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Review

Guidelines for seagrass restoration: Importance of habitat selection and donor population, spreading of risks, and ecosystem engineering effects

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ABSTRACT

Large-scale losses of seagrass beds have been reported for decades and lead to numerous restoration programs. From worldwide scientific literature and 20 years of seagrass restoration research in the Wadden Sea, we review and evaluate the traditional guidelines and propose new guidelines for seagrass restoration.

Habitat and donor selection are crucial: large differences in survival were found among habitats and among donor populations. The need to preferably transplant in historically confirmed seagrass habitats, and to collect donor material from comparable habitats, were underlined by our results. The importance of sufficient genetic variation of donor material and prevention of genetic isolation by distance was reviewed. The spreading of risks among transplantation sites, which differed in habitat characteristics (or among replicate sites), was positively evaluated. The importance of ecosystem engineering was shown in two ways: seagrass self-facilitation and facilitation by shellfish reefs. Seagrass self-facilitative properties may require a large transplantation scale or additional measures.

1. Introduction

Seagrass beds are among the most valuable ecosystems in the world (Costanza et al., 1997). Yet, these systems are relatively unknown and therefore often underappreciated by the general public (Orth et al., 2006). Large-scale losses have been reported for decades. For instance, worldwide seagrass loss between the mid-1980s and mid-1990s was estimated to be 12,000 km^2 (Short and Wyllie-Echeverria, 2000). This has led to numerous restoration programs (e.g., Paling et al., 2009).

Traditional guidelines in restoration literature suggest that it is necessary to reverse habitat degradation, to select transplantation habitats carefully, and to optimise the transplantation techniques (Hobbs and Norton, 1996; den Hartog, 2000; Calumpong and Fonseca, 2001; Campbell, 2002; Short et al., 2002; McKay et al., 2005). An unwritten rule is to spread risks in space and/or time. Recently, the importance of ecosystem engineering for seagrass beds was studied and described (Bouma et al., 2005; Bos and van Katwijk, 2007; Bos et al., 2007; van der Heide et al. 2007), and, as a new guideline, these studies should be accounted for in restoration projects (Byers et al., 2006). In this paper, we evaluate the traditional, and formulate new, guidelines by reviewing literature and 20 years of research from the Wadden Sea.

2. Study site: Wadden Sea and historical records of seagrass vegetation

The Wadden Sea is one of the world's largest international marine wetland reserves. The area covers circa 6000 km^2 and borders the coasts of The Netherlands, Germany, and Denmark (Fig. 1). The western Wadden Sea was inhabited by seagrasses since ancient times. The first record dates back to 1329 (den Hartog and Polderman, 1975). A treatise in the 18th century (Martinet, 1782), and a detailed mapping in the 19th century (Oudemans et al., 1870) are also early studies of its perceived importance, indeed providing hundreds of families with an income thanks to its economic value as isolating and filling material. Furthermore, seagrass was used to enforce the internal structure of the main dikes (to protect the polders against flooding) until the 18th century. The economic interest focused on the robust form of *Zostera marina* (eelgrass) that grew around the low tide level and deeper. The flexible, annual form of *Z. marina* as well as *Zostera noltii* (dwarf eelgrass) – both growing in the inter-tidal area that is around or

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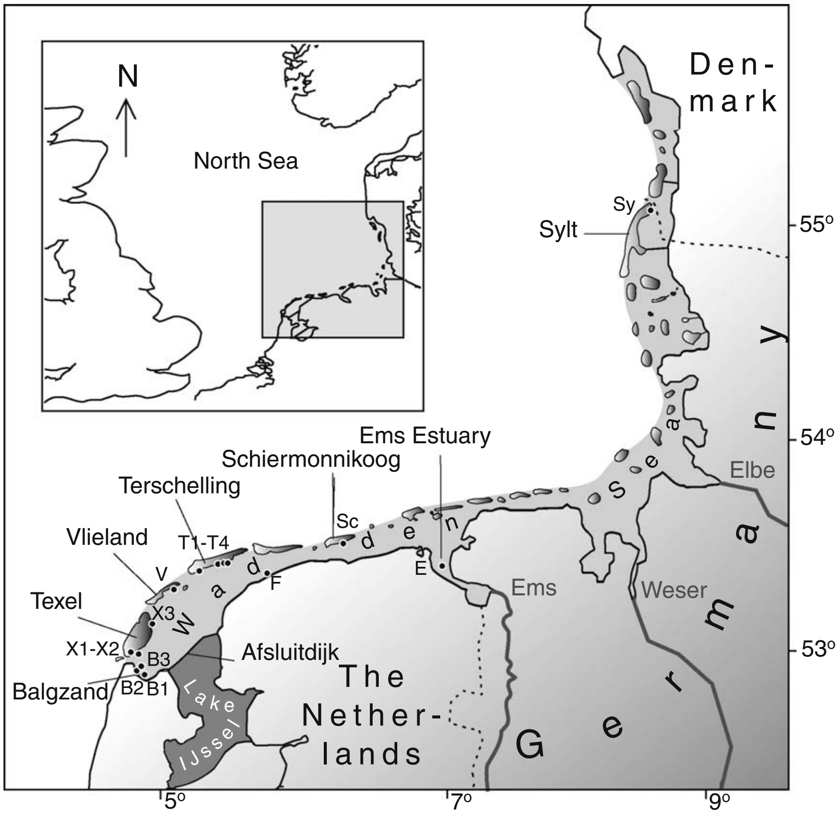

