

# Suppressing antagonistic bioengineering feedbacks doubles restoration success

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**Abstract.** In a seagrass restoration project, we explored the potential for enhancing the restoration process by excluding antagonistic engineering interactions (i.e., biomechanical warfare) between two ecosystem engineers: the bioturbating lugworm *Arenicola marina* and the sediment-stabilizing seagrass *Zostera noltii* Hornem. Applying a shell layer underneath half of our seagrass transplants successfully reduced adult lugworm density by over 80% and reduced lugworm-induced microtopography (a proxy for lugworm disturbance) at the wave-sheltered site. At the wave-exposed site adult lugworm densities and microtopography were already lower than at the sheltered site but were further reduced in the shell-treated units. Excluding lugworms and their bioengineering effects corresponded well with a strongly enhanced seagrass growth at the wave-sheltered site, which was absent at the exposed site. Enhanced seagrass growth in the present study was fully assigned to the removal of lugworms' negative engineering effects and not to any (indirect) evolving effects such as an altered biogeochemistry or sediment-stabilizing effects by the shell layer. The context-dependency implies that seagrass establishment at the exposed site is not constrained by negative ecosystem-engineering interactions only, but also by overriding physical stresses causing poor growth conditions. Present findings underline that, in addition to recent emphasis on considering positive (facilitating) interactions in ecological theory and practice, it is equally important to consider negative engineering interactions between ecosystem-engineering species. Removal of such negative interactions between ecosystem-engineering species can give a head start to the target species at the initial establishment phase, when positive engineering feedbacks by the target species on itself are still lacking. Though our study was carried out in a marine environment with variable levels of wave disturbance, similar principles may be expected to apply to other ecosystems that are inhabited by ecosystem engineers.

**Key words:** *Arenicola marina*; bioturbation; conservation; Eastern Scheldt estuary, southwestern Netherlands; ecosystem engineers; exclusion; lugworm; negative feedbacks; restoration; seagrass meadow; *Zostera noltii* Hornem.

## INTRODUCTION

Approximately 30–50% of the Earth's coastal ecosystems have been severely degraded in the last decades, often due to anthropogenic disturbances such as eutrophication or overexploitation (Orth et al. 2006, Barbier et al. 2008). Even though these areas make up

just 4% of the Earth's total surface, systems such as salt marshes, coral reefs, and seagrass meadows are of great economic and ecological importance because large human populations depend on them for storm buffering, fisheries, and enhanced water quality (Orth et al. 2006, Barbier et al. 2008). Moreover, they serve as key habitat in the life cycles of many marine animal species. Although these ecosystems were initially considered highly resilient to human disturbance, we now know that most coastal ecosystems do not respond linearly to change, but may often collapse without warning (Silliman et al. 2005, van der Heide et al. 2007, Hughes et al. 2010). It has also emerged that recovery or restoration of

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coastal ecosystems is extremely difficult (Bakker et al. 2002, Orth et al. 2006, Halpern et al. 2007, Omori 2010).

Various studies have shown that sudden collapse and lack of recovery in coastal ecosystems may follow alternative stable state behavior and can be attributed to disturbance of positive feedback mechanisms (e.g., van de Koppel et al. 2001, van der Heide et al. 2007). Such feedbacks typically arise from the ability of the foundation species (e.g., corals, seagrasses, reef-forming shellfish, marsh plants) to ameliorate environmental stress (i.e., “ecosystem engineering”) (e.g., Jones et al. 1994, Madsen et al. 2001). Because these (self-) facilitation mechanisms typically act above a certain density or size (e.g., van der Heide et al. 2007, 2008, Bouma et al. 2009), coastal ecosystems are prone to threshold behavior. The ecosystem seems stable above the threshold size or density, while recovery and restoration are nearly impossible when the threshold is not bridged (Hobbs and Norton 1996, Halpern et al. 2007, Suding and Hobbs 2009).

