Reprint from: W.J. Wolff, K. Essink, A. Kellermann & M.A. van Leeuwe (eds.) – Challenges to the Wadden Sea. Proceedings of the 10th International Scientific Wadden Sea Symposium, Groningen, 2000. Ministry of Agriculture, Nature Management and Fisheries / University of Groningen, Dept. of Marine Biology, 2003.

Reintroduction of eelgrass (*Zostera marina* L.) in the Dutch Wadden Sea: a research overview and management vision

M.M. van Katwijk
Department of Environmental Studies, University of Nijmegen, PO Box 9010, 6500 GL Nijmegen, The Netherlands (e-mail: mvkatwyk@sci.kun.nl)

Key words: mussel beds, nutrients, restoration, salinity, seagrass, water dynamics

Abstract

A research overview and management vision are presented, resulting from 13 years of research into the possibilities of reintroduction of the seagrass *Zostera marina* in the Dutch Wadden Sea. It is concluded that presently (1) suitable donor populations are available, (2) light is not limiting to *Z. marina* to at least 0.80 m below mean sea level, (3) below -0.20 m mean sea level, water movements (particularly the duration) are too severe, unless shelter is available, (4) high nutrient loads restrict the area of high potential *Z. marina* habitats to areas with freshwater influences, (5) muddy sediments and a permanent layer of water during low tide are favourable, (6) two types of *Z. marina* occurred in the pre-1930s Wadden Sea, each suitable for a different tidal depth. Main recommendations are to (1) restore estuarine gradients, (2) decrease nutrient (particularly nitrogen) loads, (3) restore areas with shelter (for example created by mussel beds, which have largely disappeared but probably can be restored, actively or passively), (4) carefully select transplantation sites: locally (muddy sediments with a permanent layer of water during low tide) and regionally (freshwater influence and shelter) (5) improve the present GIS map with the *Z. marina* habitat suitability of the Dutch Wadden Sea by including data on salinity and nutrient loads, and (6) prohibit fisheries activities in potential seagrass habitats.

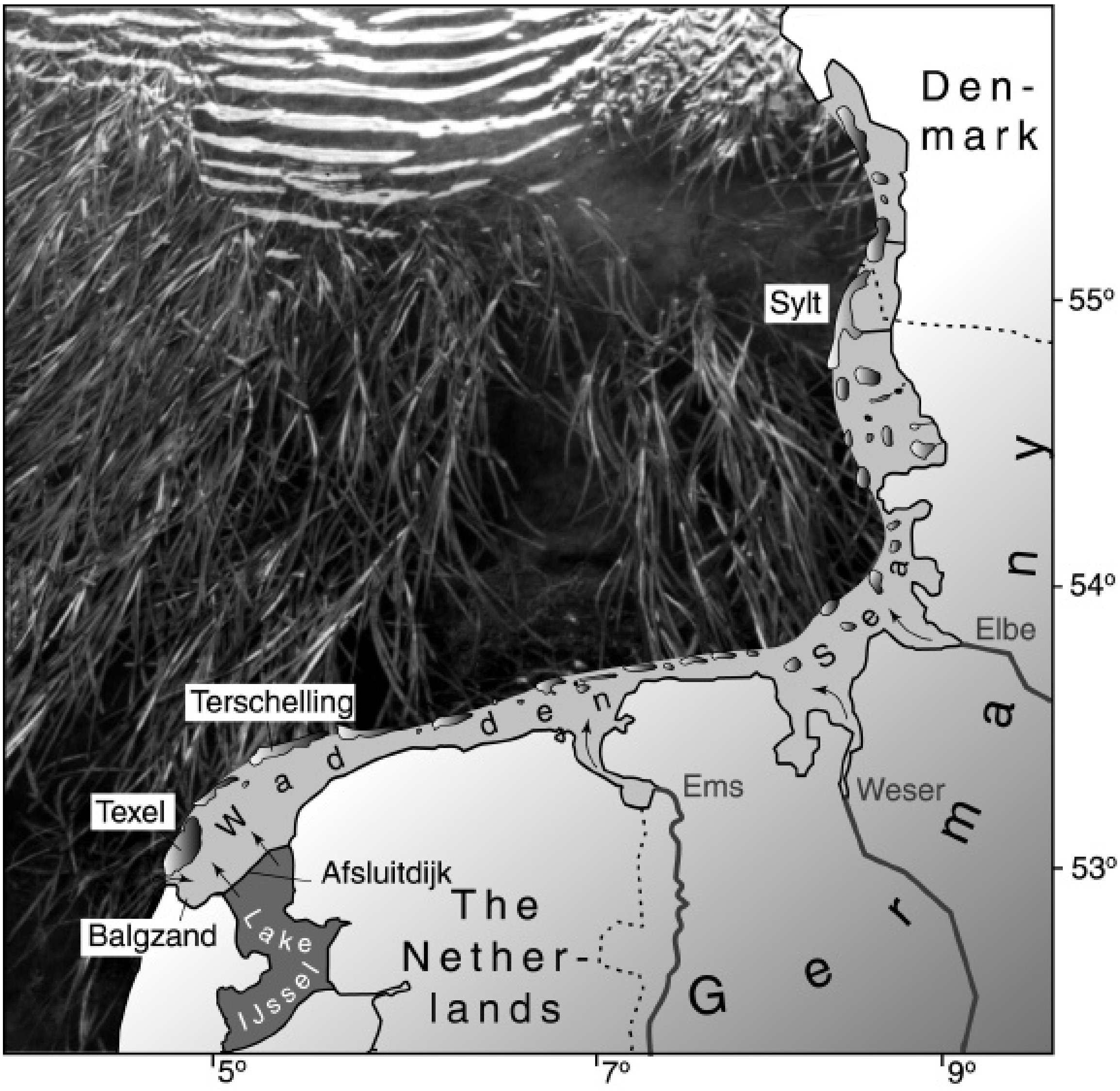
Introduction

In this review, the results of 13 years of research into the possibilities of reintroduction of the seagrass *Zostera marina* L. in the Dutch Wadden Sea are summarised and a management vision is presented. To make scientific knowledge more accessible to policymakers and stakeholders, a more receptive presentation is required, particularly by visualisation (de Jonge *et al.*, this volume). Therefore, it was chosen to break academic tradition of minimising the number of figures: the main information provided in this review can be acquired by reading the figures with the figure captions and subsequently the lists provided in the paragraphs ‘conclusions’, ‘recommendations’ and ‘new questions’.

Use and history of seagrass in the Wadden Sea

In the Wadden Sea, two species of seagrass occur, a smaller species, *Zostera noltii* Hornemann, and a larger species, *Z. marina* L., or eelgrass (Fig. 1). This study focuses on *Z. marina*. Seagrasses are higher plants, having flowers, seeds, rhizomes and roots. In the Dutch Wadden Sea *Z. marina* beds were of great economic importance. The plants were collected from the beaches, and later they

Figure 1. The Wadden Sea, and sites that are referred to in the text; major freshwater (riverine) influences are indicated by arrows. Two species of seagrass occur in the Dutch Wadden Sea: *Zostera noltii* (a) and *Z. marina*. This study focuses on *Z. marina* (photograph taken at Terschelling).



were fished or even mown (Fig. 2). The freshwater-rinsed and dried seagrass plants were used as roofing and isolation material, and to fill mattresses and cushions. Before 1857, it was used to build dikes (Martinet, 1782; Sloet tot Oldhuis, 1855; Oudemans *et al*., 1870). The first written references to the building of dikes of seagrass date back to the 13th century (Oudemans *et al*., 1870). Already in the 18th century the urgency was felt for the development of a method to multiply eelgrass, as 'one cannot have too much of it' (Fig. 3; Martinet, 1782). Less is known about the past German and Danish beds. Probably, these beds had small or no economic value (van den Hoek *et al.*, 1979).

Habitat and nursery, sediment stabilisation

Apart from this direct economic value of seagrass, numerous indirect economic advantages are reported for seagrass beds.

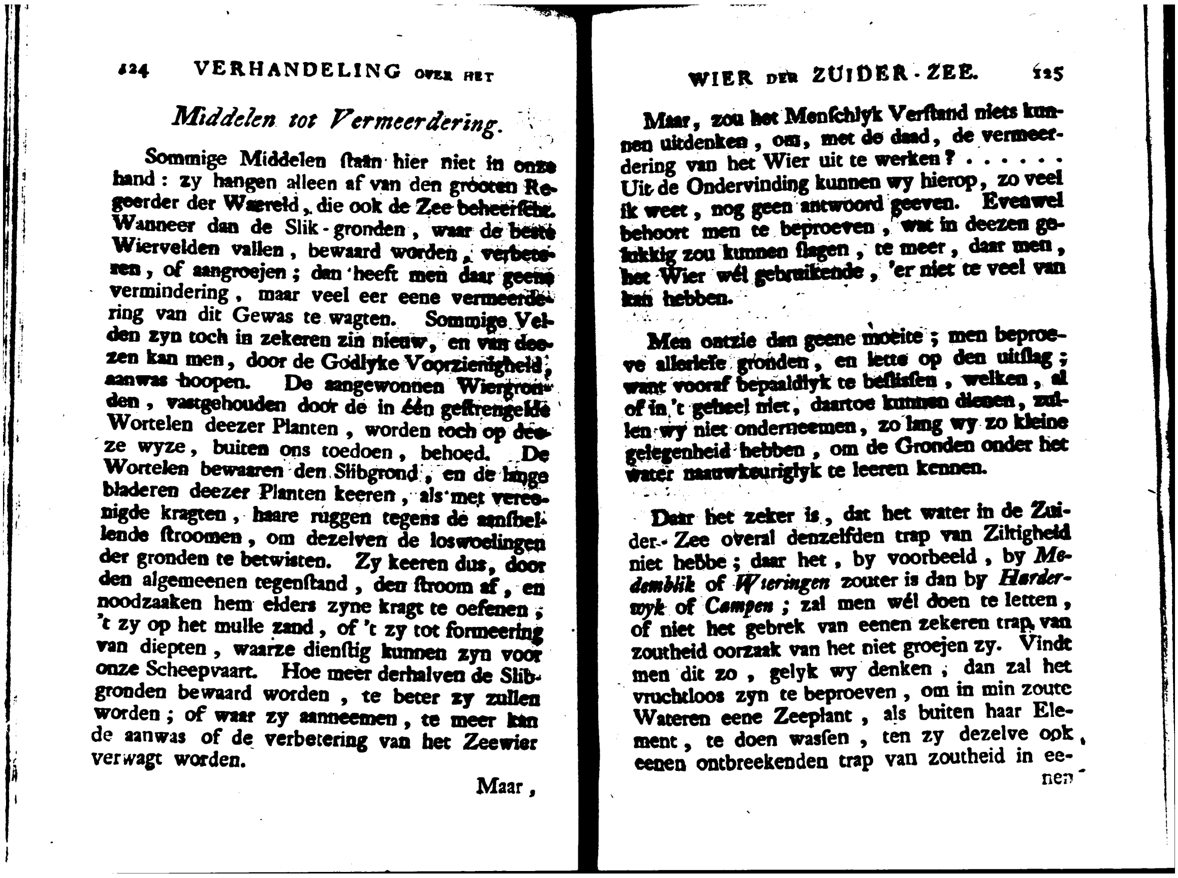
Figure 2. Harvesting of *Zostera marina* at the beginning of the 20th century. The plants were mown or collected. The seagrass had direct economical value (e.g. roofing and isolation material, filling of cushions and mattresses). Indirectly economic values of seagrasses are their nursery and habitat function (e.g. juvenile fish and crustaceans) and sediment stabilisation effect. The photographs were kindly supplied by T. Duinker.