Fig. 1. Map of the Wadden Sea, NW Europe with transplantation locations.

above mean sea level – received no interest until the 20th century (Nienburg, 1927; Harmsen, 1936; den Hartog and Polderman, 1975; van Katwijk et al., 2000a, Fig. 2). The robust form of *Z. marina* completely disappeared during the early 1930s, due to a combination of factors, and never recovered (Reise et al., 1989; Giesen et al., 1990a, b). The flexible type of *Z. marina*, as well as *Z. noltii*, disappeared during the 1970s, shortly after they had been mapped (den Hartog and Polderman, 1975). Both species still occur in the inter-tidal zone in the middle, eastern, and northern parts of the Wadden Sea (Reise et al., 2005).

In 1987, a seagrass restoration program was started for *Z. noltii* and the flexible form of *Z. marina*, as a preamble on measures that should be taken to improve water quality and habitat-providing conditions (Anonymous, 1989; de Jonge et al., 2000). Natural recovery was not conceivable in the western part of the Wadden Sea because the potential donor populations were located leeward of the predominantly western winds. It was decided not to focus on the sub-tidal, robust form because it had already disappeared in the 1930s, and environmental changes had been tremendous since that time (de Jonge and de Jong, 1992). In particular, the turbidity of the water increased (van den Hoek et al., 1979; Giesen et al., 1990a; van der Heide et al., 2007). However, light does not limit seagrass growth in the inter-tidal belts around mean sea level (van Katwijk et al., 1998; van Katwijk and Hermus, 2000).

3. Transplantations

Between 1991 and 2004, 42 seagrass transplantations were carried out at four locations in the Wadden Sea, using approximately 10,000 *Z. noltii* shoots, and 23 000 *Z. marina* plants (Table 1). Four out of the 42 seagrass transplantations were carried out at presently vegetated sites as a control. Twenty-six were carried out at sites where vegetation had disappeared during the 1970s, eight were carried out at sites where vegetation had disappeared before

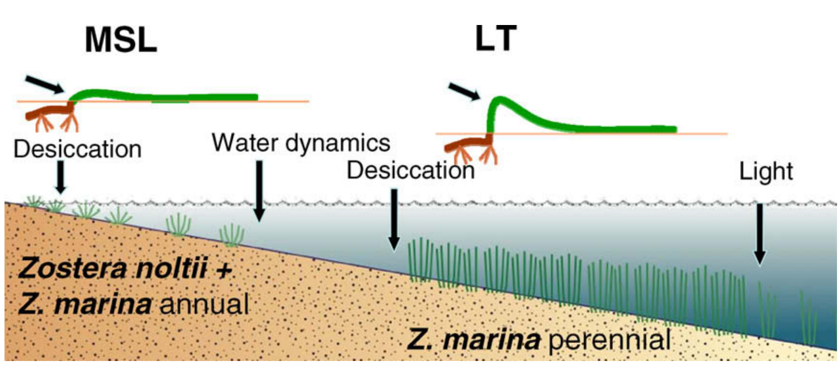

Fig. 2. *Zostera* zonation in the Wadden Sea. The perennial type of *Z. marina* went extinct in the 1930s.

Table 1
Success of seagrass transplantations (*Z. noltii and Z. marina*) in the western Wadden Sea with different techniques at varying sediment types from 1991 until 2004.

Loc[a]	Sediment type	Year	Month	Technique	Success (healthy development)	N[b]	Source
Zostera noltii							
B1	Sand	1992	April	Bare root	Few patches; possibly contrib. to present pop	2000	1,2
B1	Sand	1993	May	Bare root	Yes, and still spreading (>13 years)	2400	2,3
V	Mud/sand	1993	August	Bare root	No	75	2
T3	Sand	1992	April	Bare root,	Yes (3 years)[c]	2000	1,2
T3	Sand	1993	May	Bare root	Yes (2 years)[c] and mixed with natural pop.	2400	2,3
T3	Mud	1993	August	Bare root	No	25	2
Sy	Mud	1992	April	Bare root	Yes, merged with natural bed	800	2
Zostera marina							
B1	Sand	1992	April	Bare root	Only one growing season	1440	1,2
B1	Sand	1993	June	Bare root	Only one growing season + few[d]	1728	2,4
B1	Sand/mud	1994	June	Bare root + sods	Only one growing season[c]	432 3 s	2
B2	Mud	1998	December	Seed shoots[f]	Yes, (8 years) with varying numbers of plants, almost extinct (Fig. 3)	10-20 kg	5
B1	Sand	2002	June	Bare root	No (prob. too deep and/or exposed)	1332	5
B1	Sand	2002	July	Bare root	No (prob. too deep and/or exposed)	481	5
B1	Sand	2002	December	Seed shoots	No	0.5 kg	5
B2	Mud	2003	June	Bare root + sods	First growing season + few[d]	774 3 s	5,6
B1	Sand	2003	June	Bare root	First growing season + few[d]	444	5,6
B2	Mud	2004	June	Bare root	First growing season + few[d]	222	5
B1	Sand	2004	June	Bare root	First growing season + few[d]	1176	5
B2	Mud	2004	December	Seed shoots	very few plants	0.5 kg	5
B3	Sand/mud	2003	June	Bare root	No (facilitation by mussel bed)	444	5,6
X1	Mud	2003	June	Bare root	No	444	5
X2	Sand	1991	May	Bare root	One growing season (four populations, performed equally), though deep and exposed	Ca. 1000	1
X2	Sand	1993	June	Bare root	No	1296	2
X3	Sand	1994	June	Bareroot + sods	No	432 6 s	2
V	Mud/sand	1993	August	Bare root	Only first growing season	40	2
T1	Mud	1993	October	Seed shoots	Yes, mingled with natural population	1.5 kg	2
T3	Sand	1992	April	Bare root	No (low survival during the first growing season)	1440	1
T3	Sand	1992	June	Bare root + stab. techn	Only first growing season	2592	1,2
T3	Sand	1993	June	Bare root + stab. techn	Only first growing season + few[d]	1728	2,4
T3	Sand	1993	July	Bare root + stab. techn	Only first growing season + few[d]	630	2,4
T2[e]	Mud	1993	August	Bare root	No (but monitoring perhaps too late)	30	2
T3	Mud	1993	August	Bare root	No	10	2
T3	Sand	1993	October	Seed shoots	No	2 kg	2
T2[e]	Mud	1994	June	Bare root	One growing season[c]	432	2
T4	Sand?	1994	June	Bare root	No (prob. too deep)	432	2
F	Mud	1994	June	Bare root	No (prob. desiccation, too high)	432	2
Sc	Sand	1992	April	Bare root	No	1440	1
E	Mud/sand	1992	April	Bare root	No	1440	1
Sy	Sand/Mud	1992	April	Bare root	No (low survival)	432	1