Today, (self-) facilitation and positive feedbacks are well recognized as important factors to consider for coastal ecosystem conservation and restoration (Crain and Bertness 2006, Halpern et al. 2007). The potential role of negative interactions between contrasting ecosystem engineers in restoration efforts has recently been neglected, despite the early recognition of its potential importance in marine habitats (see review in Peterson 1980, 1991). For example, this has been shown for the negative effect of deposit feeders on filter feeders by making sediment more erosive, causing filter feeding to be hampered by more turbid water (i.e., trophic group amensalism; Rhoads and Young 1970). Several studies have also demonstrated that negative interactions between benthos and vegetation can be very strong (Philippart 1994, Hughes et al. 2000, Hughes and Paramor 2004, Siebert and Branch 2006, Berkenbusch et al. 2007, van Wesenbeeck et al. 2007). For instance, “biomechanical warfare” between ecosystem-engineering salt marsh vegetation and infauna can cause a bimodal species distribution on the salt marsh–mudflat interface, as bioturbation prevented plant colonization in the invertebrate-dominated state and invertebrates were excluded by sediment compaction in the plant-dominated state (van Wesenbeeck et al. 2007).

Meadows of the seagrass *Zostera noltii* Hornem are notoriously hard to restore, and initial establishment is especially difficult as positive feedbacks are still lacking (i.e., Byers et al. 2006, van der Heide et al. 2007, van Katwijk et al. 2009). Historically, *Zostera* meadows are found to co-occur with the bioturbating lugworm *Arenicola marina* (Jacobs et al. 1983), though they may encounter negative worm effects (i.e., Philippart 1994, Reise and Kohlhus 2008). At present, in some areas of northwestern Europe the *Zostera noltii* biomass distribution appears to be correlated with the presence of shallow layers of clay, compressed peat, or shells that

naturally exclude bioturbating lugworms (Reise 2002, Reise and Kohlhus 2008; D. J. de Jong, W. B. J. T. Giesen, M. M. van Katwijk, and W. Suykerbuyk, *personal observation* in Scheldt Estuary). Moreover, settlement of *Zostera noltii* has been observed in plots where lugworms were excluded for experimental purposes (Reise 1983, Reise and Kohlhus 2008). The absence of seagrass recovery on former seagrass grounds that are now inhabited by lugworms, despite the improved water quality with respect to increased transparency and reduced nutrient concentrations over the last decades, may suggest that the lugworm presence and/or activity may hamper recolonization by seagrass within our study area.

In this study we test to what extent restoration of *Zostera noltii* meadows at formerly suitable seagrass habitats would benefit from removal of negative effects by the bioturbating lugworm *Arenicola marina* and how this depends on abiotic conditions (sheltered vs. wave exposed). Removal of these negative ecosystem-engineering effects on initial seagrass establishment was tested in a large-scale *Zostera noltii* restoration by comparing sod transplantations with and without lugworm reduction by means of a shallow shell layer (cf. Reise 2002). To test the general relevance of excluding such negative engineering interactions, we tested this method under contrasting abiotic conditions (wave exposed vs. wave sheltered) that may cause other sources of sediment disturbance. We hypothesize that minimizing lugworm-induced sediment disturbance will enhance seagrass growth, unless other sources of abiotic stress cause sediment disturbance.

## METHODS

### Study area

Our experiment was performed in the Eastern Scheldt estuary (southwestern Netherlands), a former arm in the river Scheldt delta (Fig. 1A). After a severe flood in 1953, the estuary was heavily engineered to secure safety against flooding: freshwater input openings in the eastern part of the estuary were cut off by dams and the estuary mouth in the west was partially closed by a storm surge barrier. Since then, the system has changed (e.g., Louters et al. 1998), and the extensive seagrass meadows (up to 1000 ha) have decreased during the building of these so-called Delta Works. More surprisingly, this seagrass decline has persisted long after the completion of the Delta Works and is ongoing today, despite the higher transparency of the water column and lower nutrient loading.

Presently, only several dozen hectares of the seagrass *Zostera noltii* Hornem remain (data from the Dutch Ministry of Infrastructure and the Environment), which appear to be concentrated on relatively stable sediments without lugworm presence (e.g., natural shell layers, heavy clay from former dikes, or salt marsh remnants; D. J. de Jong, W. B. J. T. Giesen, M. M. van Katwijk, and W. Suykerbuyk, *personal observations*). Exact

mechanistic causes of this massive and persistent seagrass decline have not yet been identified. It has been observed that the lugworm relief had increased at many intertidal former seagrass locations (D. J. de Jong, W. B. J. T. Giesen, M. M. van Katwijk, and W. Suykerbuyk, *personal observations*). No previous seagrass transplantation or restoration efforts have been performed in the Eastern Scheldt estuary. Renewal of the stone cladding of the defense walls requires mitigating measures for the directly endangered seagrass that follow European Union regulations. This led to the present transplantation project.

