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Habitat suitability of the Wadden Sea for restoration of *Zostera marina* beds

Abstract A conceptual model is proposed, describing potential *Zostera marina* habitats in the Wadden Sea, based on reported data from laboratory, mesocosm and field studies. Controlling factors in the model are dynamics, degree of desiccation, turbidity, nutrients and salinity. A distinction has been made between a higher and a lower zone of potential habitats, each suitable for different morphotypes of *Z. marina*. The model relates the decline of *Z. marina* in the Wadden Sea to increased sediment and water dynamics, turbidity, drainage of sediments (resulting in increased degree of desiccation) and total nutrient loads during the twentieth century. The upper and lower delineation of both the higher and the lower zone of potential *Z. marina* habitats appear to be determined by one or a combination of several of these factors. Environmental changes in one of these factors will therefore influence the borderlines of the zones. The lower zone of *Z. marina* will be mainly affected by increased turbidity, sediment dynamics, degree of desiccation during low tide and nutrient load. The higher zone will be affected by increases in water and sediment dynamics, desiccation rates and nutrient loads. Potential *Z. marina* habitats are located above approx. –0.80 m mean sea level (when turbidity remains at the same level as in the early 1990s) in sheltered, undisturbed locations, and preferably where some freshwater influence is present. At locations with a high, near-marine, salinity, the nutrient load has to be low to allow the growth of *Z. marina*. The sediment should retain enough water during low tide to keep the plants moist. Our results suggest that the return of *Z. marina* beds within a reasonable time-scale will require not only suitable habitat conditions, but also revegetation measures, as the changes in the environment resulting from the disappearance of *Z. marina* may impede its recovery, and the natural import of propagules will be unlikely. Furthermore, the lower zone of *Z. marina* may require a genotype that is no longer found in the Wadden Sea.

Key words Restoration · *Zostera marina* · Habitat suitability · Zonation · Wadden Sea

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Introduction

Seagrass beds have drastically declined during the last century. Most of the recorded declines are attributable to human activity (Short and Wyllie-Echeverria 1996). In the western part of the Wadden Sea, one of the world's largest international marine wetland reserves (approximately 6,000 km²), an area of subtidal and low-intertidal *Zostera marina* L., ranging between 65 and 150 km², was lost during an outbreak of wasting disease in the 1930s (van Goor 1921; den Hartog and Polderman 1975; den Hartog 1987; de Jonge and Ruiter 1996). No old records exist for the eastern and northern Wadden Sea, except for Königshafen in Sylt (Nienburg 1927; Fig. 1). Here also, a subtidal *Z. marina* bed was damaged beyond recovery by wasting disease during the 1930s (Wohlenberg 1935; den Hartog 1987; Reise et al. 1989). At present, approximately 2 km² of *Z. marina* remains in the Dutch Wadden Sea, at Terschelling and in the Ems estuary (D.J. de Jong, unpublished results; Fig. 1). In the German Wadden Sea, *Z. noltii* and *Z. marina* together
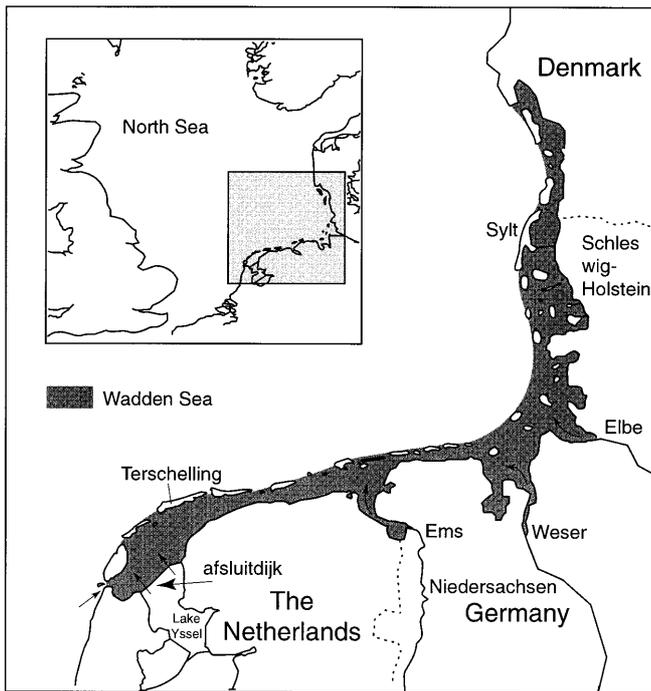
Fig. 1 The Wadden Sea with locations mentioned in the text. Indirect and direct riverine influences are indicated by *arrows*

cover approximately 170 km², and about 30 km² in the Danish part (Reise and Buhs 1991). In 1987, the Ministry of Transport, Public Works and Water Management in The Netherlands initiated the project "Reintroduction of seagrass in the Dutch Wadden Sea". The present literature study is a part of this project.

The presence of potential seagrass habitats is a prerequisite for successful revegetation. Important factors influencing the occurrence of *Z. marina* are: turbidity (e.g. Giesen et al. 1990a,b; van Katwijk et al. 1998), disturbance, which in the Wadden Sea is mainly caused by shellfish exploitation (de Jonge and de Jong 1992), water dynamics (Hermus 1995; Fonseca and Bell 1998; M.M. van Katwijk and D.C.R. Hermus, submitted), sediment dynamics (Boley 1988; Fonseca 1996), degree of desiccation (Harmsen 1936), nutrient level (e.g. Short and Wyllie-Echeverria 1996; van Katwijk et al. 1997) and salinity (Kamermans et al. 1999; van Katwijk et al. 1999).