Seagrass beds are a source of food for young fish and for crustaceans: particularly its luxuriant epiphytic flora and fauna are the main source of food for many small fish and invertebrates, which in their turn are eaten by commercially important fish species, whereas their remains, the detritus, form the basis for a complex food web (*e.g.*, van Goor, 1919; den Hartog, 1970; Thayer *et al.*, 1984; Fonseca *et al.*, 1990; Heck *et al.*, 1995; Horinouchi & Sano, 1999; Mattila *et al.*, 1999). This nutrient cycling ability of seagrass and algal beds led Costanza *et al.* (1997) to estimate their value as 19,000 US$ per ha per year (in comparison: coral reefs 6100; forests 969, cropland 92 US$ $ha^{-1}yr^{-1}$). Priceless, however, is their contribution to biodiversity and habitat diversity of coastal waters. Furthermore, the plants are known to stabilise sediments (*e.g.*, Rasmussen, 1977; Fonseca, 1996), to reduce particle loads (*e.g.*, Gacia *et al.*, 1999) and to act as a sink for nutrients (Asmus & Asmus, 1998), in this way improving water quality.

Why did the seagrass *Zostera marina* decline in the 1930s?

Before the 1930s the Dutch Wadden Sea contained large beds of subtidal and intertidal seagrass (*Zostera marina*) covering an area between 65 and 150 km^2

Figure 3. Already in 1782, Martinet discusses the possibilities to multiply eelgrass (courtesy library of University of Groningen).



124 VERHANDELING OVER HET

Middelen tot Vermeerdering.

Sommige Middelen ſtaan hier niet in onze hand: zy hangen alleen af van den grooten Regeerder der Waereld, die ook de Zee beheerſcht. Wanneer dan de Slik-gronden, waar de beſte Wiervelden vallen, bewaard worden, verbeteren, of aangroejen; dan heeft men daar geene vermindering, maar veel eer eene vermeerdering van dit Gewas te wagten. Sommige Velden zyn toch in zekeren zin nieuw, en van deezen kan men, door de Godlyke Voorzienigheid, aanwas hoopen. De aangewonnen Wiergronden, vastgehouden door de in één geſtrengelde Wortelen deezer Planten, worden toch op deeze wyze, buiten ons toedoen, behoed. De Wortelen bewaaren den Slibgrond, en de lange bladeren deezer Planten keeren, als met vereenigde kragten, haare ruggen tegens de aanſchellende ſtroomen, om dezelven de loswoelingen der gronden te betwisten. Zy keeren dus, door den algemeenen tegenſtand, den ſtroom af, en noodzaaken hem elders zyne kragt te oefenen; 't zy op het mulle zand, of 't zy tot formeering van diepten, waarze dienſtig kunnen zyn voor onze Scheepvaart. Hoe meer derhalven de Slibgronden bewaard worden, te beter zy zullen worden; of waar zy aanneemen, te meer kan de aanwas of de verbetering van het Zeewier verwagt worden.

Maar,

WIER DER ZUIDER-ZEE. 125

Maar, zou het Menſchlyk Verſtand niets kunnen uitdenken, om, met de daad, de vermeerdering van het Wier uit te werken? . . . . . . Uit de Ondervinding kunnen wy hierop, zo veel ik weet, nog geen antwoord geeven. Evenwel behoort men te beproeven, wat in deezen gelukkig zou kunnen ſlagen, te meer, daar men, het Wier wél gebruikende, 'er niet te veel van kan hebben.

Men ontzie dan geene moeite; men beproeve allerleie gronden, en lette op den uitſlag; want vooraf bepaaldlyk te beſliſſen, welken, al of in 't geheel niet, daartoe kunnen dienen, zullen wy niet onderneemen, zo lang wy zo kleine gelegenheid hebben, om de Gronden onder het water naauwkeuriglyk te leeren kennen.

Daar het zeker is, dat het water in de Zuider-Zee overal denzelfden trap van Ziltigheid niet hebbe; daar het, by voorbeeld, by *Medemblik* of *Wieringen* zouter is dan by *Harderwyk* of *Campen*; zal men wél doen te letten, of niet het gebrek van eenen zekeren trap van zoutheid oorzaak van het niet groejen zy. Vindt men dit zo, gelyk wy denken; dan zal het vruchtloos zyn te beproeven, om in min zoute Wateren eene Zeeplant, als buiten haar Element, te doen waſſen, ten zy dezelve ook, eenen ontbreekenden trap van zoutheid in ee-

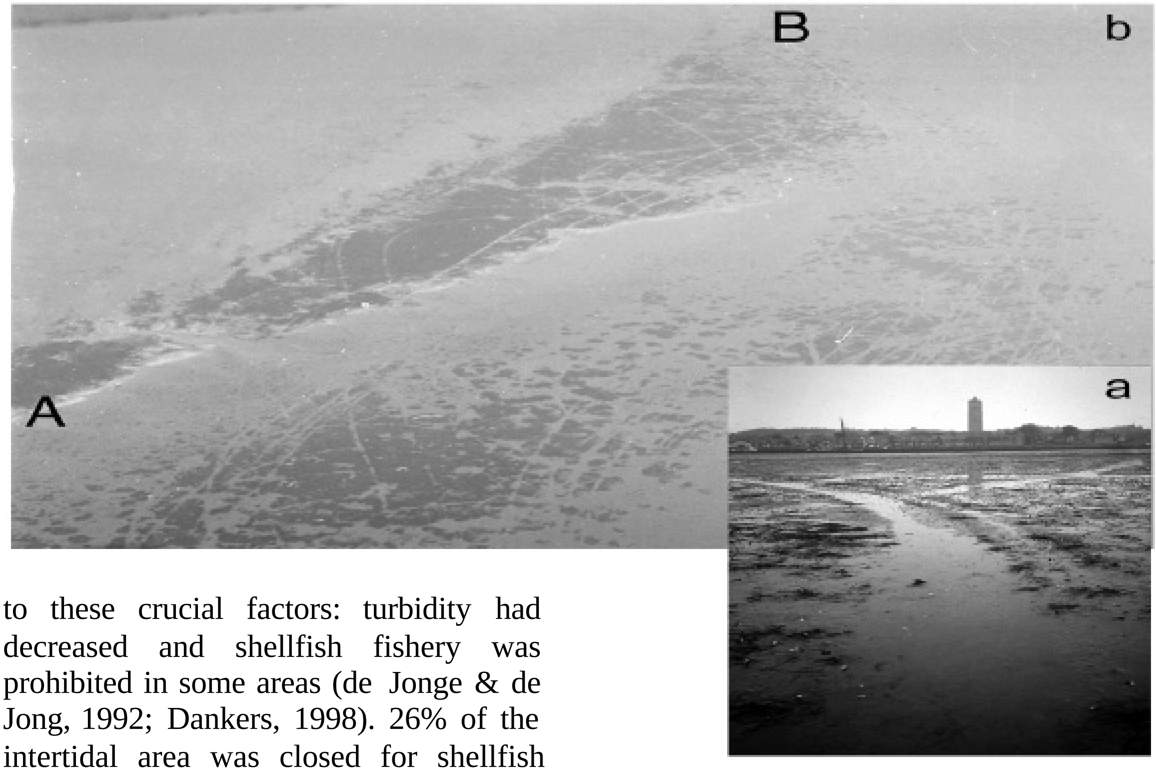
nen

(Oudemans *et al.*, 1870; den Hartog & Polderman, 1975). During the 1930s, the seagrass cover in the Wadden Sea was largely lost and the beds never recovered (*e.g.*, den Hartog, 1987; Reise *et al.*, 1989). Presently, *Z. marina* occurs only in the mid-littoral: approximately 0.87 km^2 of *Z. marina* and 0.26 km^2 *Z. noltii* in the Dutch Wadden Sea (de Jong, 2000). In the German Wadden Sea, *Z. noltii* and *Z. marina* together cover approximately 170 km^2, and in the Danish part ca. 30 km^2 (Reise & Buhs, 1991). The large-scale decline of *Z. marina* coincided with (1) the outbreak of wasting disease caused by the slime-mold *Labyrinthula zosterae*, (2) increased diking and damming activities, particularly the construction of the 'Afsluitdijk' and (3) two subsequent years with a considerable deficit of sunlight. There is no consensus about which of these events (or combination of events) caused this decline (reviews in den Hartog, 1996; de Jonge *et al.*, 1996).

Why didn't the beds recover?

Whereas in other North Atlantic areas eelgrass beds recovered after the wasting disease epidemic in the 1930s, the Dutch Wadden Sea beds failed to recover (review in den Hartog, 1996). Main causes for the lack of recovery of eelgrass stands in the Dutch Wadden Sea were thought to be high turbidity, and later shellfish fishery (Fig. 4, van den Hoek *et al.*, 1979; Giesen *et al.*, 1990a; b; de Jonge & de Jong, 1992). In the late 1980s, the eelgrass habitat in the Wadden Sea had partly been restored with respect

Figure 4. Destructive effects of shellfish fishery on seagrass beds. (a) tracks in the *Zostera marina* at the Plaat, Terschelling (photograph by V.N. de Jonge), (b) tracks in a *Z. noltii* bed at Oosterend, Terschelling (aerial photograph by the author; the distance between A and B is approximately 500 m).



to these crucial factors: turbidity had decreased and shellfish fishery was prohibited in some areas (de Jonge & de Jong, 1992; Dankers, 1998). 26% of the intertidal area was closed for shellfish fishery in 1993 (Dankers, 1998). For this reason, restoration was thought to be feasible. The Dutch government is currently attempting to return seagrass to the Wadden Sea, in order to 'restore natural values' (Anonymous, 1989).