Source: (1) van Katwijk and Schmitz (1993), (2) Hermus (1995), (3) www.zeegras.nl, (4) van Katwijk and Hermus (2000), (5) Bos and van Katwijk (2005), (6) Bos and van Katwijk (2007).

[a] Locations, see Fig. 1. A sandy site was also intermediately exposed, and a muddy site relatively sheltered.
[b] Number of transplanted plants; s, sods; kg, wet weight.
[c] No further monitoring.
[d] Few seedlings came up in the second growing season and developed well, but no seagrasses in a third year.
[e] Consolidated mud, drowned saltmarsh.
[f] Seed shoots, seed-bearing shoots.

the 1970s (eight transplantations), and one transplantation site had never been vegetated before. Thirty of all the transplantations were transplanted over a depth gradient, and planting was usually done in June. We used mostly annual but some perennial *Z. marina* donor populations from several locations in the Wadden Sea or the southern Netherlands. In experimental transplantations, several planting techniques were tested for *Z. marina*.

The 1993 *Z. noltii* transplantations were successful. At Balgzand, they were still present in 2006 and continue to spread (van Katwijk et al., 2006; personal observation). Also, at Terschelling, transplantations were successful during at least 2.5 years. No monitoring was done from 1995 to 1999, but in 2000, the transplant proliferated to such an extent (or the neighbouring natural population invaded the area) that it gained the attention of the seagrass surveillance team (www.zeegras.nl).

The *Z. marina* transplantations were successful only in the short-term, although one transplant survived for eight years, and a few plants still remain at present (Fig. 3). A 30-fold proliferation in numbers was observed between 2002 and 2003. This seagrass increase coincided with low macro-algal cover in 2002. In other years, at this sheltered, muddy location, macro-algal cover in September severely hampered seed production, because the plants with largely unripe seeds were suffocated (Bos and van Katwijk, 2005; Bos and van Katwijk, 2007). This illustrates that floating green algae can have a severe negative effect on transplantation success.

On sandy, relatively exposed sites, with low macro-algal cover, recruitment from the seeds was also limited (Table 1). In contrast to muddy sites, seed production was high (Bos and van Katwijk, 2005; Bos and van Katwijk, 2007). A sediment transplantation

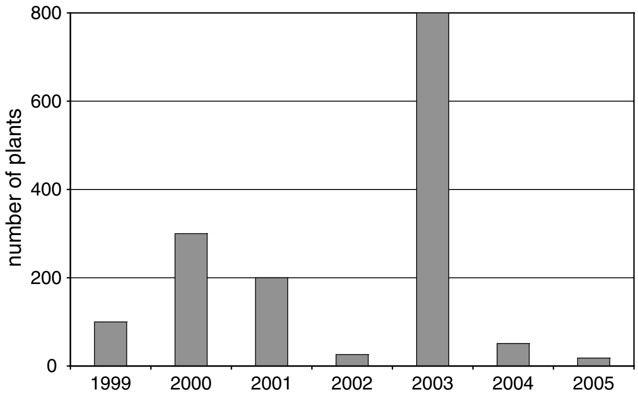

Fig. 3. Number of *Zostera marina* plants after a transplantation of seed-bearing shoots that were deposited at one spot (0.5 m^2) in December 1998 and expanded over an area of approximately 5 ha in 2003.

experiment using buried seed bags showed that sandy (relatively more exposed) sites supported low recruitment from seeds in comparison to muddy (more sheltered) sites, and that this was largely due to hydrodynamic exposure and not to sediment type. Germination however, was favoured in muddy sediments (van Katwijk and Wijgergangs, 2004; Table 3).

In the future, sheltered locations with a local water drainage function could be selected; the locally enhanced tidal currents at these types of locations may prevent macro-algal accumulation. Also, a lower eutrophication level might reduce macro-algal loads. Illustrating this point is the proliferation of seagrass beds in the northern Wadden Sea (Reise and Kohlus, 2008), which is an area with less eutrophication (van Beusekom, 2005).