As well as the role played by wasting disease in the large-scale decline of *Z. marina* in the western Wadden Sea, the construction of the Afsluitdijk dam closed off the Zuyderzee (now the freshwater Lake IJssel) from the Wadden Sea (Fig. 1), altered water dynamics, erosion and sedimentation patterns and increased turbidity temporarily (de Jonge and de Jong 1992). Furthermore, two subsequent years with a considerable deficit of sunlight occurred (Giesen 1990). There is no consensus over which of these events (or combination of events) caused the decline in seagrass beds (see review in den Hartog 1996; de Jonge et al. 1996). The main causes for the lack of recovery of eelgrass stands in the Dutch Wadden Sea were thought to be high turbidity and disturbance caused

by shellfish fishing (van den Hoek et al. 1979; Giesen et al. 1990a,b; de Jonge and de Jong 1992). Also, in the northern part of the Wadden Sea, the same three factors coincided with *Z. marina* losses: the outbreak of wasting disease (Wohlenberg 1935), sunlight deficit in spring (Giesen 1990), and the construction of the Hindenburg dam in 1927, although the latter had less impact than the construction of the Afsluitdijk dam, as it was built on tidal flats and no large channels were dammed.

In the present study, knowledge about the habitat requirements of *Z. marina* was derived from published results of laboratory, mesocosm and field experiments. This was used to construct a conceptual model which assessed the influence of the relevant factors on the potential habitats of *Z. marina* along a tidal gradient in the Wadden Sea. The model considered the physical, chemical and biological properties of the Wadden Sea.

The model creates a basis for the selection of potential sites for restoration, and for measures and policies to increase the chance of successful restoration of *Z. marina*. Moreover, the likelihood of a natural recovery of *Z. marina* will be discussed on the basis of the model.

Zonation of *Z. marina* in the Wadden Sea

In the 1930s, Harmsen (1936) investigated *Z. marina* at several locations in the Wadden Sea. Two *Z. marina* zones, separated by a large bare strip of sediment, were noted. This was also observed by Nienburg in Königshafen, Sylt, Germany (in Wohlenberg 1935; Reise et al. 1989). The zones are inhabited by different morphotypes of *Z. marina* (Fig. 2), and can be described as follows:

1. *Z. marina* beds in the intertidal zone (around mean sea level, the mid-intertidal zone), consist mostly of annual plants. When exposed, the plants lay flat on the moist sediment, and so are protected against desiccation (Harmsen 1936). The degree of desiccation during low tide determines the upper limit of *Z. marina* occurrence (Hermus 1995; Leuschner et al. 1998). The lower end of this zone is most probably limited by higher water dynamics (Hermus 1995; M.M. van Katwijk and D.C.R. Hermus, submitted; Fig. 2).
The tidal depth of the upper limit varies between mean sea level and 30 cm above it (Schellekens 1975 and unpublished Rijkswaterstaat results; Boley 1988; Hermus 1995) and was even higher before the closure of the Zuyderzee in 1932 (Harmsen 1936). The lower limit is maximally situated a few decimetres below mean sea level (Harmsen 1936; Schellekens 1975; Boley 1988; Hermus 1995; de Jonge et al. 1996). Only in sheltered areas (Königshafen) it may have extended to the low tide line (Nienburg 1927).
2. *Z. marina* in the low intertidal to subtidal zone are perennial plants (van Goor 1919; Harmsen 1936). Harmsen (1936) observed throughout the Wadden Sea that this zone never occurred more than 0.20 m above mean low tide. The plants were more robust than the
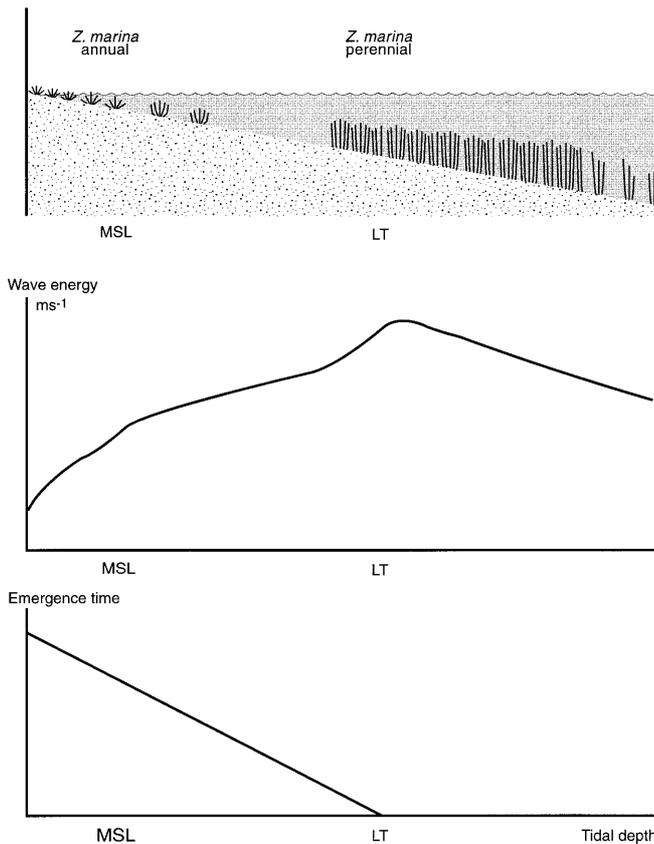
Fig. 2 Zonation of *Z. marina* in the Wadden Sea in relation to emergence time during low tide (*LT*) and wave energy (orbital velocity at the sediment surface, based on model calculations by M. van Helvert and D.J. de Jong). The shape of the wave energy profile is independent of slope, fetch and tidal range, although the height of the profile varies depending on these factors. With increasing wind velocity the maximal wave energy shifts down from –0.1 m to –0.4 m below low tide during severe storms. *MSL* Mean sea level