Seagrass restoration projects worldwide

Restoration efforts of diminished seagrass beds have been performed in many parts of the world, for example in North and Central America (review in Fonseca *et al.,* 1998; Sheridan *et al.*, 1998; Orth *et al.*, 1999), Australia (*e.g.*, Paling *et al.*, 1998; 2000a, b; Lord *et al.*, 1999), Japan (*e.g.*, Kawasaki *et al.*, 1988; Watanabe & Terawaki, 1986), but also in Europe: Great Britain (Ranwell *et al.*, 1974), Denmark (Christensen *et al.*, 1995), Italy (Balestri *et al.*, 1998; Piazzi *et al.*, 1998), and France (Meinesz *et al.*, 1991; 1992; 1993; Molenaar *et al.*, 1993). In the Dutch Wadden Sea, perhaps the eldest history of seagrass restoration was recorded by Reigersman *et al.* (1939), describing transplantation efforts of Mr. F. Duinker in Texel after the seagrass catastrophy in the 1930s. Transplantations at an experimental, small scale were performed in the Wadden Sea in the same period by Harmsen (1936), in a cross-transplantation of subtidal and intertidal seagrass.

Particularly in the case of mitigation (compensation of permitted seagrass losses caused by for instance land reclamation, port building or dredging activities), restoration projects are carried out at a large scale. In the United States, a total of 78 ha has been transplanted according to a review by Fonseca *et al.* (1998). In some cases, mechanical injection of a nutrient and

Figure 5. Overseas, restoration projects are sometimes carried out at a large scale, particularly when donor beds are due to be destructed by permitted dredging or construction activities (mitigation). Two examples of the use of boats in seagrass restoration projects are shown: (a) in Florida, as a fertiliser/hormone injection machine (Kenworthy et al., 2000, photographs kindly supplied by J. Anderson), and in SW Australia where the 'EcosubII" (b, c) is used to transplant seagrass sods (Paling et al., 2000a, photographs reproduced with permission of Cockburn Cement Limited, Western Australia).

growth hormone solution was used (Fig. 5a; *e.g.,* Kenworthy *et al.,* 2000). In Australia, 2 ha have been transplanted (Lord *et al.* 1999), mostly by a mechanical harvester and planter (Fig. 5b and c, Paling *et al.*, 2000a). In Japan several tens of hectares were transplanted near Hiroshima in recent years (many publications in the 1990s in Japanese, A. Meinesz pers. comm.).

Approach in the Dutch Wadden Sea

In the Dutch programme for reintroduction of eelgrass in the Wadden Sea, the approach is as follows: (1) to estimate the possibilities, (2) to optimise the chances, and then (3) to transplant at the smallest scale possible.

Maximum depth and donor populations

We empirically assessed the maximum depth of possible *Zostera marina* growth in Wadden Sea water in an outdoor mesocosm experiment (Fig. 6). In the same experiment, we tested donor suitability of five northwest European populations. Three out of five *Z. marina* populations were successfully transplanted into the Wadden Sea mesocosm. If turbidity in the Wadden Sea remains at the level of the 1990s

Intermezzo 1. Minimum viable population size

Survival of a population, for instance over a period of 100 years, is threatened by three types of risks: demographic, environmental and genetic stochasticity. Demographic risks are determined by birth and death rates. This involves, amongst others, seed production and the effectiveness of pollen and seed distribution. This is density-dependent: both pollen and rafting seed shoots can be 'trapped' by the plants; a lower plant density increases the chance of pollen and seed shoots to drift to the open sea. It is also area dependent: the larger the area of the seagrass colony, the larger the chance that pollen or seed shoots become eventually trapped. Once released, the seeds travel not more than a few metres (Orth et al., 1994). Environmental risks involve stochastistic events like storms, but also simple ecology: favourable conditions promote rapid expansion of a founding colony, and decrease the risk of extinction of even very small colonies. Genetics risks occur when genetic diversity is insufficient to keep the population fit, both in long term, when the environment might alter, and in short term. Recently, Williams (2001) showed that more *Zostera marina* seeds germinated from a genetically diverse, untransplanted population than from a transplanted population with low genetic diversity. Also, leaf shoot density in high-diversity eelgrass increased almost twice as fast as in low-diversity eelgrass over 22 months (Williams, 2001). Natural *Z. marina* populations generally have a large genetic diversity (Reusch *et al*., 2000; in press); inbreeding depression is known to occur (Reusch, 2001), and reduced genetic diversity has negative effects on *Z. marina* leaf shoot density and recruitment from seed (Williams 2001).

Note that the environmental, demographic and genetic factors cannot be considered as independent variables. Several interactions are known, for instance fertility can be affected by inbreeding (e.g. Booy *et al*., 2000); the rafting of seed shoots or pollen will be lower in sheltered conditions (see above), and, in general, site conditions affect birth and death rates.

(k=1.5 m^{-1} or less; de Jonge *et al.*, 1996), the mesocosm study predicted that *Z. marina* depth limits are at least -0.80 m Mean Sea Level (MSL), which corresponds to approximate low tide in most of the Dutch Wadden Sea (van Katwijk et al., 1998).

Pilot transplantations fail

These positive results led to experimental transplantations on a number of tidal flats in 1993. Mainly historical seagrass locations were selected, *i.e.*, beds were present in the 1970s. The transplanted plants survived in a narrow zone around MSL. However, in the second growing season, insufficient seedlings emerged to maintain the population (van Katwijk & Schmitz, 1993; Hermus, 1995; van Katwijk & Hermus, 2000). Three possible causes for these losses are likely: (1) germination and/or seedling survival is reduced at the transplantation site in comparison to the donor site, (2) coincidental climatologic circumstances, *e.g.*, an extreme salinity drop in January 1994 (caused by exceptionally high river discharges in the winters of 1993/1994), causing unusually early germination, followed by a prolonged cold period during which the young seedlings froze to death. (3) A large part of the seed stalks containing seeds may have drifted towards the open sea before they released their seeds.

Intermezzo 2. Nomenclature

The flexible type with less rigid bases, lying flat on the sediment, was named *Zostera hornemanniana* by Tutin (1936; 1938; 1942). Subsequently, Tutin called it *Z. angustifolia* (Hornem.) Rchb. (Clapham et al., 1962; Tutin et al., 1980), a name still in use in Great Britain (overview by Kay et al., 1998). By Harmsen (1936) it was named *Z. marina* var. *stenophylla* Aschers. & Graebner. The robust type with bases that stick up in the air for a centimetre or two when exposed at low tide is unanimously called *Z. marina* L. Presently, in white literature, both types are referred to as *Z. marina* L., as no taxonomically distinctive features could be found (den Hartog, 1972). According to den Hartog (pers. comm.) the difference in length of style + stigmas being longer in *Z. marina* than in *Z. hornemanniana* (Tutin, 1936) is an artefact: presumably the examined specimen of *Z. hornemanniana* was collected after fertilisation, when the upper part of the styles had fallen off, whereas the specimen of *Z. marina* was collected before fertilisation.

Figure 6. Experiments with a mesocosm basin in Texel showed that light was sufficient to at least –0.80 m MSL, and suitable donor populations were available (two Wadden Sea populations and one population from SW Netherlands were suitable, as opposed to an Atlantic and a Baltic population).

Figure 7. *Zostera marina* transplantation experiments (planting units of 1 m^2) showed that plants disappeared below –0.20 m MSL. It was hypothesised that this was due to either (1) water quality (lower tidal depth -> longer period of exposure to the water), or (2) increasing water dynamics with increasing tidal depth. Both hypotheses were tested.

Measures to support sustainable settlement

Proceeding from these three possible causes for insufficient recruitment from seed, measures to increase the chances for long-term survival of transplantations are:

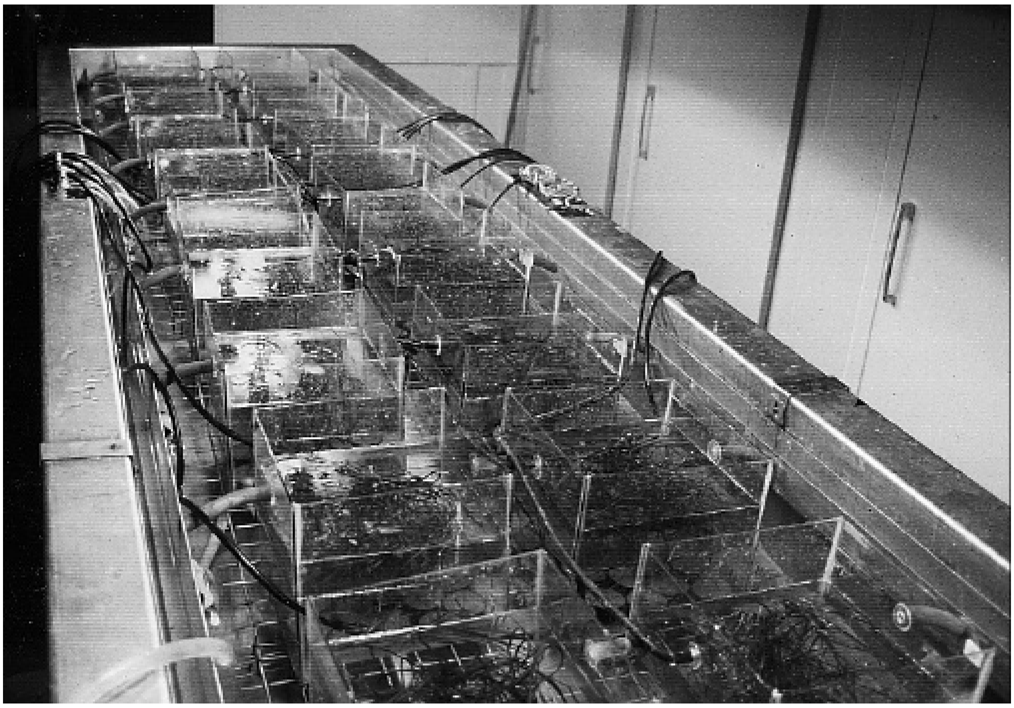
Measure 1. Selection of locations where the conditions are not only suitable for adult plants, but also for germination and/or seedling survival. Field experiments at Balgzand (Fig. 1) revealed that germination was favoured by muddy sediments (footprint depth circa 3 cm) as compared to sandy sediments; seedling survival and proliferation was favoured by a permanent layer of water covering the plants at low tide, for instance in local depressions, as compared to sites with complete emergence at the same tidal depth, and by a sheltered location (van Katwijk & Wijgergangs, 2000).