4. Guideline 1. Reverse habitat degradation

Prior to any restoration or restoration effort, the *causes of the decline should be known and alleviated or reversed* (e.g., Hobbs and Norton, 1996; den Hartog, 2000). Many seagrass recoveries have been reported following habitat improvements like reduced eutrophication and altered hydrology (Lenzi et al. 2003; Cunha et al., 2005; Greening and Janicki 2006, review in Paling et al. 2009). Studies in the western Wadden Sea showed that the cause of waning of both inter-tidal seagrass species probably could be attributed to a combination of (i) increased turbidity related to changes in freshwater discharge in combination with the disposal of dredged material, (ii) increased mechanical cockle fishery and the fishery for mussel spat of *Mytilis edulis* and (iii) increased eutrophication during the 1970s and 1980s (Giesen et al., 1990a,b; de Jonge and de Jong, 1992; Philippart et al., 1992).

In the 1990s however, turbidity had decreased (de Jonge and de Jong, 1992, 2002), eutrophication had decreased (de Jonge, 1997; van Katwijk et al., 2000a; van Beusekom and de Jonge, 2002; van Beusekom, 2005; Philippart et al., 2007), and shellfish fisheries had been banned from large areas of the Wadden Sea (Dankers, 1998). The reduction of the turbidity might be related to a changed dredging regime in Rotterdam Harbour and altered freshwater discharges (de Jonge and de Jong, 2002). Turbidity in the western Wadden Sea, however, did not – or only to a limited extent–relate to primary production (van der Heide et al., 2007). Furthermore, mesocosm and field experiments showed that light was not limiting in the mid–inter–tidal zone (van Katwijk et al., 1998; van Katwijk and Hermus, 2000).

There is very limited knowledge about the negative effect of toxic substances such as heavy metals, pesticides, and anti-foulings on seagrasses (Derksen et al., 1994; Lewis et al., 2007; Nielsen and Dahllof, 2007). At any rate, a reduction of levels was monitored in the Wadden Sea during the last decades (Marijnissen et al., 2001). Moreover, careful comparison of the data from Kastler and Michaelis (1999) with the data from Bester (2000) regarding seagrass beds in the eastern Wadden Sea reveals that seagrass decline was not related to pesticide loads.

The guideline to *reverse habitat degradation* is tentatively supported by our findings that *Z. noltii* has been successfully re-established, and *Z. marina* transplants survived for eight years in an area that had experienced total seagrass loss in a period when the habitat was more degraded in a number of aspects than at present (i.e., turbidity has declined, and shellfish fisheries were fully prohibited).

5. Guideline 2. Select appropriate habitat

Careful site selection is an important guideline, and several conceptual models to optimise site selection have been developed (e.g., Calumpong and Fonseca, 2001; Campbell, 2002; Short et al., 2002). The general improvement of the habitat in the western Wadden Sea as outlined above indicated that seagrass restoration was feasible in the western Wadden Sea. However, local site selection required additional insights into the habitat requirements and characteristics of the potential habitats. The transplantation location (i) should preferably have a history of seagrass growth, (ii) its depth should be similar to nearby natural seagrass beds, and (iii) the habitat requirements should be met as much as possible (e.g., Calumpong and Fonseca, 2001; Campbell, 2002). Ad (i): 41 out of the 42 Wadden Sea transplantations were carried out at sites with previous seagrass growth. Ad (ii): in the Wadden Sea, the lower limit of inter-tidal eelgrass is related to increasing water dynamics (van Katwijk and Hermus, 2000). The upper limit is, like in other parts of the world, related to desiccation (e.g., Harmsen, 1936; Leuschner et al., 1998; Boese et al., 2005).

Additional habitat requirements were assessed from literature and experiments and subsequently modelled. In the Wadden Sea, both *Z. noltii* and *Z. marina* prefer a relatively sheltered location (van Katwijk and Hermus, 2000; van Katwijk et al., 2000a; Schanz et al., 2002; Schanz and Asmus, 2003; Bos and van Katwijk, 2007). Otherwise, additional local shelter to hydrodynamic forces might be applied, such as a mussel ridge or a wave screen (see transplantation techniques, below). Freshwater influences are favourable: 22–26 PSU is preferred over 30 PSU (Kamermans et al., 1999; van Katwijk et al., 1999). However, when yearly averages are below 18 PSU, seagrass is seldom encountered in the Wadden Sea (Bos et al., 2005). However, there are records showing that before the 1930s, seagrass presence showed a 10 PSU yearly average (Oudemans et al., 1870; Reigersman et al., 1939; van der Hoeven, 1982).

Sediments of seagrass habitats in the Wadden Sea are described as mud and muddy sand with median grain sizes ranging from 50 to 130 μm (Philippart et al., 1992; van Katwijk et al., 2000b; van Katwijk and Wijgergangs, 2004). However, sediment composition seems not to be vital for seagrass transplantations and is probably not a habitat requirement. Firstly, seagrass modifies the sediment composition by its mere presence (e.g., Bos et al., 2007), and secondly, the sediment composition often reflects the prevailing water dynamics at a location, the latter being important to seagrass (see above). Additionally, seagrass, particularly *Z. noltii*, often grows in compact clay banks that are remnants of former salt marshes. In these clay banks, seagrasses can grow at less sheltered sites (Reise and Kohlus, 2008).