annual forms, and possessed stiff sheaths that could not lie flat on the sediment. The plants tolerated only short periods of emersion before the sheaths desiccated (Harmsen 1936). This morphotype of *Z. marina* protruded maximally one or two decimetres above low tide (van Goor 1920; Wohlenberg 1935; Harmsen 1936). Recent calculations with old data suggest that about half these plants were located above low tide level and the other half below it (de Jonge and Ruiter 1996). The lower limit of this zone was probably determined by light limitation and strong currents (e.g. Oudemans et al. 1870).

Using the model, this means that at most locations in the Wadden Sea, a bare intertidal zone exists which is not suitable for Z. marina growth. This zone is located somewhere between mean sea level and low tide and its width varies, depending on water dynamics and degree of desiccation. Water dynamics in this bare zone are too high for the mid-intertidal morphotype, and the robust morphotype from the lower zone will desiccate during prolonged periods of low tide.

Areas with reduced water dynamics are an exception to this proposition. For example, the population at "de Plaat", Terschelling (Fig. 1) is located at –0.50 m mean sea level. This tidal flat is protected by embankments. Also, in areas with barriers which retain water at all tidal levels, the robust morphotype of *Z. marina* may extend to higher levels, as has been observed in Roscoff, France (van Katwijk 1992). In Königshafen, in the German Wadden Sea, a permanent water layer of a few centimetres covers the intertidal flats. However, the robust morphotype of *Z. marina* was not encountered here (Wohlenberg 1935). Probably, the sheaths would have still protruded above the water surface and desiccated.

The extent of genetic differentiation between these morphotypes is unknown. In the United States, some genetic differentiation between intertidal (not necessarily annual) and subtidal populations was found with regard to aspects of habitat response, morphology, and DNA sequence (McMillan and Phillips 1979; Backman 1991; Fain et al. 1992; Alberte et al. 1994), although limited gene flow may occur (Laushman 1993). Along the North Atlantic coast, seeds from perennial plants developed into annual plants and vice versa, although 90–95% of the seeds developed into plants of the parent morphotype (Keddy and Patriquin 1978).

In the Wadden Sea, reciprocal transplantation experiments between high intertidal and subtidal populations were carried out by Harmsen (1936). He used intertidal seedlings, but subtidally he could only find mature plants, so he used rhizome cuttings with young shoots for his transplantations (bare root). The transplanted seedlings were lost in the subtidal zone, whereas they survived in the intertidal zone. The transplanted subtidal plants died in the intertidal environment, but survived in the subtidal. These results may indicate genetic differences, but there is also another possible explanation: the sheaths of subtidally-raised plants were probably already too stiff and desiccated in the intertidal area. When raised in the intertidal zone from seed, this might not have happened. The loss of seedlings originating from the intertidal that were transplanted to the subtidal, may have been caused by high water dynamics or shading by other plants. This is supported by the absence of seedlings in natural subtidal *Z. marina* beds in the Dutch Wadden Sea (van Goor 1919). A mesocosm experiment, using five west European populations originating from subtidal and intertidal populations, showed partial reductions in morphological, physiological and reproductive differences after transplantation to the mesocosm, suggesting both phenotypic plasticity and genetic differentiation (van Katwijk 1992; van Katwijk et al. 1998).

Dynamics and desiccation

The term dynamics entails both water and sediment dynamics. Figure 3 depicts the causes and consequences of increased dynamics. Increased dynamics occur mainly as a consequence of disturbances like increased construc-

Fig. 3 Causes and consequences of increased dynamics in the Wadden Sea
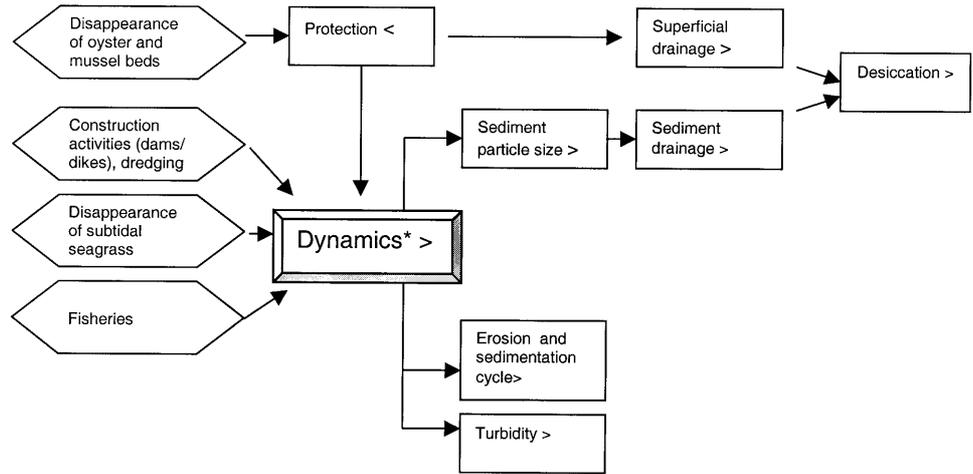
*Sediment and/or water dynamics

