopy below a critical threshold, in order for sediment suspension to be prevented (James et al. 2020), and this critical threshold depends on the sediment composition in terms of grain size. To achieve a reduction in bed shear stress below or near the determined critical threshold for sediment suspension, the designed ASG should be tested in a flume beforehand. If the magnitude of erosion is known at the site, the planting depth of the shoots should be higher than the potential erosion depth by using shoots with longer and deeper rhizomes. If this is not possible, other means, e.g., wooden pegs or staples could anchor the shoots (van Katwijk et al. 2016).

Acknowledgements

We thank Raúl Villanueva and Magnus Asmussen for gathering the plant material and the whole SeaArt team for inspirations on the experiments and the manuscript. We furthermore thank Lennart van IJzerloo for technical support at the NIOZ.

Funding

The work was funded by MWK Lower Saxony Niedersächsisches Vorab as part of the collaborative project "SeaArt - Long term establishment of SEAgrass ecosystems through biodegradable ARTificial meadows", funded by the Federal State of Lower Saxony" (Grant No. ZN3187).

References

Adams MP, Hovey RK, Hipsey MR, Bruce LC, Ghisalberti M, Lowe RJ, Gruber RK, Ruiz-Montoya L, Maxwell PS, Callaghan DP, Kendrick GA, et al. 2016. Feedback between sediment and light for seagrass: where is it important? Limnol Oceanogr. 61(6): 1937–1955.

Balke T, Bouma TJ, Horstman EM, Webb EL, Erftemeijer PL, Herman PM. 2011. Windows of opportunity: Thresholds to mangrove seedling establishment on tidal flats. Mar Ecol Prog Ser. 440:1–9.

Balke T, Herman PMJ, Bouma TJ. 2014. Critical transitions in disturbance-driven ecosystems: identifying Windows of Opportunity for recovery. J Ecol. 102(3): 700–708.

Balke T, Webb EL, van den Elzen E, Galli D, Herman PMJ, Bouma TJ. 2013. Seedling establishment in a dynamic sedimentary environment: a conceptual framework using mangroves. J Appl Ecol. 50(3):740–747.

Barbier EB, Hacker SD, Kennedy C, Koch EW, Stier AC, Silliman BR. 2011. The value of estuarine and coastal ecosystem services. Ecol. Monogr. 81(2):169–193.

Bos AR, van Katwijk MM. 2007. Planting density, hydrodynamic exposure and mussel beds affect survival of transplanted intertidal eelgrass. Mar Ecol Prog Ser. 336: 121–129.

Bouma TJ, van Belzen J, Balke T, Zhu Z, Airoldi L, Blight AJ, Davies AJ, Galvan C, Hawkins SJ, Hoggart SP, et al. 2014. Identifying knowledge gaps hampering application of intertidal habitats in coastal protection: opportunities & steps to take. Coastal Eng. 87:147–157.

Bouma TJ, Vries M. d, Low E, Peralta G, Tánczos IC, van de Koppel J, Herman PMJ. 2005. Trade-offs related to ecosystem engineering: a case study on stiffness of emerging macrophytes. Ecology. 86(8):2187–2199.

Bouma TJ, Vries MD, Herman PMJ. 2010. Comparing ecosystem engineering efficiency of two plant species with contrasting growth strategies. Ecology. 91(9): 2696–2704.

Bower W.F. 2007. Seagrass -Sediment interactions, positive feedbacks and critical thresholds for occurrence: a review. Hydrobiologia. 591(1):5–24.

Cabaço S, Santos R. 2007. Effects of burial and erosion on the seagrass *Zostera noltii*. J Exp Mar Biol Ecol. 340(2): 204–212.

Campbell ML. 2002. Getting the foundation right: a scientifically based management framework to aid in the planning and implementation of seagrass transplant efforts. Bull Mar Sci. 71(3):1405–1414.

Campbell ML, Paling EI. 2003. Evaluating vegetative transplant success in *Posidonia australis*: a field trial with habitat enhancement. Mar Pollut Bull. 46(7): 828–834.

Cao H, Zhu Z, Balke T, Zhang L, Bouma TJ. 2018. Effects of sediment disturbance regimes on Spartina seedling establishment: Implications for salt marsh creation and restoration. Limnol Oceanogr. 63(2):647–659.

Carr JA, D'Odorico P, McGlathery KJ, Wiberg PL. 2016. Spatially explicit feedbacks between seagrass meadow structure, sediment and light: habitat suitability for seagrass growth. Adv. Water Resour. 93:315–325.

Carus J, Paul M, Schröder B. 2016. Vegetation as self-adaptive coastal protection: reduction of current velocity and morphologic plasticity of a brackish marsh pioneer. Ecol Evol. 6(6):1579–1589.