To determine suitable locations for transplantation, a habitat suitability map was modelled for the seagrasses in the Dutch Wadden Sea. The map was based on a GIS-model using the duration of exposure to air, current velocity, wave exposure, salinity, and ammonium load (Bos et al., 2005; de Jong et al., 2005). The relationship between seagrass habitat suitability and these factors was based on monitoring the data of the Ministry of Transport Public Works and Water Management and on studying the available literature. The habitat suitability map correctly predicted the currently existing eelgrass locations and most of the previous beds (Bos et al., 2005; de Jong et al., 2005).

The Wadden Sea transplantation results tentatively confirm the general rule of thumb, which is to *select locations with a history of seagrass growth*: best results were obtained in the beds still present (control transplantations), and secondly, in the seagrass beds that had only disappeared recently, that is, during the 1970s (Table 1, present *Z. marina* beds were Sy, T1 and E. Beds that declined during the 1970s are: T2, T3 and B. Beds that had already declined before the 1970s were V and X. Finally, F was never vegetated by *Z. marina*; it was a tidal flat which had silted up to a suitable level due to land reclamation) (den Hartog and Polderman, 1975).

Still, this is not a rule that should be strictly followed. We found exceptions, but it should also be considered that coastal habitats are highly dynamic, and unsuitable areas may become suitable as a result of changes in geomorphology. In the Wadden Sea, this was witnessed in 2001 when a new seagrass bed appeared within the propagule plume of a natural bed at a distance of 4 km, in an area where tidal depth had become suitable after considerable silting up (www.zeegras.nl). Also, a number of Australian restoration attempts have successfully transplanted into areas previously lacking seagrass (e.g., Paling et al., 2000; Campbell and Paling, 2003). Finally, as argued by Campbell (2002), various successful seagrass invasions (e.g., *Zostera japonica*, *Halophila stipulacea*, *H. johnsonii* and *Halophila decipiens*) evidence that seagrasses are capable of utilizing areas outside of their realised niche.

In the Wadden Sea, natural beds occur in a narrow zone around mean Sea Level, but when shelter is present or sediments are stabilised, they protrude deeper (Harmsen, 1936; van Katwijk and Hermus, 2000; Katwijk et al., 2000; Bos and van Katwijk, 2007; Reise and Kohlus, 2008). This pattern was exactly copied in our transplantation results (Table 1, van Katwijk and Hermus, 2000), which confirmed the guideline that *depth should be similar to nearby natural seagrass beds*, but it also shows that the suitability of a depth range may vary, depending on other habitat characteristics. In our case, the presence of shelter or stable sediments was crucial, but many other interacting factors are feasible, such as in light-limited depth ranges, turbidity or stability of sediments (re-suspension), all of which may cause shifts in the suitable depth range.

The guideline that *seagrass habitat requirements should be met* has knowledge constraints. Particularly, hydrodynamics are difficult to measure or predict. Also, many environmental parameters are highly variable, and the habitat requirements of the plants are not often fully understood, particularly regarding interactive effects. When sufficient information is available, a habitat suitability model can be helpful for large-scale site selection. We cannot evaluate this guideline, as it largely coincides with the first rule of thumb, which is to select locations with a history of seagrass growth.

6. Guideline 3: Select an appropriate donor population

The general criteria for the suitability of potential donor populations for restoration are based upon (i) suitable plant traits that are needed to survive and expand at the transplantation site, meaning that the plants should be adapted to the local environmental conditions, and (ii) having suitable gene characteristics to survive in the long-term. In other words, the transplantation should have sufficient genetic variation to be able to adapt to environmental changes and avoid inbreeding. Suitable genetic settings can be achieved, on the one hand, by using coarsely adapted genetic mixtures, which bear the risk of an out-breeding depression (e.g., Rice and Emery, 2003; McKay et al., 2005). On the other hand, suitable genetic settings can be achieved by gene flow or genetic reinforcement from neighbouring populations. To do this, isolation by distance should be prevented (e.g., Olsen et al., 2004; Vergeer et al., 2004).

The guidelines formulated in the literature for seagrass transplantation follow these general criteria. Suitable plant traits can be achieved by *transplanting from locations that are environmentally similar* (e.g., Calumpong and Fonseca, 2001; McKay et al., 2005). The notion that seagrass donor populations might differ in suitability for restoration was, to our knowledge, first addressed by Meinesz et al. (1993), who found differences in survival and development among several *Posidonia oceanica* populations from the Mediterranean. In 2007, the populations were still different (A. Meinesz, personal communication).

Piazzi et al. (1998) tested two *P. oceanica* populations and found no differences between them. Plant performance in water originating from the western Wadden Sea was tested for a number of potential donor populations (van Katwijk et al., 1998). Differential response to various salinity and nutrient levels was tested for two Wadden Sea populations (van Katwijk et al., 1999). Also, the ability to recruit from seed was tested *in situ* for two potential donor populations in various sediment types and hydrodynamic exposure levels (van Katwijk and Wijgergangs, 2004). These tests indicated that Wadden Sea populations, as well as nearby populations in the southwestern Netherlands, were suitable for transplantation to the western Wadden Sea.