#### *Experimental set-up*

A total of 441 m<sup>2</sup> of native *Zostera noltii* Hornem sods (196 sods of 1.5 × 1.5 m) with a vegetation cover ranging from 10% to 70% (sod vegetation cover, 33% ± 2% [mean ± SE]) were transplanted to two tidal flats, one sheltered (Krabbenkreek flat) and one relatively more exposed (Slikken van den Dortsman), in the Eastern Scheldt estuary early in the growing season (June 2007) (Fig. 1B, C). Sod were mechanically harvested in custom-made wooden boxes from a natural meadow at the donor site Slikken van Viane. They were protected against desiccation during transport and replanted within 24 h to 28 plots divided over the sheltered (16) and exposed (12) sites. Plots were distributed evenly 10 m apart in rows at an average emerging time of 50–60% (Fig. 1B, C). To test the effect of plot size, plots consisted of either five or nine sods placed in a checkerboard configuration (Fig. 1D). Planting configurations were evenly applied over the control and exclusion plots at both locations (Fig. 1B, C). In every second transplantation plot, adult lugworms (*Arenicola marina*) were excluded by placing a 10 cm thick shell layer (local cockle shell fragments with a diameter of 4 cm) at a depth of 8–18 cm below the sediment surface, both underneath the seagrass sods and the surrounding plot sediment (Fig. 1E, F) (after Reise 2002). In the control plots, sediment was similarly removed and replaced to adjust for sediment handling.

Basic transplant characteristics (i.e., plant coverage and area), as well as lugworm and other biological parameters, were monitored at monthly intervals during the growing season from June until October. The area covered by seagrass (in square meters) is considered to be the main indicator for transplantation success (Schanz and Asmus 2003), with area being measured and cover being estimated by eye using a 25 × 25 cm grid and cross-checking between workers. Lugworm fecal cast counts per area were used as a quantitative proxy for the numbers of worms present (cf. Farke and Berghuis 1979, Flach and Beukema 1994). Juvenile and adult lugworms were divided by the diameter of the cylindrical-shaped cast; rule of thumb: juvenile < diameter cast 1 mm < adult. In order to prevent severe underestimation of lugworm numbers, cast counts were not performed on a rainy day or prior to 2 h after the

transplants emerged from the water (sensu Cadée 1976). Lugworm-induced microtopography (also referred to as lugworm relief) was measured as the vertical height difference between a lugworm's pit and adjacent mound. This parameter was used as a simple integrative proxy for the potential negative engineering effects of lugworm-induced sediment disturbance (e.g., direct burial, unearthing rhizomes, and sediment instability) on seagrass survival, as it accounts for size and activity differences between local lugworm communities and can easily be compared across sites with other sources of sediment disturbance such as wave exposure.

#### *Sediment characteristics*

Additional measurements of pore water nutrients (alkalinity, pH, NO<sub>3</sub><sup>-</sup>, NH<sub>4</sub><sup>+</sup> and ortho-PO<sub>4</sub>, sheltered sites only) and sediment composition (grain size distribution and organic content, both sites) were performed just after maximum seagrass biomass and area were reached in the growing season (early September). Alkalinity (by titration with 0.01 mol/L HCl to pH 4.2; Lamers et al. 1998) and pH were determined directly after sampling, whereupon samples were frozen (–20°C) until further analysis. Ammonia and ortho-phosphate concentrations were measured colorimetrically on an auto-analyzer (Bran+Luebbe, Almere, The Netherlands), using hypochlorite (Berthelot reaction) and ammonium-molybdate, respectively. Organic matter content in freeze-dried sediments (upper 5 cm) was estimated as mass loss by ignition at 550°C after acidifying samples with HCl. Grain size distribution on the same sediment sieved over 1 mm was measured by laser diffraction on a particle sizer (Malvern, Worcestershire, UK).

#### *Statistical analysis*

All results are summarized as means ± SE. In advance of statistical analysis, data were checked for normality and if necessary transformed (Table 1). As planting configuration had no effect on seagrass survival (data not shown), plots are treated as replicates in further statistical analysis. Differences between transplantation sites and anti-lugworm treatments were analyzed using ANOVA with treatment nested in location, followed by post hoc Tukey's honestly significant differences (HSD) multiple means comparison tests at the 0.05 confidence limit. Effects of control and shell treatment on pore water and sediment data were tested by independent-samples *t* test. All tests were performed using Statistica (StatSoft, Tulsa, Oklahoma, USA).