Chen S-N, Sanford LP, Koch EW, Shi F, North EW. 2007. A nearshore model to investigate the effects of seagrass bed geometry on wave attenuation and suspended sediment transport. Estuaries Coasts. 30(2): 296–310.

Christianen MJA, van Belzen J, Herman PMJ, van Katwijk MM, Lamers LPM, van Leent PJM, Bouma TJ. 2013. Low-canopy seagrass beds still provide important coastal protection services. PloS One. 8(5):e62413.

Davis RC, Short FT. 1997. Restoring eelgrass, *Zostera marina* L., habitat using a new transplanting technique: The horizontal rhizome method. Aquat. Bot. 59(1-2): 1–15.

Fonseca MS, Cahalan JA. 1992. A preliminary evaluation of wave attenuation by four species of seagrass. Estuarine Coastal Shelf Sci. 35(6):565–576.

Fonseca MS, Koehl MA, Fourqurean JW. 2019. Effect of Seagrass on Current Speed: Importance of Flexibility vs. Shoot Density. Front Mar Sci. 6:376.

Fonseca MS, Zieman JC, Thayer GW, Fisher JS. 1983. The role of current velocity in structuring eelgrass (*Zostera marina* L.) meadows. Estuarine Coastal Shelf Sci. 17(4):367–380.

Ganassin C, Gibbs PJ. 2008. A review of seagrass planting as a means of habitat compensation following loss of seagrass meadow. Cronulla: NSW Department of Primary Industries.

Hengst A, Melton J, Murray L. 2010. Estuarine restoration of submersed aquatic vegetation: the nursery bed effect. Restor Ecol. 18(4):605–614.

Hu Z, Lei J, Liu C, Nepf H. 2018. Wake structure and sediment deposition behind models of submerged vegetation with and without flexible leaves. Adv Water Resour. 118:28–38.

Infantes E, Orfila A, Bouma TJ, Simarro G, Terrados J. 2011. Posidonia oceanica and Cymodocea nodosa seedling tolerance to wave exposure. Limnol Oceanogr. 56(6):2223–2232.

James RK, Christianen MJA, Katwijk MM, Smit JC, Bakker ES, Herman PMJ, Bouma TJ. 2020. Seagrass coastal protection services reduced by invasive species expansion and megaherbivore grazing. J Ecol. 108(5): 2025–2037.

James RK, Silva R, van Tussenbroek BI, Escudero-Castillo M, Mariño-Tapia I, Dijkstra HA, van Westen RM, Pietrzak JD, Candy AS, Katsman CA, van der Boog CG, et al. 2019. Maintaining tropical beaches with seagrass and algae: a promising alternative to engineering solutions. BioScience. 69(2):136–142.

Koch E. 1999. Preliminary evidence on the interdependent effect of currents and porewater geochemistry on *Thalassia testudinum* Banks ex König seedlings. Aquat Bot. 63(2):95–102.

Koch EW, Ackerman JD, Verduin J, van Keulen M. 2007. Fluid dynamics in seagrass ecology—from molecules to ecosystems. In: Larkum AWD, Orth RJ, Duarte CM, editors. Seagrasses: Biology, ecology and conservation, 2nd ed. Dordrecht: Springer. p. 193–225.

Lei J, Nepf H. 2019. Wave damping by flexible vegetation: connecting individual blade dynamics to the meadow scale. Coastal Eng. 147:138–148.

Malcherek A. 2018. Gezeiten und Wellen: In Küsteningenieurwesen und Ozeanographie. 2nd ed. Wiesbaden: Springer Vieweg.

Manca E, Cáceres I, Alsina JM, Stratigaki V, Townend I, Amos CL. 2012. Wave energy and wave-induced flow reduction by full-scale model Posidonia oceanica seagrass. Cont Shelf Res. 50-51:100–116.

McCullough P, Nelder JA. 1989. Generalized linear models. Monographs on Statistics and Applied Probability, 2 ed. vol. 37, London: Chapman and Hall.

Mills KE, Fonseca MS. 2003. Mortality and productivity of eelgrass *Zostera marina* under conditions of experimental burial with two sediment types. Mar Ecol Prog Ser. 255:127–134.

Newell RIE, Koch EW. 2004. Modeling seagrass density and distribution in response to changes in turbidity stemming from bivalve filtration and seagrass sediment stabilization. Estuaries. 27(5):793–806.

Nielsen P. 1992. Coastal bottom boundary layers and sediment transport: Singapore: World scientific, 340p.