Suitable gene characteristics for long-term survival can be achieved by *transplanting genetically diverse donor material*. This contributes to transplantation success, seagrass productivity, and recovery potential (Procaccini and Piazzi, 2001; Williams, 2001; Hughes and Stachowicz, 2004; Reusch et al., 2005; Reusch and Hughes, 2006). Genetic research of both *Z. marina* and *Z. noltii* indicated that the genetic variety of Wadden Sea donor material is ample (Olsen et al., 2004; Coyer et al., 2004). During the restoration program in the western Wadden Sea, the importance of genetic variation in *Z. marina* transplants became known by the publication of Williams (2001): reduced genetic diversity affected the growth and fitness of the transplants. Therefore, since 2001, we collected the seedlings in such way as to maximise their genetic variation. Fortunately, the donor population in the Ems Estuary was well studied by J.L. Olsen, who advised us to collect plants minimally 2 m apart and from two to three locations 2 km apart.

Suitable gene characteristics for long-term survival of the transplant can also be achieved by *preventing isolation by distance* (e.g., Olsen et al., 2004). When the transplanted seagrass bed is located too far away from natural or other transplanted beds, the gene flow is hampered, and genetic variation may reduce with the consequences listed above. Isolation by distance has never, to our knowledge, been part of considerations in seagrass restoration programs. In the Wadden Sea, this distance is approximately 150 km (Olsen et al., 2004; Coyer et al., 2004). Since the closest natural populations present were located at less than 50 km from the transplantation site, isolation by distance presented no risks in the Wadden Sea, though the predominant western winds may increase the isolation of the most western transplantation sites.

The importance of the guideline that *donor plants should be recruited from populations in comparable environments* (van Katwijk et al., 1998; Calumpong and Fonseca, 2001) could be confirmed in the Wadden Sea case (van Katwijk et al., 1998). Moreover, results from additional studies show that small differences in performance exist between the donor population of comparable environments (van Katwijk and Hermus, 2000; van Katwijk et al., 1999; van Katwijk and Wijgergangs, 2004). For example, transplants of a donor population with longer leaves showed larger losses at hydrodynamically more exposed transplantation sites

(Hermus 1995). Also, in a seed recruitment experiment, one donor population showed more vigorous seedling expansion than another (van Katwijk and Wijgergangs, 2004). Ideally, for optimal transplantation results, donor suitability should also be tested between those populations.

The genetic variation of the presently expanding *Z. noltii* transplant in the western Wadden Sea has not yet been investigated. The *Z. marina* transplantation is presently too small for such an evaluation (only a few plants remained in 2006).

7. Guideline 4: Spread risks

In a dynamic coastal and estuarine environment, the spreading of the risk of plant losses (due to storms, droughts, ice scour, salinity fluctuations, El Niño effects, temperature fluctuations and so forth) in time and space is important. Natural populations survive extreme conditions by maintaining genetic variation, phenotypic plasticity, multiple reproductive or growth strategies, (meta-) population dynamics and the like. In the transplantation practice, spreading of risks is often intuitively done, particularly in spreading risks in space, for example, by applying replicates.

Risks that particularly apply to the seagrasses in the Wadden Sea are ice scour that may remove the top of the sediments containing rhizomes and seeds or prematurely germinated seedlings (Davis and Short, 1997; van Katwijk and Hermus, 2000). Prematurely germinated seedlings are vulnerable to prolonged periods of cold weather in early spring (Churchill, 1983; van Katwijk and Hermus, 2000). Rapid and complete germination may occur when the salinity is extremely low (e.g., Hootsmans et al., 1987), which sometimes happens during the winter, due to rainfall and high temperatures (snowmelt) in the catchments of the rivers that debouche into the Wadden Sea. Prematurely germinated seedlings have low chances of surviving spring storms and low temperatures (van Katwijk and Hermus, 2000; Erftemeijer, 2004). During autumn storms, seed-bearing shoots may become detached, which is favourable for long distance dispersal (Reusch, 2002; Harwell and Orth, 2002) but unfavourable for the local maintenance. Therefore, this risk needs to be as small as possible when transplanting.

Other reasons to advocate for spreading of risks are the knowledge constraints associated with environmental processes. With reference to habitat characteristics and habitat suitability, the complex reality will always leave gaps in knowledge (related to uncertainty, indeterminacy or ignorance, Wynne, 1992). This makes the success of a transplant to a particular site in a particular year difficult to predict. Finally, for long-term transplantation success, it might be wise to include sub-optimal sites, in order to keep genetic diversity high and to maintain genotypes that might be advantageous for the transplant's survival when the environment changes (van Groenendael et al., 1998). Unpredictability, the lack of knowledge and perhaps also the suitability of sub-optimal sites are illusively illustrated by the work of Kelly et al. (2001), who constructed a predictive model on habitat suitability based upon the susceptibility of seagrass to the hydrodynamics related to storm events. The majority of the seagrass habitats in the study area were predicted to have less than 50% probability of seagrass cover.

The spreading of risks can be accomplished by:

(1) *Spreading risks at a kilometre scale*: for example, by transplanting to areas that differ in hydrodynamic exposure. Sites will probably differ in habitat characteristics.
(2) *Spreading risks at a local scale*: by applying replicates at a distance of tens of metres and hundreds of meters, but also by planting at different tidal depths. In other words, sites may differ in habitat characteristics at this scale, or may not differ (replicates).
(3) *Spreading risks at a temporal scale by transplanting in different years*.
(4) *Spreading risks at a temporal scale by transplanting at different dates*.