## RESULTS

Shell layers successfully reduced the mean numbers of adult lugworms at both the sheltered ( $P < 0.01$ ) and the exposed ( $P < 0.01$ ) transplantation sites (Fig. 2A). Although initially the ambient number of lugworms at the exposed site was almost 2.5 times lower than that at the sheltered location, the proportional reduction of



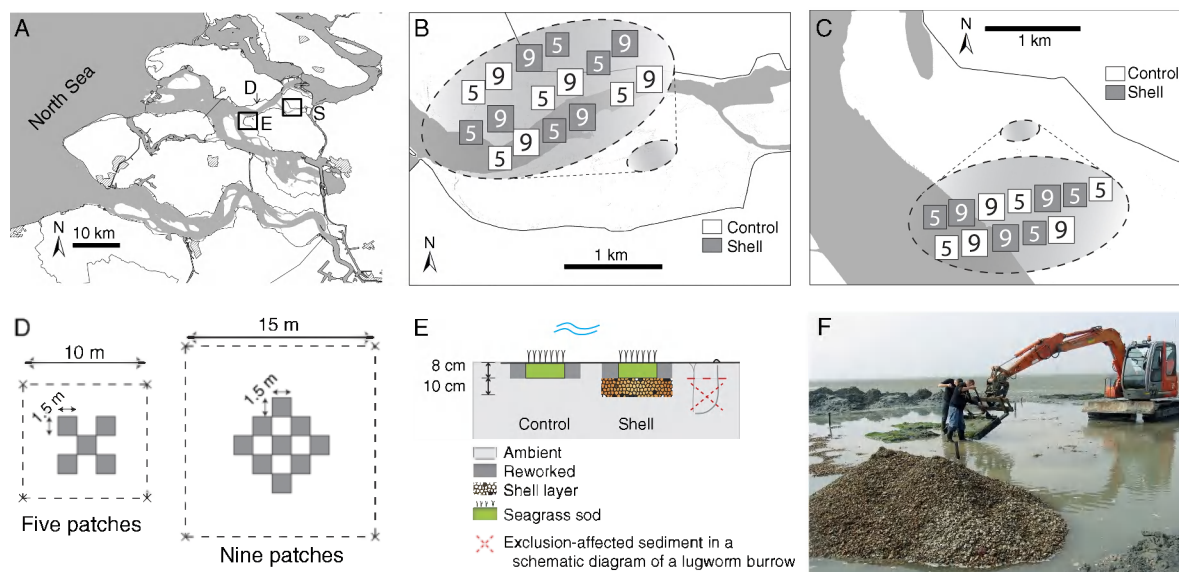


FIG. 1. (A) Location of the study areas in the southwest delta area of The Netherlands. Letters indicate the donor site (D) and the wave-exposed (E) and sheltered (S) *Zostera noltii* seagrass transplantation sites in the Eastern Scheldt estuary. (B, C) Detailed top view of (B) the wave-sheltered Krabbenkreek flats and (C) the wave-exposed Slikken van den Dortsman flats; shading indicates anti-lugworm (*Arenicola marina*) treatments (application of shells), and numbers indicate planting configuration. (D) Schematic top view of plots with two different planting densities (five and nine patches), their configuration (a checkerboard pattern), and the plot area that was reworked for the anti-lugworm treatment. (E) Schematic cross section of the plots indicating the manner in which sediments are reworked and organized. Colors indicate different sediment origins or treatments. At the far right is a schematic of a lugworm burrow indicating the significance of the anti-lugworm treatment on lugworm burrowing. (F) Large-scale seagrass transplantation in progress at the sheltered site. Shells applied to exclude lugworms are seen in the foreground. Placement of seagrass sod on the shell treatment is seen in the background.

adult worms due to the shell layer was of the same order of magnitude (81.3% vs. 86.8% for sheltered and exposed, respectively). The shell treatment significantly promoted ( $P < 0.05$ ) settlement of juvenile lugworms in the absence of adult worms at both sites (277.8% vs. 290.4% increase for shell-treated compared to control plots, respectively, both at wave-sheltered and wave-exposed sites; Fig. 2B). Adult lugworm numbers remained stable during at least three more years (data not shown).