Orth RJ, Carruthers TJB, Dennison WC, Duarte CM, Fourqurean JW, Heck KL, Hughes AR, Kendrick GA, Kenworthy WJ, Olyarnik S, et al. 2006. A global crisis for seagrass ecosystems. BioScience. 56(12):987.2.0.CO;2]

Paling EI, Fonseca MS, van Katwijk MM, van Keulen M. 2009. Seagrass restoration. In: Perillo GME, editor. Coastal wetlands: an integrated ecosystem approach, 1st ed. Amsterdam: Elsevier. p. 687–713.

Park J-I, Lee K-S. 2010. Development of transplantation method for the restoration of surfgrass, *Phyllospadix japonicus*, in an exposed rocky shore using an artificial underwater structure. Ecol. Eng. 36(4):450–456.

Paul M, Amos CL. 2011. Spatial and seasonal variation in wave attenuation over *Zostera noltii*. J Geophys Res. 116(C8):138.

Paul M, Bouma TJ, Amos CL. 2012. Wave attenuation by submerged vegetation: combining the effect of organism traits and tidal current. Mar Ecol Prog Ser. 444: 31–41.

Pebesma EJ. 2004. Multivariable geostatistics in S: the gstat package. Comput Geosci. 30(7):683–691.

Pickerell CH, Schott S, Wyllie-Echeverria S. 2005. Buoy-deployed seeding: demonstration of a new eelgrass (*Zostera marina* L.) planting method. Ecol Eng. 25(2): 127–136.

R Core Team. 2019. R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical.

Reidenbach MA, Thomas EL. 2018. Influence of the Seagrass, *Zostera marina*, on wave attenuation and bed shear stress within a shallow Coastal Bay. Front Mar Sci. 5: 1–16, Article 397.

Temmink RJ, Christianen MJA, Fivash GS, Angelini C, Boström C, Didderen K, Engel SM, Esteban N, Gaeckle JL, Gagnon K, et al. 2020. Mimicry of emergent traits amplifies coastal restoration success. Nat Commun. 11(1):3668. doi:10.1038/s41467-020-17438-4.

Unsworth RKF, McKenzie LJ, Collier CJ, Cullen-Unsworth LC, Duarte CM, Eklöf JS, Jarvis JC, Jones BL, Nordlund LM. 2019. Global challenges for seagrass conservation. Ambio. 48(8):801–815.

van der Heide T, van Nes EH, Geerling GW, Smolders AJP, Bouma TJ, van Katwijk MM. 2007. Positive feedbacks in seagrass ecosystems: Implications for success in conservation and restoration. Ecosystems. 10(8): 1311–1322.

van Katwijk MM, Bos AR, de Jonge VN, Hanssen LSAM, Hermus DCR, de Jong DJ. 2009. Guidelines for seagrass restoration: importance of habitat selection and donor population, spreading of risks, and ecosystem engineering effects. Mar Pollut Bull. 58(2):179–188.

van Katwijk MM, Hermus DCR. 2000. Effects of water dynamics on Zostera marina: transplantation experiments in the intertidal Dutch Wadden Sea. Mar Ecol Prog Ser. 208:107–118.

van Katwijk MM, Thorhaug A, Marbá NN, Orth RJ, Duarte CM, Kendrick GA, Althuizen IH, Balestri E, Bernard G, Cambridge ML, Cunha AH, et al. 2016. Global analysis of seagrass restoration: the importance of large-scale planting. J Appl Ecol. 53(2):567–578.

van Keulen M, Paling EI, Walker CJ. 2003. Effect of planting unit size and sediment stabilization on seagrass transplants in Western Australia. Restor Ecology. 11(1):50–55.

Villanueva R, Thom M, Visscher J, Paul M, Schlurmann T. 2020. Wake length of an artificial seagrass meadow: a study of shelter and its feasibility for restoration. J Ecohydraulics. Same Special Issue.

Wicks EC, Koch EW, O’Neil JM, Elliston K. 2009. Effects of sediment organic content and hydrodynamic conditions on the growth and distribution of *Zostera marina*. Mar Ecol Prog Ser. 378:71–80.

Widdows J, Pope ND, Brinsley MD, Asmus H, Asmus RM. 2008. Effects of seagrass beds (*Zostera noltii* and *Z. marina*) on near-bed hydrodynamics and sediment resuspension. Mar Ecol Prog Ser. 358:125–136.

Wilcoxon F. 1945. Individual comparisons by ranking methods. Biometrics Bull. 1(6):80–83.

Wilkie L, O’Hare MT, Davidson I, Dudley B, Paterson DM. 2012. Particle trapping and retention by Zostera noltii: A flume and field study. Aquat Bot. 102:15–22.