Measure 2. Spreading of risks, in space and time, to cope with coincidental adverse weather conditions.

Measure 3. Development of a method to keep the rafting reproductive shoots within the area that was thought to be suitable for bed development, until a minimum viable population size is reached, see intermezzo 1.

Additionally, from literature rises *Measure 4.* Application of genetically diverse donor material, to keep the transplantation adaptable and avoid inbreeding depression (Booy *et al.*, 2000; Williams, 2001, see intermezzo 1).

Figure 8. In two laboratory experiments using glass containers testing water quality, we found (1) that ammonium was toxic to *Zostera marina*, and (2) that high nutrient loads had a positive effect when salinity was low, but a negative effect when salinity was high (see Fig. 9).



Depth-related transplantation success raised new questions

Another finding of the transplantation experiments was that the transplanted seagrasses disappeared below -0.20 m MSL within one month. At that depth, light was not limiting (van Katwijk et al., 1998; van Katwijk & Hermus, 2000) from which it was hypothesised that either some water quality factor was unsuitable to sustain eelgrass, or physical disturbance was too high at larger depths.

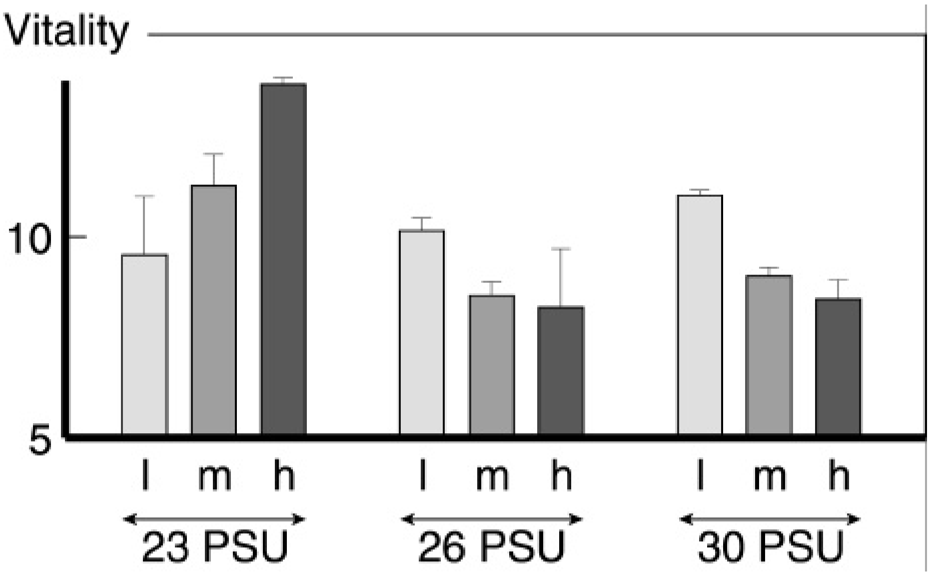
Water quality factors: nutrients and salinity

Introduction

Probably, the most influencing water quality factor is nutrient load (Short & Echeverria, 1996; Hemminga & Duarte, 2000). Nutrient loads have severely increased in the Wadden Sea (review in van Katwijk *et al.*, 2000), and particularly the following factors, that are part of, or interacting with nutrient load, were of interest:

- Nitrate: In the United States, a negative, probably toxic effect of nitrate on *Z. marina* is reported (Burkholder *et al.*, 1992).
- Ammonium: it is well known that high ammonium levels in the water layer can be toxic to plants. However, ammonium toxicity to submerged aquatic plants has been given little attention. It had been observed in a few freshwater aquatic plants (Glänzer, 1974; Grube, 1974; Agami *et al.*, 1976; Glänzer *et al.*, 1977; Roelofs, 1991; Smolders *et al.*, 1996). It had not been reported for *Z. marina* or any other seagrass.
- Salinity: patterns of distribution and decline of *Z. marina* in the Netherlands indicated a negative

Figure 9. Vitality of *Zostera marina* plants originating from the Ems estuary, after six weeks at different combinations of salinity (psu, generally equal to promille S) and nutrient loads (l low, m medium, h high). Vitality (mean + standard error of the mean) = number of shoots + size - necrosis - number of missing leaves, where size was the average between leaf length, width and total biomass of the plants; all parameters were standardised to mean 2 (to avoid negative values) and unit variance prior to the calculation. ANOVA revealed a negative effect of nutrients in the two higher salinity treatments ($p<0.01$, N=4), whereas nutrients tended to respond positively to nutrients at the lowest salinity treatment ($p=0.1$, N=2) (van Katwijk et al., 1999).



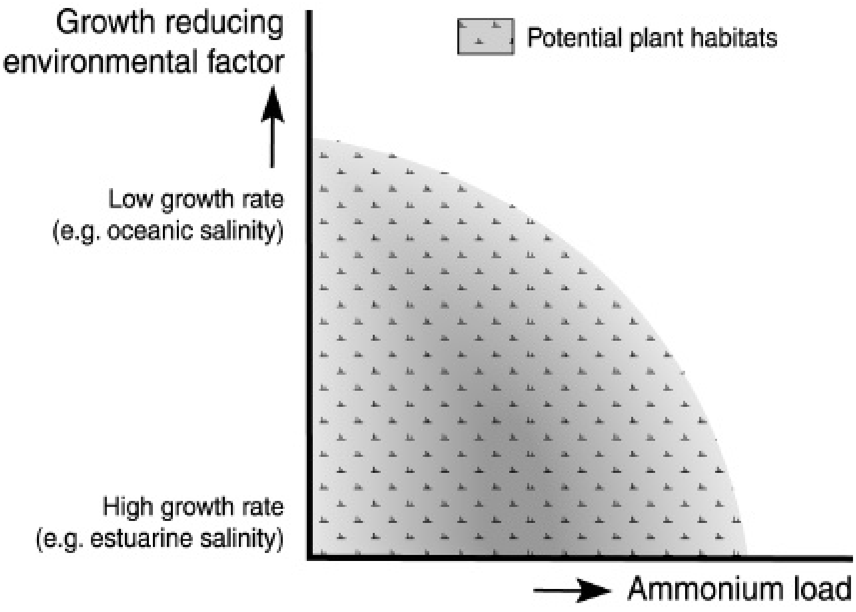
effect of a high salinity, particularly above 30.5 psu (de Jong, pers. comm.; Wijgergangs & van Katwijk, 1993; Wijgergangs, 1994; Wijgergangs & de Jong, 1999). This was confirmed by laboratory experiments with *Z. marina* shoots (Kamermans *et al.*, 1999; van Katwijk *et al.*, 1999), as well as germination and seedling development experiments (*e.g.*, Hootsman *et al.*, 1987) showing a negative effect of salinity on *Z. marina*.

Therefore, we investigated the effects of nutrients and salinity on *Zostera marina* in two laboratory experiments. One laboratory experiment revealed that high loads of ammonium are toxic to eelgrass (Fig. 8; van Katwijk *et al.*, 1997). A second laboratory experiment, simulating present nutrient loads in the present Wadden Sea showed an interactive effect with salinity on *Z. marina*: at a normal salinity (30 psu) these nutrient loads had a negative effect, whereas at a lowered salinity (23 psu) the nutrient load had a positive effect on *Z. marina* development (Fig. 9; van Katwijk *et al.*, 1999).

Comparison to the field situation

The interactive effect correlates with distribution and decline patterns of *Z. marina* in many areas of the northern hemisphere. For example, in The Netherlands, with its variety of marine (ca. 30 psu) and estuarine (15 to 25 psu) environments, we observed that the distribution of *Z. marina* in marine environments was limited to waters with low to moderate nutrient concentrations, viz. in summer, monthly median values varied between 0-4 ìM NO_3, 1-8 ìM NH_4, 2-10 ìM P_{tot} and in winter between 15-55 ìM NO_3, 7-11 ìM NH_4 3-8 ìM $P_{tot.}$ However, *Z. marina* was observed to

Figure 10. Postulated interactive effect of nutrients, viz. ammonium, and any growth reducing factor (for example high salinity) on potential plant habitats. Darker shades indicate greatest plant vitality.

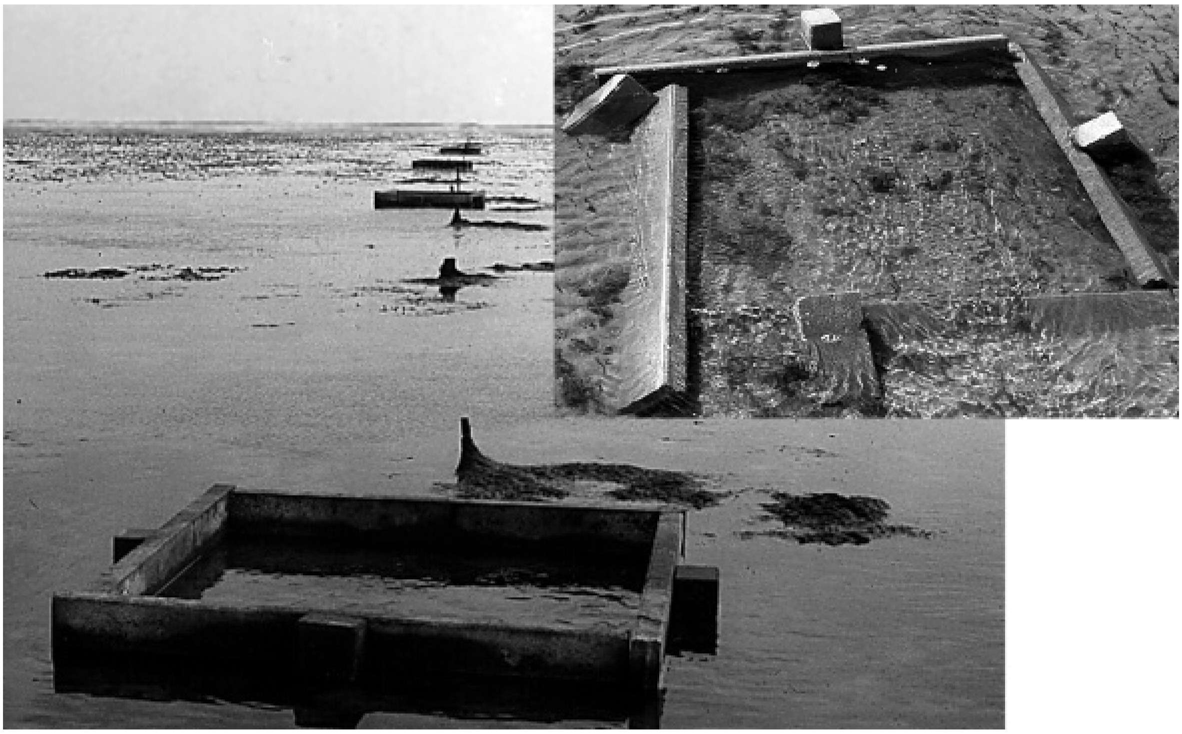


flourish in estuarine environments with relatively high nutrient concentrations, viz. in summer, monthly median values varied between 0-90 ìM NO_3, 2-11 ìM NH_4, 7-25 ìM P_{tot} an in winter between 50-260 ìM NO_3, 15-55 ìM NH_4 and 8-20 ìM P_{tot} (Ministry of Transport, Water Management and Public Works, unpublished data on the southwest Netherlands and the Dutch Wadden Sea). Furthermore, in some marine environments, seagrass distribution shifted towards areas with some freshwater influence (Burdick *et al*., 1993).