Combining the spreading of risks among sites with different characteristics *and* among replicates is, in fact, an experimental scientific setup generating ecological knowledge. This, in turn, will serve future transplantations, as was urged by Temperton (2007).

Spreading of risks at the kilometre scale was supported by our findings. Some of our sites (that are kilometres apart) that were considered to be equally suitable on the basis of existing ecological knowledge, showed, in reality, large differences in transplantation success. This stresses the need for spreading of risks in space among sites.

At a scale of tens to hundreds of metres, we can distinguish sites with seemingly similar environmental characteristics (replicates), and sites that differ in habitat characteristics, such as different depths. Our results strongly support the importance of spreading of risks over replicates, as complete losses of replicates were paralleled with the vigorous development of their neighbours. This happened in the majority of our transplantation efforts. Spreading of risks over depth gradients was also legitimated by our study, as optimal depth ranges in one year appeared sub-optimal in another year, probably related to dry and warm summers enhancing desiccation of higher zones, whereas, in cold and wet years, higher zones profit from the better light climate. In addition, slight variations between sites were found.

Spreading of risks in time can be accomplished by transplanting to the same site during two or more *years*, notwithstanding the results. This guideline found its origin when we found a large year-to-year difference in transplantation success (i.e., location TX, Table 1). Also, the year-to-year dynamics in the 1998 transplant (Fig. 3) and in natural populations (www.zeegras.nl) support the idea of the spreading of risks in time. However, other transplantation experiences appeared to be relatively consistent over time. For example, locations with a transplant success during one growing season only repeated this pattern the next year as well (e.g., locations B1 and T3, Table 1). Therefore, our evaluation is not conclusive in this respect.

The spreading of risks in time can also be accomplished by transplanting in different *months*. Usually, only few months per year yield optimal transplantation results (e.g., this study, Martins et al., 2005; Boudouresque et al., 2006; Paling et al., 2007; Park and Lee, 2007). Results are difficult to evaluate because differences in transplantation success can be attributed to a stochastic event (which would justify the spreading of risks), or to an unfavourable planting time (which would urge one to never transplant again in that month).

8. Guideline 5: Hydrodynamics: optimise techniques and account for ecosystem engineering effects

The distribution of most seagrass species is often governed by the presence of shelter. Accordingly, many transplantation results are shaped by hydrodynamic stress or disturbances (e.g., van Katwijk and Hermus, 2000; Calumpong and Fonseca, 2001; Campbell, 2002; Paling et al., 2003; van Keulen et al., 2003). Numerous stabilizing techniques have been used, ranging from mesh or wires (e.g., van Keulen et al., 2003; Boudouresque et al., 2006) to staples (Davis and Short, 1997; van Keulen et al., 2003; Paling et al., 2007), and coat hangers (reviews in Phillips, 1980, 1990; Davis and Short, 1997). Devices like cloth or netting may tear loose by waves and currents and may end up *adding* to the dynamics and destruction of the transplants instead of stabilizing them (Table 2).

Table 2
These planting techniques tested for *Zostera marina* unless indicated otherwise.

Planting techniques and additional measures	Effect	Source
Anchoring: – nets, cloth	– Negative (addition of dynamics)	1,2
– staples/pegs	– No effect	
Sediment improvement: – shell armouring	– Positive effect at exposed (=low–inter–tidal) areas, no effect at sheltered (=mid–inter–tidal) locations	2
Add shelter: – curbstone square of 1 m^2	– no effect, probably too local	1, 3, 4
– mussel ridge	– unknown (mussel ridge disappeared in winter)	
– screens	– unknown (screens disappeared in winter)	
– transplant behind natural mussel bed	– positive (but not sufficient)	
Planting unit size	– No effect (37 or 65 plants)	3
Planting density	– Negative effect for *Z. noltii* – 100–400/m^2	1, 4
	– No effect if sheltered location	
	– Positive effect if relatively exposed location 5–13/m^2	

Source: (1) van Katwijk and Schmitz (1993), (2) van Katwijk and Hermus (2000), (3) Bos et al. (2005), (4) Bos and van Katwijk (2007).

Table 3
Zostera marina experiments to grow plants from seed-bearing shoots or seeds buried at the transplantation site.

Activity	Month	Year	Result	Source
Cupola's of gauze 1 mm and 10 mm placed over the transplants during autumn and winter unless washed away (in the end, all were washed away).		1993	Result not interpretable, no controls and $t = 0$ situation too variable (as one growing season had already finished with intrinsically variable results)	1
Seed-bearing shoots			(success measured by visible seedlings)	
October: buried 4 cm deep 3 kg in total	October	1993	Muddy site successful, sandy site	1
December: no burial but just dropping about 10 kg	December	1998	not successful 8 years (muddy site) Fig. 3	
	December	2002	not successful (sandy site)	2
Burial + stabilising	December	2004	Successful (10%), (muddy site)	2
Burial of seeds				
Seeds buried 2–4 cm	September	1993	Muddy sand successful, sandy site not	1
Mesocosm testing two sediment types	December	1993	Sandy sediment successful, muddy sand not	1
Seeds in seed bags	April	1994	Muddy sediment successful, sandy site not	1
Seeds in seed bags in transplanted sediments at exposed and sheltered site	March	1999	Muddy and sandy sediments both successful for germination and seedling survival, seedling expansion higher at sheltered site as compared to exposed site	3

Source: (1) Hermus (1995), (2) Bos and van Katwijk (2005), (3) van Katwijk and Wijgergangs (2004).