Lugworm-induced microtopography, and thereby the negative engineering effect of lugworms on seagrass, was

significantly reduced by the shell treatment at the sheltered location ( $P < 0.01$ ; Fig. 2C). Exclusion plots could be easily recognized by the reduction of this characteristic pit and mound landscape. At the exposed site, similar anti-lugworm measures and their proportional effects on lugworm relief between control and treated plots of the exposed site compared to the sheltered site (50.5% vs. 37.0% reduction, respectively). Surprisingly, this reduction in relief was not found significantly different from that found at the sheltered site.

TABLE 1. Results of nested ANOVA on the number of adult and juvenile lugworms (*Arenicola marina*), their induced microtopography, and the related seagrass (*Zostera noltii*) area detected at each treated plot on two tidal flats.

Dependent variable	Transformation	Factor	SS	df	MS	F	P
Adult lugworms	square root	location	23.14	1	23.14	8.28	0.006
		treatment(location)	122.74	2	61.37	21.96	<0.001
		error	120.16	43	2.79		
Juvenile lugworms	fourth root	location	1.75	1	1.75	1.53	0.223
		treatment(location)	14.39	2	7.19	6.29	0.004
		error	49.21	43	1.14		
Lugworm relief	fourth root	location	128.31	1	128.31	22.84	<0.001
		treatment(location)	71.81	2	35.91	6.39	0.004
		error	235.91	42	5.62		
Seagrass area	log	location	1.23	1	1.23	4.12	0.054
		treatment(location)	3.67	2	1.84	6.13	0.007
		error	7.19	24	0.30		

Note: The study was conducted in the southwest delta area of The Netherlands.

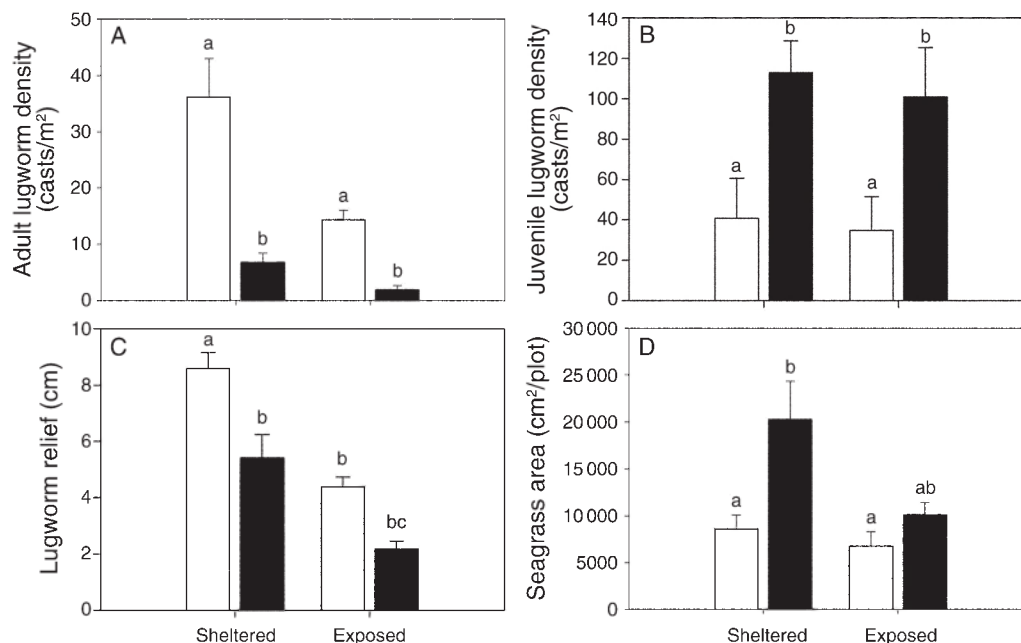


FIG. 2. Effects of hydrodynamic forcing (wave sheltered vs. wave exposed) and lugworm exclusion method (control in white vs. exclusion in black) on density of (A) adult and (B) juvenile lugworms (counts of fecal casts), (C) lugworm relief (lugworm-induced microtopography, used as proxy for lugworm disturbance), and (D) seagrass area per plot (used as proxy for restoration success). Data are from 17 and 18 July 2008, 13 months after transplantation. Bars represent mean + SE. Different letters above bars indicate significant differences (Tukey's HSD,  $P < 0.05$ ).