tion and fishery activities, and the disappearance of subtidal seagrass beds. Water dynamics affect a number of other parameters. Firstly, increased water dynamics may result in increased sediment dynamics, intensified sedimentation and erosion cycling, until a new equilibrium between bottom morphology and water dynamics has been reached (de Jonge 1983). Secondly, an increased suspension of fine material may occur, subsequently resulting in increased turbidity and a larger average grain size of the sediment (e.g. Ehlers 1988). The latter may increase water drainage and so lead to the rapid desiccation of plants in the intertidal zone during low tide (Fig. 4).

Dynamics

The importance of low water dynamics, both wave energy and current velocity, to seagrass distribution in the western Atlantic is well documented (e.g. Fonseca and Bell 1998). In the Wadden Sea, it is likely that water dynamics directly determine the lower limit of the high *Z. marina* belt (M.M. van Katwijk and D.C.R. Hermus, submitted).

Increased erosion and sedimentation negatively affect *Z. marina* establishment. On the west coast of the United States, it is suggested that erosion rates of 0.5 mm day^{-1} and burial rates of 0.3 mm day^{-1} are the limits for *Z. marina* survival (Merkel 1992, in Fonseca et al. 1998). However, little is known about detrimental erosion and sedimentation rates in the Wadden Sea. To our knowledge, only one study, performed in the German Wadden Sea, dealt with this subject. It was found that *Z. marina* disappeared when the sedimentation rate exceeded 1 cm year^{-1} on average, over a period of 13 years (Boley 1988).

Oyster beds disappeared in the intertidal zone of the Wadden Sea at the beginning of the twentieth century. Stable mussel beds disappeared around 1990, except
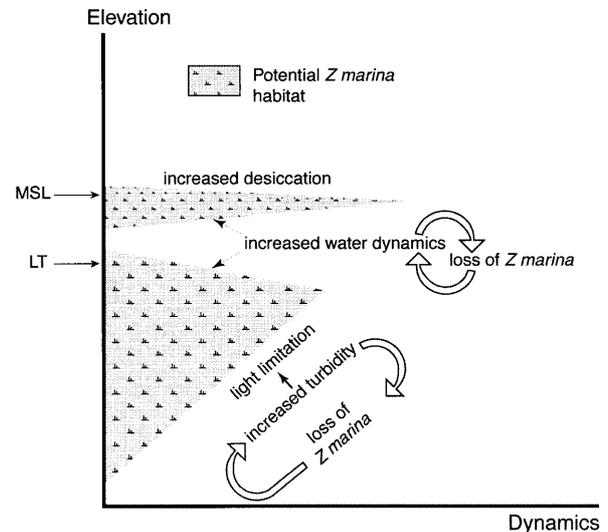
Fig. 4 Potential *Z. marina* habitats in relation to dynamics and related factors (see Fig. 3 and text). *MSL* Mean sea level, *LT* low tide

for a few in the German Wadden Sea (Beukema 1992; Rudfeld 1992; Dankers 1993; Nehls and Thiel 1993; Beukema and Cadée 1996; Reise 1998b). Stable, elevated oyster and mussel beds act as effective wave-breaks, especially when located around low tide level (Consemulder 1984; van der Linden 1985). Their decrease may therefore have contributed to an increase in wave dynamics, resulting in an upward shift of the lower limit of the high belt of potential *Z. marina* habitats (Fig. 4). Secondly, the removal of mussel beds around 1990 resulted in increased phytoplankton blooms, which increased turbidity (Beukema and Cadée 1996).

In the western Wadden Sea, water dynamics changed following the closure of the Zuyderzee. Since then, the tidal amplitude has increased by 0.3–0.5 m (Thijsse 1972; de Jonge and de Jong 1992). Furthermore, the clo-

sure of the Zuyderzee resulted in a change in the locations of the channels and, as a consequence, altered erosion and sedimentation patterns. Turbidity also increased temporarily (Thijsse 1972; van den Hoek et al. 1979; den Hartog 1987; Glim et al. 1987; Ehlers 1988; de Jonge and de Jong 1992). In other parts of the Wadden Sea, the construction of dams and dykes have had similar effects (e.g. Asmus and Asmus 1998; Reise 1998a).

Desiccation

The Wadden Sea sediments have become coarser, as a result of (1) the loss of vast areas of *Z. marina* (Rasmussen 1977; Fonseca 1996), (2) the extensive coastal engineering works in the south-west of The Netherlands that have resulted in a reduced transport of fluvial mud to the sea (de Jonge et al. 1993), and (3) the increased intensity of land reclamation and dyke construction activities during the last century (e.g. Flemming and Nyandwi 1994). Increased sediment grain size, and the rapid superficial run-off of tidal water due to the disappearance of elevated mussel beds, may have resulted in an increased degree of desiccation of the sediment surface during low tide (Fig. 3). A more rapid desiccation in the intertidal zone will result in a downward shift of the upper limit of the low *Z. marina* belt (Fig. 4).