Our findings refer to a general principle

Probably, the interactive effect of nutrients having a positive effect on *Z. marina* at low salinity, and a negative effect at high salinity, relates to a general principle: probably faster growing *Z. marina* can accommodate for the higher nutrient availability by fast uptake and incorporation. In this case, accumulation of N is prevented. However, in slower growing marine populations, increased nutrient availability cannot be used for growth. N will accumulate, leading to inhibition of plant development and eventually death by toxicity. The same interactive effect was found when comparing slow-growing seagrasses with fast-growing macroalgae (Pedersen, 1995) and in several terrestrial and freshwater species and vegetation types (*e.g.*, Roelofs, 1986; Roelofs *et al*., 1996; Bobbink *et al*., 1998). This means that in the process of eutrophication, relatively slow-growing species can maintain themselves only when conditions are optimal in all other aspects, keeping their growth rate as high as possible (Fig. 10). Growth rates of *Z. marina* drop when salinity is high (32 psu as compared to 22 psu) (Kamermans *et al*., 1999). In the Wadden Sea, nutrient loads have increased during the last century (*e.g.*, van Katwijk *et al*., 2000), thus confining the potential seagrass habitat to areas with freshwater influence, or to areas where nutrient loads are still relatively low, *e.g.*, the northern Wadden Sea, where no large rivers discharge. N-loadings from rivers through Lake IJssel

Figure 11. Over the investigated depth range (+0.15 - -1.05 m Mean Sea Level, MSL), the average maximum wave intensity is equal, whereas, obviously, the duration of exposure increases with increasing depth. The effect of this increasing exposure period is illustrated by the kerbstones (1 x 1 m) placed on the tidal flat near Wierschuur, Terschelling (a), but displaced after one month at -0.60 m MSL (b), which did not occur at 0 m MSL (sediments were similar).



provide the main N-source to the western Wadden Sea (Philippart & Cadée, 2000). N-loading from mineralisation of influxing organic matter from the North Sea are in the same order of magnitude in the western and northern Wadden Sea (van Beusekom et al., 1999; in press).

Physical disturbance

Introduction

Transplanted seagrass disappeared below -0.20 m MSL. This was neither a local nor an incidental phenomenon: it occurred at three locations in the Dutch Wadden Sea, and in two subsequent years (van Katwijk & Schmitz, 1993; Hermus, 1995). From several observations it appeared that water dynamics increased with increasing depth. For instance, kerbstones that were placed on the tidal flats, were severely displaced within one month at -0.60 m MSL (Fig. 11), whereas no such displacement occurred at 0 m MSL. Also, with increasing depth, erosion pits and sedimentary elevations arose at a higher pace around exclosures that were placed on the tidal flat at several depths (Hermus, 1995; D.C.R. Hermus, pers. comm.). Model calculations revealed that, obviously, the duration of the exposure increased with increasing depth, however the maximum wave intensity was equal at all tidal depths investigated (van Katwijk & Hermus, 2000).

Figure 12. Experiments with exclosures showed that below -0.20 m MSL additional shelter is required to support transplantation success.

Experiments show that wave dynamics prevents transplantation success below -0.20 m MSL

Transplantation experiments in the Dutch Wadden Sea showed that reduced wave dynamics by exclosures (Fig. 12), prevented the loss of plants in the zone -0.40 - -1.15 m MSL, and removal of the exclosures after 1 month caused loss of all plants within a few days. Light limitation could not explain these results (van Katwijk *et al*., 1998; van Katwijk & Hermus, 2000). Bioturbation, often causing transplantation losses along the eastern and southern shores of the United States (Fonseca *et al*., 1994; 1998; Davis *et al*., 1998; Hammerstrom *et al*., 1998), had no effects on the transplantations in the Dutch Wadden Sea (van Katwijk & Hermus, 2000). We concluded that the depth-related transplantation success could be attributed to increasing periods of exposure to wave dynamics at increasing depth. At these sites, the average maximal orbital velocity at the sediment reached circa 0.40 ms^{-1}. Transplantation failed below -0.20 m MSL, corresponding to a relative period of exposure to wave action of circa 60%. If water dynamics are even higher (viz. average maximal orbital velocity at the sediment > 0.60 m s^{-1}, they become too high for the establishment and maintenance of intertidal *Z. marina* at all tidal depths (van Katwijk & Hermus, 2000).

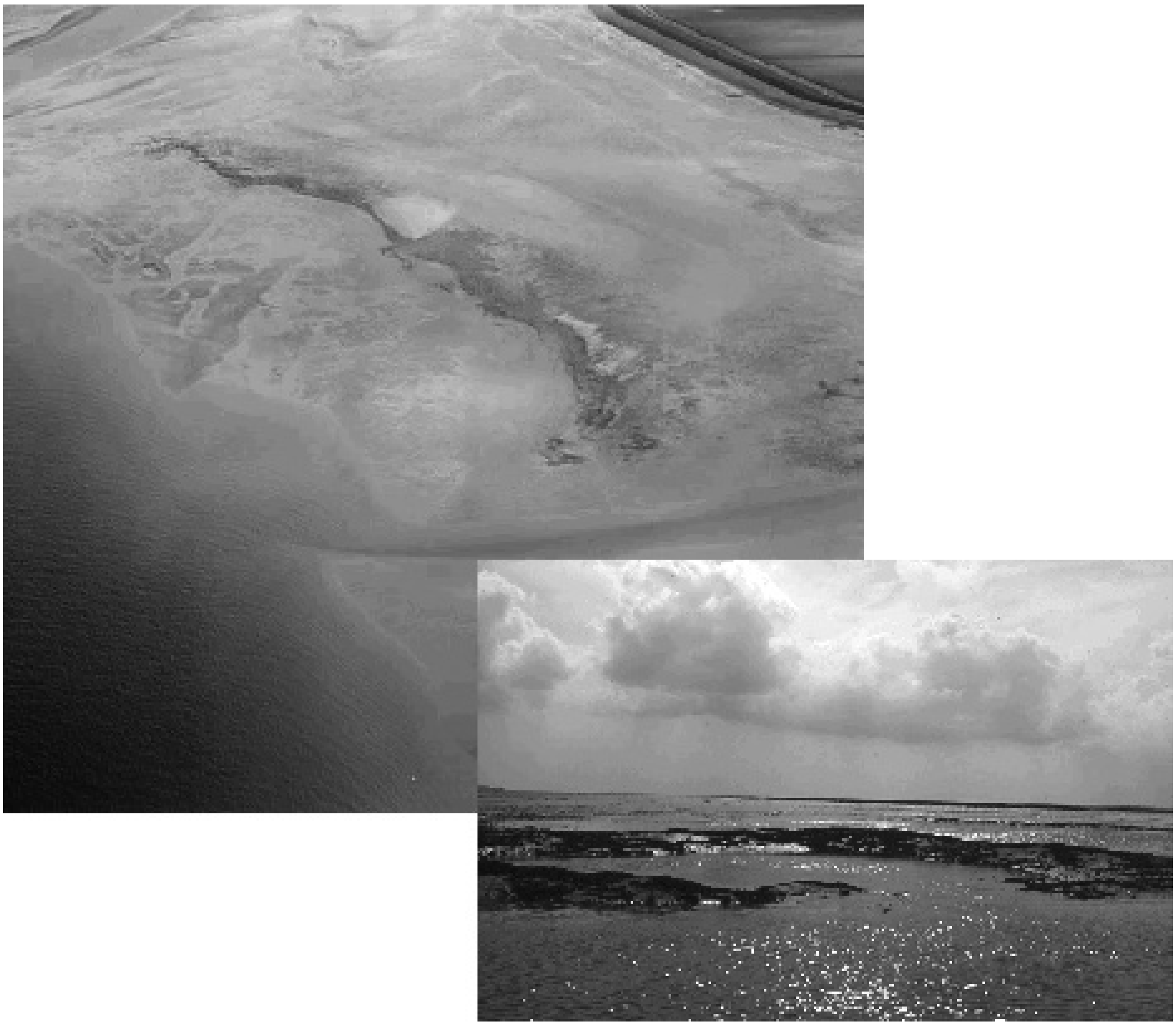
This is also visible in several distribution patterns of eelgrass found elsewhere in NW Europe

The importance of water dynamics determining the lower limit of eelgrass beds is furthermore supported by zonation patterns of intertidal *Z. marina* beds in the Dutch and German Wadden Sea, southwest Netherlands, and for example, the Thames estuary (at present, but also in the period that subtidal eelgrass was still present, so light was not limiting): plant cover diminished with increasing depth (Harmsen, 1936; C. den Hartog, pers. comm.; pers. obs. author), which could not be attributed to light limitation (Harmsen, 1936; Wijgergangs & de Jong, 1999; van Katwijk & Hermus, 2000). Moreover, intertidal *Z. marina* beds penetrate to larger depths when shelter is present, *i.e.*, behind a mussel bed at the low tide level in Sylt Germany (K. Reise, pers. comm.), behind the dam encompassing the eelgrass bed at The Plaat, Terschelling, located at -0.50 m MSL (pers. obs. author, L.J.M. Wijgergangs, pers. comm.) and directly behind an island at Roscoff, France (C. den Hartog, pers. comm.).