Although reduction of lugworm microtopography was comparable at both sites, surprisingly no such comparable effects on seagrass growth were found. That is, at the sheltered site, seagrass growth was significantly promoted in plots that excluded *Arenicola* by shells as compared to the control plots ( $P < 0.05$ ; Fig. 2D) (data 17 and 18 July 2008). However, no such difference was found at the exposed transplantation site, where seagrass growth was low both in the presence and absence of worm exclusion. Seagrass growth responses at the sheltered site could not be ascribed to shell layer effects on sediment and pore water characteristics, as these were unaffected (Table 2) except for a slightly lower median grain size ( $D_{50_{SED}}$ ) in the exposed lugworm-exclusion plots ( $t_{14} = 2.38$ ,  $P < 0.05$ ). Planting configuration (five or nine sods) had no effect on seagrass survival at either site at any point in time (data not shown).

#### DISCUSSION

The use of facilitative interactions is now a common recommendation in restoration and conservation efforts, and ecosystem engineers causing such interactions are increasingly considered to be conservation and restoration target species (Boogert et al. 2006, Byers et al. 2006, Crain and Bertness 2006, Halpern et al. 2007). Surprisingly, however, these papers neglect the potential restoration benefits of the removal of negative interactions originating from ecosystem engineers, despite the fact that such interactions can play an important role in

marine habitats (Rhoads and Young 1970, Philippart 1994, Hughes et al. 2000, Hughes and Paramor 2004, Siebert and Branch 2006, Berkenbusch et al. 2007, van Wesenbeeck et al. 2007). In this study, we show that suppressing such negative ecosystem-engineering effects could be a useful approach in restoration and conservation efforts by giving at least a better start during the initial establishment phase. Using the seagrass (biostabilizer)–lugworm (biodestabilizer) interaction as a model system, we showed that seagrass growth was significantly enhanced by excluding lugworms in a lugworm-dominated area. Removing negative engineering interactions may be especially important for reestablishing those species whose initial establishment is hampered by thresholds but who subsequently benefit from self-facilitating positive feedbacks. The latter is clearly the case in seagrass (van der Heide et al. 2007, 2011, van Katwijk et al. 2010).

Enhanced seagrass growth in the present study was fully assigned to the lugworm exclusion and not to any (indirect) evolving effects such as an altered biogeochemistry (Table 2) or sediment-stabilizing effects by the shell layer. From previous studies on *Zostera* it is known that sediment stabilization improves success at relatively exposed locations (van Katwijk and Hermus 2000, Reise and Kohlus 2008), but that this is not always the case at sheltered locations (van Katwijk and Hermus 2000). In our study the reverse holds true: the success was only promoted at sheltered sites. Therefore, this explanation does not hold for our situation. At the relatively exposed

TABLE 2. Sediment and pore water composition in control and exclusion (shell) plots at sheltered and exposed transplantation sites.

Parameter	Treatment	Sheltered		Exposed	
		Mean	SE	Mean	SE
D50 <sub>SED</sub> (μm)	control	159.13	8.54	<b>179.08</b>	<b>1.19</b>
	shell	168.70	5.74	<b>175.40</b>	<b>0.98</b>
Org C <sub>SED</sub> (%)	control	1.27	0.13	0.55	0.09
	shell	1.04	0.14	0.69	0.12
NH <sub>4</sub> (μmol/L)	control	91.82	11.18	...	...
	shell	104.17	13.15	...	...
ortho-PO <sub>4</sub> (μmol/L)	control	13.14	2.62	...	...
	shell	14.24	1.34	...	...
pH	control	7.48	0.02	...	...
	shell	7.49	0.03	...	...
Alkalinity (meq/L)	control	2.75	0.12	...	...
	shell	3.03	0.10	...	...