Conclusion

The effects of the direct and indirect consequences of altered dynamics on potential *Z. marina* habitats along the tidal gradient are depicted in Fig. 4. The horizontal axis "dynamics" includes water dynamics, sediment dynamics and the derived effects, grain size of the sediment, turbidity and the degree of desiccation. We have assumed that increased water dynamics will also affect the upper limit of the low *Zostera* belt, as the zone just below low tide experiences the highest wave energy at the sediment surface (Fig. 2). We speculate that increased water dynamics may reach a level that is too high even for these robust *Z. marina* plants, to withstand. In this case, we conclude that the disappearance of *Z. marina* belts will begin at the upper limit of this zone (Fig. 4).

Nutrients, salinity, turbidity and direct disturbance

Nutrients

Z. marina is adapted to low nitrogen concentrations (Borum et al. 1989; Hemminga et al. 1991; Pedersen and Borum 1992). Enrichment of the water column, with either nitrate, ammonium or phosphate, or a combination of these, can lead either to increased growth of *Z. marina* (Harlin and Thorne-Miller 1981; Bohrer et al. 1995), or to negative effects on its growth or productivity (Burkholder et al. 1992, 1994; Neckles et al. 1993;
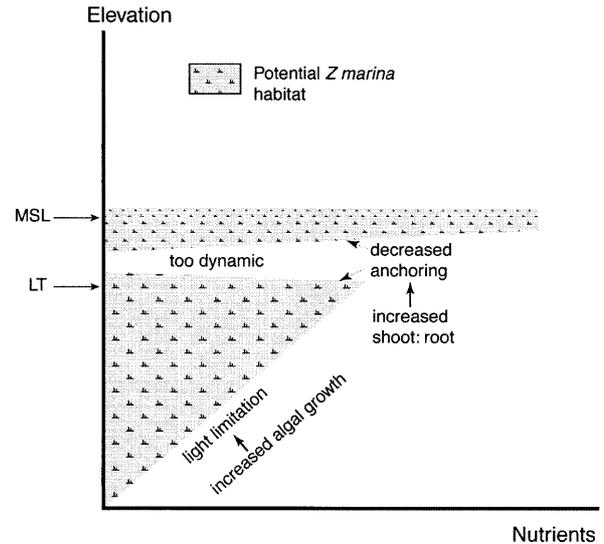
Fig. 5 Potential *Z. marina* habitats in relation to nutrients

Williams and Ruckelshaus 1993; Taylor et al. 1995; Boynton et al. 1996; Nelson and Waaland 1997; van Katwijk et al. 1997). The effects may be direct (Burkholder et al. 1992, 1994; van Katwijk et al. 1997) or indirect, as a consequence of light limitation or oxygen deprivation due to increased algal growth (Neckles et al. 993; Williams and Ruckelshaus 1993; den Hartog 1994; Harlin 1995; Short et al. 1995; Taylor et al.1995). Figure 5 shows the direct and indirect effects of nutrient enrichment on *Z. marina* along the tidal gradient in the Wadden Sea.

In general, experimental nutrient enrichment of sediments has positive effects on *Z. marina* (Orth 1977; Short 1983; Roberts et al. 1984; Short 1987; Kenworthy and Fonseca 1992; Murray et al. 1992; Williams and Ruckelshaus 1993; van Lent et al. 1995). However, in many cases, nutrient enrichment of the total system (increased loads) leads to the disappearance of *Z. marina* (e.g. Taylor et al. 1995; Boynton et al. 1996; Short and Wyllie-Echeverria 1996). It seems that prolonged exposure to increased nutrient loads has a negative effect on *Z. marina*, whereas temporary increases have a stimulating effect. N-enrichment of the water layer affects *Z. marina* negatively. Leaves, unlike roots, cannot regulate N uptake, and assimilation requires energy from the plant (see van Katwijk et al. 1997).

The processes that contribute to eutrophication are related to increased human populations and have significantly increased with industrialisation, and these were further accelerated when artificial fertilisers were introduced. In the Wadden Sea, nutrient loads increased until the mid-1980s, as a consequence of increased inputs of riverine origin (e.g. de Jonge and Postma 1974; Höpner 1991; de Jonge 1997). Nutrients reach the Wadden Sea directly from Lake IJssel, the Rivers Ems, Weser and Elbe, and indirectly from the River Rhine via the Dutch coastal zone (Fig. 1).

Secondly, internal eutrophication occurs as a consequence of mineralisation processes. These processes are driven by the input of organic matter (Postma 1966), for which the Wadden Sea acts as a sink (e.g. Postma 1954). The result of mineralisation is increased levels of N (Helder 1974) and P (de Jonge and Postma 1974). The input of living and dead organic matter into the Wadden Sea has increased, mainly due to increased phytoplankton levels in the coastal zone of the North Sea. (de Jonge and Postma 1974; de Jonge 1990; de Jonge et al. 1993). Thirdly, the nutrient load of the Wadden Sea has increased due to a 2- to 4-fold increase of the atmospheric deposition of N, assuming an original load of 5 kg N ha^{-1}year^{-1} (de Jonge and van Meerendonk 1990; Isermann 1990; Houdijk and Roelofs 1991; Schlünzen 1994; Mansfeldt and Blume 1997).