However, pre-1930s beds did occur deeper than -0.20 m MSL. Why?

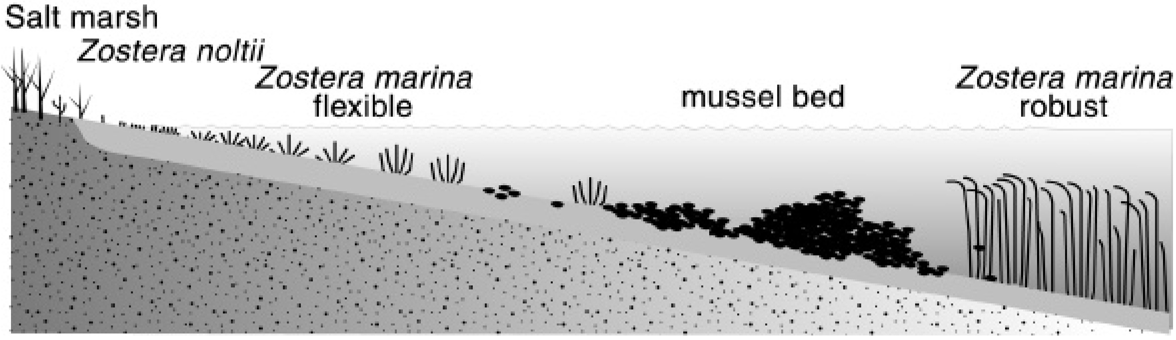
In a seeming contrast with our findings is the luxurious growth of *Z. marina* around

Figure 13. Mussel beds protect the hinterland against water dynamics, providing a suitable location for seagrass restoration in this respect (photographs copyright ALTERRA, courtesy to N. Dankers).



the low tide level in the Wadden Sea at the beginning of the twentieth century. Maximal orbital velocity at the sediment is equal at all tidal depths down to a point just below the low tide level. Below this point, the maximal orbital velocity decreases (van Katwijk & Hermus, 2000; M.M. van Katwijk, unpubl.). At the low tide level, the duration of exposure is almost 100%, which is much higher than the 60% exposure that was found to be critical! At that time, two (not necessarily genetically based) morphotypes of *Z. marina* were present, a robust perennial morphotype, and a flexible (often annual) morphotype of *Z. marina* (Harmsen, 1936). These morphotypes were also described for other parts of the world (Harmsen, 1936; Tutin, 1938; Keddy & Patriquin, 1978; intermezzo 2). The larger type that occurred in the low-intertidal-subtidal zone can withstand higher water dynamics, because of its robustness, and its relatively larger belowground biomass providing better anchoring facilities. It could not extend towards higher tidal levels because it is more susceptible to desiccation than the flexible type of *Z. marina* that grows in the mid-intertidal zone (Harmsen, 1936; Tutin, 1938; Keddy & Patriquin, 1978; van Katwijk et al., 2000). Knowing this, our results can explain why non-vegetated zones existed at non-sheltered

Figure 14. Zones of communities protecting each other from deep to shallow against water dynamics and erosion. Old literature revealed that two morphotypes of eelgrass were present before the decline in 1930s: a robust perennial morphotype and a flexible morphotype of *Zostera marina*. Restoration should aim at the latter type, as it disappeared last and is still present in eastern and northern parts of the Wadden Sea, including the Ems estuary. Before the robust morphotype can be reintroduced, additional research is necessary to select suitable donor populations and test habitat requirements. MSL Mean Sea Level, LT low tide.



locations in the Wadden Sea and in the Thames estuary in the 1930s (Harmsen, 1936): the water dynamics were too high for the flexible type of *Z. marina*, and the period of emergence during low tide was too long for the robust type of *Z. marina*.

What do these findings imply for the reintroduction of seagrass in the Dutch Wadden Sea?

Apart from the obvious requirement of prohibition of shellfish fisheries (*e.g.*, Fig. 4) to facilitate reintroduction of *Zostera marina*, a careful selection of the transplantation sites should be made. At a local scale, relatively muddy sediments and a thin layer of water during low tide are preferred; at a regional scale, particularly freshwater influence and the availability of shelter are recommended. It is of importance to quantify these factors in the Wadden Sea, and map the *Z. marina* habitat suitability in the Wadden Sea. A start in this direction was made for the Dutch Wadden Sea by de Jonge *et al.* (1997; 2000), using the factors wave energy, currents, grain size and tidal depth in a GIS model.

Creation of shelter: seagrasses and mussel beds protect each other and saltmarshes in an undisturbed Wadden Sea

Shelter can also be created, which is not as artificial as it seems. Ecosystems in a natural coastal gradient often protect each other: sublittoral *Z. marina* beds can protect mussel beds against storms (Reusch & Chapman, 1995), mussel beds can provide shelter to mid-littoral *Z. marina* and *Z. noltii* populations (Fig. 13, van Katwijk & Hermus, 2000; van Katwijk *et al*., 2000; N. Dankers, pers. comm.), as is supported by the extension of *Z. marina* beds towards mussel beds at low tide level (K. Reise, pers. comm.). The shelter that is provided by mussel beds will additionally stimulate the accumulation of fine sediments and a lesser degree of desiccation of the sediment (van Katwijk *et al*., 2000), which is favourable to *Z. marina* (van Katwijk & Wijgergangs, 2000). The overall positive effect of mussel beds on *Z. marina* in the Wadden Sea is supported by the eyewitness accounts in 1938 by Reigermans and coworkers (1939), who observed at several locations in the western Wadden Sea that near mussel beds, seagrass had survived the wasting disease.

In turn, the presence of mid-littoral *Z. marina* and *Z.noltii* beds can reduce erosion of salt marshes, as seagrasses accumulate sediments, in this way providing a natural barrier in front of the salt marsh edge (*e.g.*, Rasmussen, 1977; Beardall *et al*., 1988; Gacia *et al*., 1999; Koch, 2001; Granata *et al*., 2001; D.J. de Jong, pers. comm.). This zonation is depicted in Fig. 14.

Subtidal and low-intertidal seagrass beds disappeared in the 1930s (see introduction). Stable mussel beds disappeared around 1990, except for a few in the German Wadden Sea (Beukema, 1992; Rudfeld, 1992; Dankers, 1993; Nehls & Thiel, 1993; Beukema & Cadée, 1996; Reise, 1998).

Management vision: Zostera marina *bed restoration by restoring the coastal gradient*

The coherence of the seagrass and mussel bed zones makes restoration of one of the separate zones less feasible than simultaneous restoration of the complete zonation. However, restoration of the sublittoral *Z. marina* beds is complex, as the morphotype that is suitable for this zone probably has become extinct in the Wadden Sea. A practical solution would be to first restore stable mussel beds, as these can maintain themselves without sublittoral seagrass. Secondly, mid-littoral *Z. marina* and *Z. noltii* can be transplanted, which will probably reduce salt marsh erosion (Fig. 14). Finally, to complete the gradient, sublittoral *Z. marina* can be transplanted, provided a suitable donor population has been found.

It should be noted that in a pristine Wadden Sea eelgrass beds flourished on (locally and/or temporarily) unsheltered locations as well. Here they led a dynamic and uncertain existence, as becomes apparent from notes by Martinet (1782), Oudemans *et al*. (1870) and den Hartog & Polderman (1975). Likewise, it is known that stable mussel beds are incidentally destroyed by storms, though subsequently colonising the same location or in the close vicinity (Dankers & Koelemaij, 1989). Recovery is possible if sufficient sources and numbers of propagules are available. In the present situation, without such sources present, a direct return to dynamic eelgrass beds is not possible. This underlines our plea for an indirect approach, through the construction of more or less stable centres of proliferation acting as refugia.

Conclusions

1. Suitable donor populations are available.
2. Light is not limiting to at least -0.80 m MSL, which is the approximate mean low tide level in the Dutch Wadden Sea.
3. Below -0.20 m MSL, water dynamics are too severe, unless shelter is available.
4. High nutrient loads inhibit *Zostera marina*, unless freshwater influences are present.
5. Muddy sediments and a permanent layer of water during low tide are favourable.
6. Two types of *Zostera marina* occurred in the pre-1930s Wadden Sea, each suitable for another tidal depth.

Recommendations

1. Restoration of estuarine gradients (which is presently discussed as a policy option in The Netherlands, Anonymous, 1998).
2. Decrease of nutrient (particularly nitrogen) loads.

3. Restoration of areas of shelter (for example mussel beds), active or passive.
4. Careful selection of transplantation sites; locally (muddy sediments with a permanent layer of water during low tide) and regionally (freshwater influence and shelter).
5. Improvement of the present GIS map of the *Z. marina* habitat suitability of the Dutch Wadden Sea with data on salinity and nutrient loads.
6. Prohibition of fisheries activities in potential seagrass habitats.
7. Find answers to the new questions that follow from the presented results, as listed below.

New questions

1. What is the minimum size of a founding population for a sustainable re-establishment?
2. How can we keep the seed containing shoots within the target area until a minimum population size is achieved (viz. develop a technique to culture the seagrass in situ)?
3. Is there a genetic basis for the differences between the flexible and robust type of *Zostera marina*? If so,
4. What donor population (robust type) would be suitable for the zone around low tide?

Acknowledgements

Main contributors to the project “Reintroduction of Zostera marina in the Dutch Wadden Sea” were C. den Hartog, V.N. de Jonge, D.J. de Jong, W.J.B.T. Giesen, G.H.W. Schmitz, D.C.R. Hermus and L.J.M. Wijgergangs. Three anonymous referees, C. den Hartog, and J.M. van Groenendael are thanked for valuable comments. Photographs were kindly provided by: J. Anderson, N. Dankers, V.N. de Jonge, T. Duinker, the Library of the University of Groningen and M. van Keulen (reproduced with permission of Cockburn Cement Limited, Western Australia). The Ministry of Transport, Public Works and Water Management provided funding for most of the research.

References

Agami M, Litav M, Waisel Y (1976) The effects of various components of water pollution on the behaviour of some aquatic macrophytes of the coastal rivers of Israel. Aquat Bot 2:203-213

Anonymous (1989) Water voor nu en later. Derde Nota Waterhuishouding. Ministry of Transport, Public Works and Water Management. Tweede Kamer 1988-1989 21250, Den Haag

Anonymous (1998) Vierde Nota Waterhuishouding. Regeringsbeslissing.