Transplantation of plants with intact sediments, such as sods (or turfs), plugs or growth of seedlings in peat blocks, generally yields the highest chances of success, but it is cost and labour intensive (Phillips, 1990; Davis and Short, 1997; Fonseca et al., 1998). In the Wadden Sea, only a few *Z. marina* sod transplantations were carried out, which did not perform better than the bare root transplantations (Table 1).

Seagrass plants have been observed to facilitate each other, i.e., by increasing density or planting unit size (van Keulen et al., 2003; Bos and van Katwijk, 2007). In other words, the ecosystem engineering properties of seagrass (Bouma et al., 2005; Bos et al., 2007) can be used in transplantation technology. If the water dynamics are too strong, mutual facilitation compensates little, if at all (Paling et al., 2003): plant disappearance is delayed when plugs or densities are larger (van Keulen et al., 2003; Bos and van Katwijk, 2007). At lower water dynamics, self-facilitative effects were evident, but at sheltered locations, this effect is absent again (Bos and van Katwijk, 2007). This is logical if one assumes that the self-facilitation is related to water dynamics. In flume studies with different current velocities, this relationship was confirmed (Bouma et al., unpublished results). Obviously, a density that is too large will lead to competitive effects (e.g., van Katwijk et al., 1998; Granger et al., 2000).

To cope with hydrodynamic stress and disturbances, the habitat can be locally stabilised. We tested (i) kerbstones forming a miniature dike around a square meter plot, (ii) shell armouring of the sediment and (iii) the presence of mussel ridges. The kerbstone mini-dikes had no effect, and even became slightly trans-located themselves at the most exposed sites (Table 2). Shell armouring of the sediment favoured transplant survival at exposed sites but had no effect at sheltered sites (van Katwijk and Hermus, 2000), again showing the importance of hydrodynamic exposure interacting with the measures taken. The presence of mussel beds favoured *Z. marina* transplant survival, probably because they protrude 0.1 or 0.2 m above the sediment, providing shelter in the open spaces between them (Bos and van Katwijk, 2007). The relationship between this facilitating effect and hydrodynamics was confirmed in flume studies (Bouma et al., unpublished results).

Our results support the recommendation to *search for optimal transplantations techniques* (e.g., Calumpong and Fonseca, 2001), since we found large differences between transplant survival using different techniques. The guideline to *account for ecosystem engineering effects*, though formulated by Byers et al. (2006), was not yet formulated in seagrass restoration, or transplantation guidelines. It was applied in the Wadden Sea case, and we were able to elucidate self-facilitative effects and facilitation by mussels. In general, ecosystem engineering by seagrass beds might establish positive feedback that hampers restoration when the scale is small (e.g., van Katwijk et al. 2000a; van der Heide et al. 2007).

9. Conclusions

The experiences of 20 years of ecological research and transplantations of seagrass at the inter-tidal flats in the Wadden Sea allow us to evaluate traditional and new guidelines concerning restoration of seagrass. At a regional scale, we conclude that the inter-tidal flats of the western Wadden Sea are well suited for *Z. noltii* restoration, and they are less suitable for small-scale *Z. marina* restoration. The *Z. marina* transplants remained over eight years, with years of large expansion and years of decrease, but they eventually disappeared. The bottlenecks were either in the seed production phase (muddy sites, prone to high macro-algal cover) or in the seed/seedling survival phase (sandy sites). We postulate that the reproductive strategy, being annual in *Z. marina* and perennial in *Z. noltii*, gives an advantage to the latter. It should not be excluded that *Z. marina* could successfully settle in the Wadden Sea when transplanted at a larger scale because (i) natural population fluctuations are usually not synchronous in The Netherlands (Erftemeijer, 2005; www.zeegras.nl), such that spreading of risks among sites within a re-colonisation distance could balance the year-to-year differences in survival, and (ii) several self-facilitative properties of eelgrass have been established (Bos and van Katwijk, 2007; van der Heide et al., 2007).

The successfully reintroduced inter-tidal *Z. noltii* patches in the western Wadden Sea are not yet evaluated on the return of functional traits (e.g., Evans and Short, 2005), like the nursery and spawning functions (Polte et al., 2005; Polte and Asmus, 2006a,b), or sediment-stabilising functions (e.g., Bos et al., 2007). These items remain to be investigated.

More generally, reviewing and evaluating guidelines on seagrass restoration lead us to:

(i) Underline the well-known guidelines in restoration ecology, which are to study the causes of disappearance and assess whether environmental conditions have improved, to conduct careful site selection, preferably with seagrass history, to perform careful selection of donor populations and to develop stabilizing techniques (Guidelines 1, 2 and 3).
(ii) Formulate an additional guideline: to spread risks in space and time, so as to anticipate the natural dynamics *and* acknowledge the lack of knowledge. It will not only increase chances for success, but it will also allow for improvement of our ecological knowledge (Guideline 4).
(iii) Stress the importance of ecosystem engineering. Since transplantation success of many seagrass species was related to low water dynamics, the stabilisation of the plants and their local environment could be accomplished by using the self-facilitative properties of seagrass and by using the facilitative properties of, for instance, mussel beds to create beneficial shelter (Guideline 5).

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