Since the 1980s, nutrient levels in the Wadden Sea have stabilised or decreased, although in the more unspoilt areas in the north, an increase has been measured in recent years (Martens 1989a,b; Bakker et al. 1991; Schneider and Martens 1994; de Jonge 1997; Martens and Elbrächter 1998).

Increasing nutrient loads in the Wadden Sea will have consequences for potential Z. marina habitats. In cases where increased algal concentrations decrease light penetration, the depth limit for the lower Z. marina belt may rise (e.g. Taylor et al. 1995). Secondly, the high Z. marina belt may be hindered by the increased amount of opportunistic macroalgae such as Ulva spp. and Enteromorpha spp., that can suffocate the plants (den Hartog 1994). In both belts, N loads may eventually become toxic (Burkholder et al. 1992, 1994; van Katwijk et al. 1997) (Fig. 5).

Frequently, increased nutrient concentrations in nutrient-limited aquatic systems result in an increased shoot:root ratio of water plants (e.g. Roelofs et al. 1984, 1994). In Z. marina, this was found in a field experiment in which the sediment was enriched with ammonium (van Lent et al. 1995). In another field study, Short (1983) observed that root development and the number of root hairs were lower when sediment ammonium concentrations were high, as compared with low sediment ammonium concentrations. As a consequence of the increased shoot:root ratio, anchoring ability decreases, making the plants more vulnerable to water dynamics. Therefore, the zone where no Z. marina growth is possible due to increased water dynamics is expected to widen (Fig. 5).

In the high Z. marina zone, the plants can probably tolerate the adverse effects of water quality better than when the plants are permanently submerged, because the plants are exposed to the water for a shorter period (during high tide). During low tide, they remain photosynthetically active as long as the leaves remain moist (Leuschner and Rees 1993). Therefore, we assume that the low Z. marina belt will disappear at lower nutrient loads than the high Z. marina belt (Fig. 5).
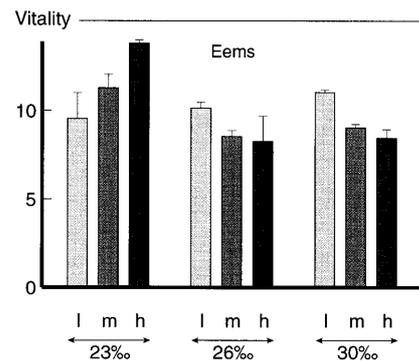
Fig. 6 Vitality of Z. marina originating from an intertidal estuarine bed in the Eems estuary, after 6 weeks at three different combinations of salinity and nutrient loads: l low, m medium, h high nutrient load (N:P, 20:20, 95:45, 625:100 kg ha^{-1}year^{-1}, respectively). Means (columns) and SEM (bars) are indicated

Salinity

High (near-marine) salinity is unfavourable to Z. marina (Kamermans et al. 1999; van Katwijk et al. 1999). Assuming that plants living in unfavourable conditions will tolerate less stress from other factors, high salinity will magnify the negative effects of high water dynamics and high nutrient concentrations. Van Katwijk et al. (1999) found an interaction between salinity and nutrients; at a salinity of 26 or 30 PSU, a moderate nutrient enrichment of the water layer had a negative effect, while the same nutrient application had a stimulating effect at a lower salinity (Fig. 6). "Vitality" in Fig. 6 is a combined factor derived from the number of shoots, size, necrosis and number of missing leaves (van Katwijk et al. 1999). At high salinity, Z. marina performed well when nutrient loads were low. This finding is reflected in the distribution pattern of Z. marina in The Netherlands where it is absent at high nutrient loads, except where salinity is low (van Katwijk et al. 1999).

Although some adaptation to high salinity, genetically or phenotypically, is likely (van Katwijk et al. 1998; Kamermans et al. 1999), we hypothesise that Z. marina will still be more vulnerable to other stress factors when subjected to high salinity. Salinity-stressed plants, having a lower growth rate (Kamermans et al. 1999) will not be able to use the extra nutrients for growth (Pedersen 1995). These surplus nutrients will actually burden the plants (Burkholder et al. 1992, 1994; van Katwijk et al. 1997, 1999). This hypothesis concerning potential habitats with regard to salinity and nutrients is depicted in Fig. 7. We assumed that the plants will respond to nutrients in a bell-shaped gaussian manner (log-transformed – see Slob 1987) at each salinity level.

The salinity regime of the Dutch Wadden Sea changed after the closure of the Zuyderzee in 1932. Based on yearly averages, salinity has decreased since 1932 (van der Hoeven 1982). However, the estuarine gradient was replaced by a variable salinity regime, with the input of fresh water being regulated by sluices. In the
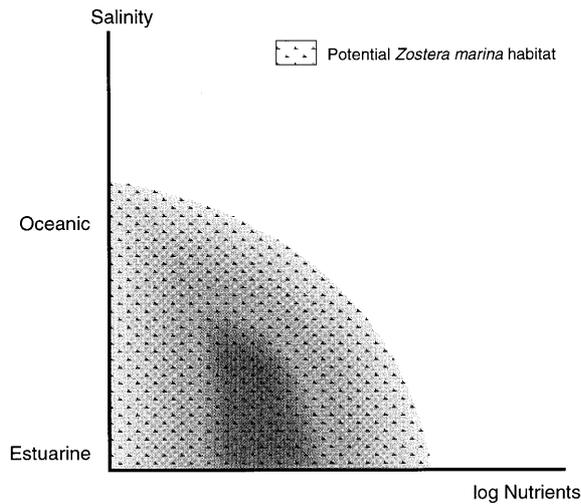
Fig. 7 Interactive effect of nutrients and salinity on potential *Z. marina* habitats, deduced from a laboratory experiment and field observations (van Katwijk et al. 1999). *Darker shading* indicates greatest *Z. marina* vitality