Notes: Sampling was conducted in early September 2007, three months after transplantation. Significant differences between treated and untreated plots are indicated in bold (*t* test, *P* < 0.05). Abbreviations are: D50<sub>SED</sub>, median grain size of the sediment; Org C<sub>SED</sub>, organic carbon fraction of the sediment. All other parameters refer to the pore water.

site no positive effect of lugworm exclusion on seagrass growth was found, although the proportional reduction of lugworm disturbance was comparable to that observed at the sheltered site. We expect this to be due to poorer growth conditions at the exposed site, due to direct physical disturbances by waves and currents (dislodgement or mechanical stress) or to indirect effects of increased hydrodynamics, such as increased sediment dynamics (resulting in burial or erosion) (e.g., Cabaço and Santos 2007; Han et al. 2012) or decreased epiphyte grazer densities (increasing algal overgrowth and thus light reduction for the seagrass plants) (Schanz and Asmus 2003). This indicates that excluding negative ecosystem-engineering interactions to initiate a population is only useful in areas where growth is not limited by other overriding (physical) stresses.

#### *Feasibility and long-term consequences of our method*

Our large-scale shell treatment proved to be a good measure for promoting initial seagrass establishment success by excluding adult lugworms and their negative effects, which is an important step in restoration. Extra costs for the application of a shell layer were ~20% of the total transplantation costs. For restoration purposes, lugworm exclusion by shells has major advantages over using nets, as have been used in scientific studies on lugworm exclusion (Reise 1983, Philippart 1994, Volkenborn and Reise 2006). First, shells are natural material that can generally be easily obtained locally. Second, in contrast to nets as used by Volkenborn and Reise (2006), shell layers only exclude large lugworms and allow smaller ones to establish. This is advantageous because the full exclusion has several side effects, such as the accumulation of fine sediment and the blockage of interstitial pores causing enhanced nutrient and sulphide levels (Volkenborn et al. 2007) that may have negative effects on seagrass performance (i.e., Touchette and Burkholder 2000, Calleja et al. 2007).

The present approach of removing negative engineering interactions was specifically aimed at improving the initial establishment for ecosystems that are difficult to restore due to establishment thresholds, but can later maintain themselves by self-facilitating positive feedbacks. Maximal establishment is the first requirement to enhance long-term success. However, although the treatment most likely will continue to diminish negative engineering interactions over the long term (the shell layer will not easily get lost), this does not necessarily warrant long-term success. During winter, when lugworms are less active and seagrass is dormant, grazing or physical disturbances from storm-driven waves, freezing, and ice rafting may form a second bottleneck to meadow persistence and thus restoration success. Unfortunately, these processes appeared to be important at our restoration sites, as seagrass transplantation suffered large losses during subsequent winters. Still, during summers, the shell treatment had a consistent positive effect on seagrass survival and growth similar to that shown in Fig. 2. Present observations suggest that the proposed method of removing negative engineering interactions will be most beneficial in those areas where biological activity causing such interactions is the main driver restricting seagrass growth year round.

#### CONCLUSIONS

Dynamic ecosystems that do not respond linearly to changes but are characterized by threshold behavior (such as coastal ecosystems) are notoriously difficult to restore (Rapport et al. 1998, Hobbs et al. 2006, van der Heide et al. 2007, Suding and Hobbs 2009) and are also sensitive to environmental perturbations (Scheffer et al. 2001, Pascual and Guichard 2005). Thorough understanding of system feedbacks, criticalities, shifts, and thresholds is needed to predict and thereby prevent transitions toward a barren state (Pascual and Guichard 2005, Scheffer et al. 2009, Firn et al. 2010). We provide

compelling experimental evidence demonstrating that exclusion of negative ecosystem-engineering interactions may be useful in initiating the reestablishment of those species whose initial establishment is hampered by thresholds but who subsequently benefit from self-facilitating positive feedbacks. Present findings underline that in addition to the recent growing awareness of the need to consider positive (facilitating) interactions in ecological theory (i.e., Bruno et al. 2003, Brooker and Callaway 2009) and ecological conservation and restoration projects (Byers et al. 2006, Crain and Bertness 2006, Halpern et al. 2007, van Katwijk et al. 2009), it is equally important to also consider negative engineering interactions between ecosystem-engineering species in restoration projects. This result reemphasizes and (by specifically focusing on negative engineering interactions) extends a wealth of older theory (Rhoads et al. 1970, Peterson 1980, 1991, Reise 1985, Wilson 1991). Similar to positive feedbacks, such negative engineering interactions may also cause threshold dynamics. Though our study was carried out in a marine environment, similar principles may be expected to apply to other ecosystems dominated by ecosystem engineers (Rietkerk et al. 2004, Scheffer et al. 2009).

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