Asmus H, Asmus R (1998) The role of macrobenthic communities for sediment-water material exchange in the Sylt-Rømø tidal basin. Senckenb Marit 29:111-119

Balestri E, Piazzi L, Cinelli F (1998) Survival and growth of transplanted and natural seedlings of Posidonia oceanica (L.) Delile in a damaged coastal area. J Exp Mar Biol Ecol 228:209-225

Beardall CH, Dryden RC, Holzer TJ (1988) The Suffolk Estuaries. The Suffolk Wildlife Trust, Saxmundham, Suffolk

Beukema JJ (1992) Long-term and recent changes in the benthic macrofauna living on tidal flats in the western part of the Wadden Sea. Neth Inst Sea Res Publ Ser 20:135-141

Beukema JJ, Cadée GC (1996) Consequences of the sudden removal of nearly all mussels and cockles from the Dutch Wadden Sea. Mar Ecol 17:279-289

Bobbink R, Hornung M, Roelofs JGM (1998) The effects of air-borne nitrogen pollutants on species diversity in natural and seminatural European vegetation. J Ecol 86:717-738

Booy G, Hendriks RJJ, Smulders MJM, Van Groenendael JM, Vosman B (2000) Genetic diversity and the survival of populations. Plant Biol 2:379-395

Burdick DM, Short FT, Wolf J (1993) An index to assess and monitor the progression of wasting disease in eelgrass Zostera marina. Mar Ecol Prog Ser 94:83-90

Burkholder JM, Mason KM, Glasgow HB (1992) Water-column nitrate enrichment promotes decline of eelgrass Zostera marina: Evidence from seasonal mesocosm experiments. Mar Ecol Prog Ser 81:163-178

Christensen PB, McGlathery KJ (1995) Transplantation of eelgrass. National Environmental Research Institute, Silkeborg

Clapham A.R., Tutin TG, Warburg EF (1962) Flora of the british Isles. Cambridge University Press, Cambridge

Costanza R, d'Arge R, de Groot R, Farber S, Grasso M, Hannon B, Limburg K, Naeem S, O'Neill RV, Paruelo J, Raskin RG, Sutton P, van den Belt M (1997) The value of the world's ecosystem services and natural capital. Nature 387:253-260

Dankers N, Koelemaij K (1989) Variations in the mussel population of the Dutch Wadden Sea in relation to monitoring of other ecological parameters. Helgol Mar Res 43:529-535

Dankers N (1993) Integrated estuarine management - obtaining a sustainable yield of bivalve resources while maintaining environmental quality. In: Dame RF (ed) Bivalve Filter Feeders. Springer-Verlag, Berlin Heidelberg, p 479-511

Dankers N (1998) Four years of Dutch shellfish fisheries policy - and now the future. Wadden Sea Newsl 1998-1:5-7

Davis RC, Short FT, Burdick DM (1998) Quantifying the effects of green crab damage to eelgrass transplants. Restor Ecol 6:297-302

de Jong DJ (2000) Werkdocument zeegraskarteringen Waddenzee. RWS/RIKZ, Middelburg

de Jonge VN, de Jong DJ (1992) Role of tide, light and fisheries in the decline of Zostera marina L. in the Dutch Wadden Sea. Neth Inst Sea Res Publ Ser 20:161-176

de Jonge VN, de Jong DJ, van den Bergs J (1996) Reintroduction of eelgrass (Zostera marina) in the Dutch Wadden Sea; review of research and suggestions for management measures. J Coast Conserv 2:149-158

de Jonge VN, van den Bergs J, de Jong DJ (1997) Zeegras in de Waddenzee, een toekomstperspectief. RIKZ, Haren, The Netherlands

de Jonge VN, de Jong DJ, van Katwijk MM (2000) Policy plans and management measures to restore eelgrass (Zostera marina L.) in the Dutch Wadden Sea. Helgol Mar Res 54:151-158

de Jonge, V. N., Ruijgrok, E. C. M., and de Vries, M. B. (This volume) Concepts and dilemma's in integrating ecology and economy in coastal policy-making.

den Hartog C (1970) The sea-grasses of the world. North-Holland, Amsterdam

den Hartog C (1972) The identity of Zostera marina var. angustifolia Hornemann (Potamogetonaceae). Blumea 20:150-150

den Hartog C, Polderman PJG (1975) Changes in the seagrass populations of the Dutch Waddenzee. Aquat Bot 1:141-147

den Hartog C (1987) "Wasting disease" and other dynamic phenomena in Zostera beds. Aquat Bot 27:3-14

den Hartog C (1996) Sudden declines of seagrass beds: "wasting disease" and other disasters. In: Kuo J, Phillips RC, Walker DI, Kirkman H (eds) Seagrass Biology: Proceedings of an International Workshop. Rottnest Island, Western Australia, 25-29 January 1996. University of Western Australia, Nedlands, p 307-314

Fonseca MS, Kenworthy WJ, Colby DR, Rittmaster KA, Thayer GW (1990) Comparisons of fauna among natural and transplanted eelgrass Zostera marina meadows: Criteria for mitigation. Mar Ecol Prog Ser 65:251-264

Fonseca MS, Kenworthy WT, Courtney FX, Hall MO (1994) Seagrass planting in the southeastern United States: Methods for accelerating habitat development. Restor Ecol 2:198-212

Fonseca MS (1996) The role of seagrasses in nearshore sedimentary processes: a review. In: Nordstrom KF, Roman CT (eds) Estuarine Shores: Evolution, Environments and Human Alterations. John Wiley & Sons Ltd., p 261-286

Fonseca MS, Kenworthy WJ, Thayer GW (1998) Guidelines for the conservation and restoration of seagrasses in the United States and adjacent waters. NOAA Coastal Ocean Program Decision

Analysis Series No. 12. NOAA Coastal Ocean Office, Silver Spring MD

Gacia E, Granata TC, Duarte CM (1999) An approach to measurement of particle flux and sediment retention within seagrass (Posidonia oceanica) meadows. Aquat Bot 65:255-268

Giesen WBJT, van Katwijk MM, den Hartog C (1990a) Eelgrass condition and turbidity in the Dutch Wadden Sea. Aquat Bot 37:71-85

Giesen WBJT, van Katwijk MM, den Hartog C (1990b) Temperature, salinity, insolation and wasting disease of eelgrass (Zostera marina L.) in the Dutch Wadden Sea in the 1930's. Neth J Sea Res 25:395-404

Glänzer U (1974) Experimentelle Untersuchung über das Verhalten submerser Makrophyten bei NH4+-Belastung. Verhandlungen der Gesellschaft für Ökologie, Saarbrucken 1973. Dr. W. Junk Publishers, Den Haag, p 175-179

Glänzer U, Haber W, Kohler A (1977) Experimentelle Untersuchungen zur Belastbarkeit submerser Flie gewasser-Makrophyten. Arch Hydrobiol 79:193-232

Granata TC, Serra T, Colomer J, Casamitjana X, Duarte CM, Gacia E (2001) Flow and particle distributions in a nearshore seagrass meadow before and after a storm. Mar Ecol Prog Ser 218:95-106

Grube H-J (1974) Belastung und Belastbarkeit von submersen Makrophyten in südniedersachsischen Fliessgewässer. Verhandlungen der Gesellschaft für Ökologie, Saarbrucken 1973. Dr. W. Junk Publishers, Den Haag, p 193-200

Hammerstrom K, Sheridan P, McMahan G (1998) Potential for seagrass restoration in Galveston Bay, Texas. Texas Journal of Science 50:35-50

Harmsen GW (1936) Systematische Beobachtungen der Nordwest-Europäischen Seegrasformen. Ned Kruidk Arch 46:852-877

Heck KL, Able KW, Roman CT, Fahay MP (1995) Composition, abundance, biomass, and production of macrofauna in a New England estuary: Comparisons among eelgrass meadows and other nursery habitats. Estuaries 18:379-389

Hemminga MA, Duarte CM (2000) Seagrass Ecology. Cambridge University Press,

Hermus DCR (1995) Herintroduktie van zeegras in de Waddenzee. Het verloop van de beplantingen in 1992-1994 & zaadexperimenten. Department of Aquatic Ecology and Environmental Biology, University of Nijmegen

Hootsmans MJM, Vermaat JE, Van Vierssen W (1987) Seed-bank development, germination and early seedling survival of two seagrass species from the Netherlands: Zostera marina L and Z. noltii Hornemann. Aquat Bot 28:275-285

Horinouchi M, Sano R (1999) Effects of changes in seagrass shoot density and leaf height on abundances and distribution patterns of juveniles of three gobiid fishes in a Zostera marina bed. Mar Ecol Prog Ser 183:87-94

Kamermans P, Hemminga MA, de Jong DJ (1999) Significance of salinity and silicon levels for growth of a formerly estuarine eelgrass (Zostera marina) population (Lake Grevelingen, the Netherlands). Mar Biol 133:527-539

Kawasaki Y, Litoka T, Goto H, Terawaki T, Watanabe Y, Kikuti K (1988) Study on the technique for Zostera bed creation. Denryoku Chuo Kenkyusho Hokoku u14, 1-231

Kay QON (1998) A review of the existing state of knowledge of the ecology and distribution of seagrass beds around the coast of Wales. Science report 296, Countryside Council for Wales, Bangor, Wales

Keddy CJ, Patriquin DG (1978) An annual form of eelgrass in Nova Scotia. Aquat Bot 5:163-170

Kenworthy WJ, Fonseca MS, Whitfield PE, Hammerstrom K, Schwarzschild AC (2000) A comparison of two methods for enhancing the recovery of seagrasses into propellor scars: mechanical injection of a nutrient an growth hormone solution vs. defecation by roosting seabirds. Center for Coastal Fisheries and Habitat Research, Beaufort, NC

Koch EW (2001) Beyond light: physical, geological, and geochemical parameters as possible submersed aquatic vegetation habitat requirements. Estuaries 24:1-17

Lord D, Paling E, Gordon D (1999) Review of Australian rehabilitation and restoration programs. In: Butler AJ, Jernakoff P (eds) Seagrass in Australia. Strategic review and development of an R&D plan. SCIRO Publishing, Collingwood, p 65-115

Martinet JF (1782) Verhandeling over het wier der Zuiderzee. Verhandelingen Hollandsche Maatschappij der Wetenschappen 20: 54-129 + plates I-VI

Mattila J, Chaplin G, Eilers MR, Heck KL, O'Neal JP, Valentine JF (1999) Spatial and diurnal distribution of invertebrate and fish fauna of a Zostera marina bed and nearby unvegetated sediments in Damariscotta River, Maine (USA). Journal of Sea Research 41:321-332