Fig. 8 Conceptual model of the potential *Z. marina* habitats (*shaded*) along a tidal gradient in the Wadden Sea, in relation to dynamics (sediment and water dynamics and related factors, turbidity, grain size and degree of desiccation), and the interactive effect of nutrients (direct and indirect effects of the enrichment of the total system) and salinity. *MSL* Mean sea level, *LT* low tide

northern Wadden Sea (Königshafen, Sylt), salinity was greater in the early 1990s than in the early 1980s (Schneider and Martens 1994).

Turbidity

Turbidity can increase due to (1) increased phytoplankton growth and (2) increased water/sediment dynamics (see previous paragraphs). Increases in turbidity during the twentieth century are thought to be the main reason for the lack of recovery of *Z. marina* in the Dutch Wadden Sea (van den Hoek et al. 1979; Giesen et al. 1990a,b; de Jonge and de Jong 1992). At present, turbidity has decreased (de Jonge and de Jong 1992; de Jonge et al. 1996). A mesocosm experiment with *Z. marina* plants originating from Terschelling and Sylt showed that light was not limiting to a depth of at least –0.80 m mean sea level, assuming a tidal range of 1.80 m (van Katwijk 1992; van Katwijk et al. 1998), provided that the average turbidity factor k is less than 1.5 m^{-1}. This has been the case in the Dutch Wadden Sea since 1989 (de Jonge et al. 1996) This was supported by calculations by de Jonge and de Jong (1992). To our knowledge, no information is present about trends in turbidity in the German and Danish Wadden Sea.

At locations where the depth limit of the low *Z. marina* belt is determined by light limitation rather than by the presence of channels with strong currents, increased turbidity will result in an upward shift of the depth limit of the low *Z. marina* belt. When the downward expansion of the low *Z. marina* belt is limited by the presence of a channel, increased dynamics in this channel may also shift the lower limit of *Z. marina* upwards (Figs. 4 and 5).

Direct disturbance

Fishery activity directly removes seagrass beds (de Jonge and de Jong 1992; van Katwijk 1993; de Jonge et al. 1997) and is unrelated to tidal depth. In the Wadden Sea, direct disturbance of *Zostera* is mainly caused by shellfish exploitation, e.g. mussel seed and cockles. Increased fishery activities during the twentieth century have contributed to the lack of recovery of *Z. marina* beds in the lower intertidal and subtidal zones (de Jonge and de Jong 1992). At present, shellfishing is prohibited in some areas of the Wadden Sea (Essink 1992; Rudfeld 1992; Philippart 1993; Wonneberger 1996; Borchardt 1997).

Conceptual model for potential *Z. marina* habitats in the Wadden Sea

Model

The previously discussed effects of dynamics, desiccation, nutrients and turbidity on the distribution of *Z. marina* over a tidal gradient are summarised in Figs. 4 and 5. The interactive effect of salinity and nutrients is shown in Fig. 7. We have integrated these "modules" into one conceptual model, depicted in Fig. 8. The axis "dynamics" is the same as that shown in Fig. 4, and involves water dynamics, sediment dynamics and derived effects, grain size of the sediment, turbidity and the degree of desiccation. The axis "nutrient*salinity" represents the interactive (multiplicative) effect of nutrients

and salinity: plants growing at near-marine salinity are negatively affected at moderately high nutrient loads, whereas at lower salinity, the plants tolerate much higher nutrient loads and their growth can even be stimulated. Direct disturbance caused by fishing activities was not integrated in the model as it acts on a local scale and is not related to tidal depth.

In Fig. 8, the environmental changes in the Wadden Sea during the twentieth century are indicated with an arrow in the direction of increasing dynamics, and increasing nutrients*salinity. In the western Wadden Sea, the latter is a consequence of increased nutrient loads, not salinity. Salinity in the western Wadden Sea has slightly decreased on average, but the degree of variation has increased (van der Hoeven 1982). Nutrients and salinity have both increased in the northern Wadden Sea (e.g. Schneider and Martens 1994). The several aspects of "dynamics" (Fig. 3) have also increased in the Wadden Sea.

The conceptual model shows that the complex interaction between increased dynamics, degree of desiccation and nutrient loads in the Dutch Wadden Sea during the last century have reduced the number of potential Z. marina habitats. In fact, all Z. marina beds around low tide and deeper were lost in the 1930s, coinciding with a disease epidemic, and these beds have failed to recover. Also, intertidal Z. marina beds have suffered in the Wadden Sea, but at a much later date (den Hartog and Polderman 1975; de Jonge et al. 1996; Kastler and Michaelis 1997; Reise 1998c).

Present situation in the Wadden Sea
and potential Z. marina habitats

Since the end of the 1980s, the turbidity of the Wadden Sea has decreased, nutrient levels have decreased or stabilised, and shellfish fisheries have been prohibited in some areas (see previous paragraphs; Table 1).