Meinesz A, Molenaar H, Bellone E, Loquès F (1991) Vegetative reproduction in Posidonia oceanica (L.) Delile I - Effects of rhizome length and time of year on development in orthotropic transplants. Mar Ecol

Meinesz A, Molenaar H, Bellone E, Loquès F (1992) Vegetative reproduction in Posidonia oceanica: I. Effects of rhizome length and transplantation season in orthotropic shoots. Mar Ecol 13:163-174

Meinesz A, Molenaar H, Caye G (1993) Transplantations de phanerogames marines en mediterranee. Bollettino di Oceanologia Teorica ed Applicata 11:183-190

Molenaar H, Meinesz A, Caye G (1993) Vegetative reproduction in Posidonia oceanica. Survival and development in different morphological types of transplanted cuttings. Bot Mar 36:481-488

Nehls G, Thiel M (1993) Large-scale distribution patterns of the mussel Mytilus edulis in the Wadden Sea of Schleswig-Holstein: Do storms structure the ecosystem? Neth J Sea Res 31:181-187

Orth RJ, Luckenbach M, Moore KA (1994) Seed dispersal in a marine macrophyte: Implications for colonization and restoration. Ecol 75:1927-1939

Orth RJ, Harwell MC, Fishman JR (1999) A rapid and simple method for transplanting eelgrass using single, unanchored shoots. Aquat Bot 64:77-85

Oudemans CAJA, Conrad JFW, Maats P, Bouricius LJ (1870) Verslag der Staatscommissie inzake de wiermaayerij. Verslag aan den Koning over de Openbare Werken in het Jaar 1869. Van Weelden en Mingelen, Den Haag, p 199-231

Paling EI, van Keulen M, Wheeler KD (1998) Seagrass rehabilitation in Owen Anchorage, Western Australia. Report no. MAFRA 98/4, Murdoch University, Murdoch

Paling EI, van Keulen M, Wheeler KD (2000a) Seagrass rehabilitation on Success Bank, Western Australia (Project S2, 1995-2000). (Report No. MAFRA 00/006) Murdoch University, Murdoch

Paling EI, van Keulen M, Wheeler K, Walker C (2000b) Effects of depth on manual transplantation of the seagrass Amphibolis griffithii (J. M. Black) den Hartog on Success Bank, Western Australia. Pac Cons Biol 5:314-320

Pedersen MF (1995) Nitrogen limitation of photosynthesis and growth: Comparison across aquatic plant communities in a Danish estuary (Roskilde Fjord). Ophelia 41:261-272

Philippart CJM, Cadee GC (2000) Was total primary production in the western Wadden Sea stimulated by nitrogen loading? Helgol Mar Res 54:55-62

Piazzi L, Balestri E, Magri M, Cinelli F (1998) Experimental transplanting of Posidonia oceanica (L.) Delile into a disturbed habitat in the Mediterranean Sea. Bot Mar 41:593-601

Ranwell DS, Wyer DW, Boorman LA, Pizzey JM, Waters RJ (1974) Zostera transplants in Norfolk and Suffolk, Great Britain. Aquaculture 4:185-198

Rasmussen E (1977) The wasting disease of eelgrass (Zostera marina) and its effect on environmental factors and fauna. In: McRoy CP, Helfferich C (eds) Seagrass ecosystems. A scientific perpective. M. Dekker Inc., New York, p 1-51

Reigersman CJA, Houben GFH, Havinga B (1939) Rapport omtrent den invloed van de wierziekte op den achteruitgang van de wierbedrijven, met Bijlagen. Provinciale Waterstaat in Noord-Holland, Haarlem

Reise K, Herre E, Sturm M (1989) Historical changes in the benthos of the Wadden Sea around the island of Sylt in the North Sea. Helgol Mar Res 43:417-433

Reise K, Buhs F (1991) Seegrasvorkommen im Nationalpark Schleswig-Holsteinisches Wattenmeer. Forschungsbericht Biologische Anstalt Helgoland, List, Sylt

Reise K (1998) Pacific oysters invade mussel beds in European Wadden Sea. Senckenb Marit 28:167-175

Reusch TBH, Chapman ARO (1995) Storm effects on eelgrass (Zostera marina L.) and blue mussel (Mytilus edulis L.) beds. J Exp Mar Biol Ecol 192:257-271

Reusch TBH, Stam WT, Olsen JL (2000) A microsatellite-based estimation of clonal diversity and population subdivision in Zostera marina, a marine flowering plant. Molecular Ecology 9:127-140

Reusch TBH (2001) Fitness-consequences of geitonogamous selfing in a clonal marine angiosperm (Zostera marina). Journal of Evolutionary Biology 14:129-138

Reusch, T. B. H. (2002) Microsatellites reveal high population connectivity in eelgrass (Zostera marina) in two contrasting coastal areas. Limnology and Oceanography 47: 78-85

Roelofs JGM (1986) The effect of airborne sulphur and nitrogen deposition on aquatic and terrestrial heathland vegetation. Experientia 42:372-377

Roelofs JGM (1991) Inlet of alkaline river water into peaty lowlands: effects on water quality and Stratiotes aloides L. stands. Aquat Bot 39:267-294

Roelofs JGM, Bobbink R, Brouwer E, de Graaf MCC (1996) Restoration ecology of aquatic and terrestrial vegetation on non-calcareous sandy soils in The Netherlands. Acta Bot Neerl 45:517-541

Rudfeld L (1992) The Danish Wadden Sea - 25 years of protection. Neth Inst Sea Res Publ Ser 20:199-213

Sheridan P, McMahan G, Hammerstrom K, Pulich WJ (1998) Factors affecting restoration of Halodule wrightii to Galveston Bay, Texas. Restor Ecol 6:144-158

Short FT, Wyllie-Echeverria S (1996) Natural and human-induced disturbance of seagrasses. Environ Conserv 23:17-27

Sloet tot Oldhuis BWAE (1855) Het zeewier. Tijdschr v Staatshuishoudkunde en Statistiek 11:192-210

Smolders A, van Gestel CBL, Roelofs JGM (1996) The effects of ammonium on growth, accumulation of free amino acids and nutritional status of young phosphorus deficient Stratiotes aloides plants. Aquat Bot 53:85-96

Steins, N. and Brocken, F. (This volume) Balancing fisheries and nature in the Dutch Wadden Sea.

Thayer GW, Kenworthy WJ, Fonseca MS (1984) The ecology of eelgrass meadows of the Atlantic coast: a community profile. U.S.Fish Wildl.Serv.,

Tutin TG (1936) New species of Zostera from Britain. J Bot 74:227-230

Tutin TG (1938) The autecology of Zostera marina in relation to its wasting disease. New Phytol 37:50-71

Tutin TG (1942) Zostera marina L. J Ecol 30:217-226

Tutin TG, Chater AO, Richardson IBK (1980) Flora Europaea vol. 5: Alismataceae to Orchidaceae (Monocotyledones). Cambridge University Press, Cambridge

van Beusekom JEE, Brockmann UH, Hesse KJ, Hickel W, Poremba K, Tillman U (1999) The importance of sediments in the transformation and turnover of nutrients and organic matter in the Wadden Sea and German Bight. German J Hydrogr 51:245-266

van Beusekom JEE, de Jong F, Fock H, Diel-Christiansen S, Christiansen B (In press) Wadden Sea specific eutrophication criteria. Common Wadden Sea Secretariat, Wilhelmshafen, Germany

van den Hoek C, Admiraal W, Colijn F, de Jonge VN (1979) The role of algae and seagrasses in the ecosystem of the Wadden Sea, a review. In: Wolff WJ (ed) Flora and vegetation of the Wadden Sea. Wadden Sea Working Group, Report 3, Leiden, p 9-118

van Goor ACJ (1919) Het zeegras (Zostera marina L.) en zijn beteekenis voor het leven der visschen. Rapp Verh Rijksinst Visscherij I(4):415-498

van Groenendael JM (1995) How small can minimum viable population sizes really be? Levende Natuur 96:-39

van Katwijk MM, Schmitz GHW (1993) Herintroduktie van Zeegras in de Waddenzee. Beplantingen 1991 en 1992. Department of Aquatic Ecology and Environmental Biology, University of Nijmegen

van Katwijk MM, Vergeer LHT, Schmitz GHW, Roelofs JGM (1997) Ammonium toxicity in eelgrass Zostera marina. Mar Ecol Prog Ser 157:159-173

van Katwijk MM, Schmitz GHW, Hanssen LSAM, den Hartog C (1998) Suitability of Zostera marina populations for transplantation to the Wadden Sea as determined by a mesocosm shading experiment. Aquat Bot 60:283-305

van Katwijk MM, Schmitz GHW, Gasseling AM, van Avesaath PH (1999) The effects of salinity and nutrient load and their interaction on Zostera marina L. Mar Ecol Prog Ser 190:155-165

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, Wijgergangs LJM (2000) Enkele voorwaarden voor kieming en zaailingontwikkeling van Groot zeegras (Zostera marina). Department of Aquatic Ecology and Environmental Biology, University of Nijmegen

van Katwijk MM, Hermus DCR, de Jong DJ, Asmus RM, de Jonge VN (2000) Habitat suitability of the Wadden Sea for restoration of Zostera marina beds. Helgol Mar Res 54:117-128

Watanabe Y, Terawaki T (1986) Development of techniques for marine macrophyte bed creation in the coastal zone near a power plant: 6. Assessment of a transplanting method to prevent the eelgrass (Zostera marina L.) from being washed away. Denryoku Chuo Kenkyusho Hokoku u86008, i-iii-i1-16

Wijgergangs LJM, van Katwijk MM (1993) Zeegrassterfte in het Grevelingenmeer. Een studie naar de mogelijke oorzaken van de afname van het Groot zeegras, Zostera marina L., sinds eind jaren tachtig. Department of Aquatic Ecology and Environmental Biology, University of Nijmegen

Wijgergangs LJM (1994) Zeegras in het Grevelingenmeer en de Oosterschelde, relatie met voedingsstoffen en zoutgehalte. Department of Aquatic Ecology and Environmental Biology, University of Nijmegen

Wijgergangs LJM, de Jong DJ (1999) Een ecologisch profiel van zeegras en de verspreiding in Nederland. Department of Aquatic Ecology and Environmental Biology, University of Nijmegen

Williams SL (2001) Reduced genetic diversity in eelgrass transplantations affects both population growth and individual fitness. Ecol Applic 11:1472-1488