Potential Z. marina habitats in the Dutch Wadden Sea are located above approx. −0.80 m mean sea level (when the turbidity remains at the same level as in the early 1990s). In the northern Wadden Sea, potential habitats are situated below −0.80 m, as turbidity is lower. Furthermore, potential habitats are located in undisturbed, sheltered locations, preferably where some freshwater influence is present (e.g. in estuaries, near local freshwater sources or in groundwater upwelling zones). At locations with a near-marine salinity, the present nutrient load is probably too high to allow the growth of Z. marina in most parts of the Wadden Sea (van Katwijk et al. 1999). The sediment should retain enough water during low tide to keep the plants moist, e.g. sand containing some mud (without being unstable), or the presence of barriers. In general, areas with a diverse geomorphology are suitable for Z. marina, as this provides shelter and prevents rapid water runoff.

Our model suggests that the area of habitats suitable for Z. marina can be increased by a (further) decrease in

Table 1 Restoration of Z. marina habitats in the Wadden Sea

Factor	Requirement	Present situation in the Wadden Sea	Reference	Recommendations
Dynamics and desiccation	<	In The Netherlands, plans are discussed to restore stable mussel banks	Faber (1999)	Construction of stabilisation devices or barriers (artificial, and/or stable mussel or oyster banks)
Nutrients	<	Generally reduced recently, although increased in the north / Still high in comparison with the beginning of the twentieth century	Martens (1989a,b), Schneider and Martens (1994), de Jonge (1997), Martens and Elbrächter (1998) Isermann (1990), Höpner (1991), de Jonge et al. (1993), de Jonge (1997)	Further reduction
Salinity	<	Some decline, although more fluctuation in The Netherlands / In N Germany an increase / In The Netherlands, plans are discussed to restore the estuarine gradient	van der Hoeven (1982) Schneider and Martens (1994) Anon. (1998)	Restoration of estuarine gradients; stimulation of groundwater influence
Turbidity	$\geq$<	Present turbidity allows Z. marina establishment to at least −0.80 m below mean sea level	van Katwijk et al. (1998)	Further reduction increases chances for subtidal Z. marina
Direct disturbance	<	Shellfishery activities are prohibited in some areas in the Wadden Sea	Philippart (1993), Wonneberger (1996), Borchardt (1997)	Further limitation, with particular avoidance of potential Z. marina habitats

nutrient loads, an increase of freshwater influence (e.g. restoration of estuarine gradients), a (further) decrease in activities that rework the sediment surface (fishery on mussel seedlings, mussel culture, cockle fishing, mining of shells and sand). The enhancement of geomorphological diversity would also aid *Z. marina* recovery. This could be achieved by the application of stabilisation measures such as the recovery or restoration of stable mussel banks at low tide level. Increased geomorphological diversity would reduce water dynamics and grain size of the sediment, and increase the water retention capacity of the area, thereby preventing desiccation of plants. Table 1 summarises these recommendations.

Natural or active restoration of *Z. marina*

Some processes causing *Z. marina* disappearance are accelerated by the loss of *Z. marina* itself. Among restoration ecologists, and increasingly among conservation ecologists, it is recognised that thresholds may exist in the process of degradation, where crossing a threshold precludes the return to an undegraded state without management intervention (see review in Hobbs and Norton 1996). This is probably the case for *Z. marina*. Once the bed is lost, turbidity and erosion from non-stabilised sediments and/or increased water dynamics will impair natural recovery (see Fig. 4; Fonseca et al. 1998). The return of the plants may only be possible after several consecutive years of favourable climatic circumstances at undisturbed locations; however, the time-scale required is still unknown (e.g. den Hartog 1996; Fonseca et al. 1998). Moreover, natural populations in the Wadden Sea are located in the middle, eastern and northern part. However, the prevailing winds are westerly, so propagules will have severe difficulty in reaching the western area. In general, *Z. marina* seed movement is limited to short distances (Orth et al. 1994). Finally, the genetic variation of the remaining populations may be too low to cope with the unpredictable, dynamic environment of the Wadden Sea. In particular, the morphotypes with stiff sheaths, that formerly covered the lower tidal zone and became extinct in the Wadden Sea, may not evolve from the present mid-intertidal populations.

For restoration aims, it is important to gain more insight into the genetic differences among *Z. marina* morphotypes growing at different tidal levels. If there is strong genetic differentiation in functionally important traits, it will be necessary to use donor populations that are located at approximately the same tidal level as the target location. Also, it is unlikely that an intertidal donor stock transplanted to the intertidal will expand to the lower intertidal and subtidal regions. If genetic differentiation is low, a transplanted bed will have a greater chance of survival when an intertidal and a subtidal bed are created simultaneously: if one of them is destroyed (for instance by ice scour or severe storms) recovery will be possible from the other.

In conclusion, we estimate the chance of natural restoration of mid-intertidal *Z. marina* in the western Wadden Sea on a human time-scale to be low. In other areas, careful site selection and possibly habitat restoration may be sufficient. The chance of natural recovery of *Z. marina* of the lower zone depends upon the ability of the present populations to adopt the morphology that is typical for the low *Zostera* belt.

Active restoration of the seagrass beds should be preceded by careful site selection. Natural restoration can only be expected at undisturbed locations, which means that sites having large potential for seagrass establishment should be protected from fishing activities. To serve both ends (active as well as natural restoration), it is essential to quantify the presented conceptual model, 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. Combining this model with the information used in the conceptual model presented here would provide a valuable policy instrument.

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