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Wax and wane of *Zostera noltii* Hornem. in the Dutch Wadden Sea

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Abstract

The distribution, coverage and area of *Zostera noltii* Hornem. were studied in the four main seagrass stands in the intertidal zone of the Dutch Wadden Sea, two off the island of Terschelling and two in the sedimentation fields off Groningen. In addition, the actual seagrass stands and their close surroundings were mapped for several biotic and abiotic environmental factors, which were thought to be relevant to the past and present distribution of *Z. noltii*, viz. coverage by macroalgae, lugworm density and sediment composition.

Compared with earlier findings on distribution of seagrass in the Dutch Wadden Sea, the total area of *Z. noltii* almost doubled between the beginning of the 1970s and the end of the 1980s. This increase is mainly due to the rapid re-establishment of seagrass in the outer sedimentation fields of the salt-marsh works off Groningen after a change of management. The total area of *Z. noltii* on the tidal flats off Terschelling decreased by approximately 20%.

At the Terschelling seagrass stands, the coverage of seagrass was positively related to the clay content of the sediment and negatively to the density of lugworms (*Arenicola marina* L.). The presence of macroalgae, however, seems to play a minor role in the distribution of this seagrass species in the Dutch Wadden Sea. In the sedimentation fields off Groningen, almost no significant relationships were found between seagrass and environmental factors studied, which may be due to the fact that these seagrass stands are still expanding.

1. Introduction

The Wadden Sea is a shallow coastal sea along the North Sea coasts of Denmark, Germany and the Netherlands and the largest estuarine area in Europe (10 000 km^2). Its tidal flats

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are the habitat of two seagrass species, viz. *Zostera noltii* Hornem. and *Zostera marina* L. (eelgrass). The latter was the most abundant seagrass species in the Dutch part of the Wadden Sea before 1930, occurring at that time in the intertidal as well as in the subtidal zone. However, it started to decline in 1932, most probably as the result of a wasting disease (Short et al., 1988). Since 1938, this seagrass species occurred only in intertidal areas, and it never recovered in the subtidal zone (Den Hartog, 1994). *Z. noltii* was less affected by the disease (Vergeer and den Hartog, 1991) and became the most abundant seagrass species of the Dutch Wadden Sea due to the decline of *Z. marina*. At the beginning of the 1970s (Den Hartog and Polderman, 1975), however, the stands of *Z. noltii* also started to decline. Unfortunately, little is known about the dynamics of this seagrass species in the Dutch Wadden Sea after 1970. Jacobs et al. (1983) reported a further decrease of seagrass stands in the mid 1970s, but they give detailed information only for a part of the area. Dijkema et al. (1989b) presented a map of the overall distribution of seagrasses at the end of the 1980s, but no information on the total area covered is supplied. In order to examine the historical changes in the abundance of *Z. noltii* in the Dutch Wadden Sea during the last 15 years, the areas covered by seagrass stands at the end of the 1980s were compared with those found in earlier years.

In addition, it was examined which environmental factors may be held responsible for the present patterns as well as the changes in distribution since the 1970s. In the Wadden Sea, the presence of *Z. noltii* is related to the period of emersion, sediment type, sediment stability and geographical area (Philippart et al., 1992). Other possible environmental factors involved in the distribution of this seagrass species are the presence of macroalgae and lugworms (*Arenicola marina* L.). Mass development of macroalgae probably caused a recent decline of seagrass in the German Wadden Sea (Reise, 1989). Transplantation experiments at a seagrass stand at the tidal flats off Terschelling showed that seagrass was severely affected in the presence of lugworms (Philippart, 1994). The present study describes the recent change in the *Z. noltii* stands in the Dutch Wadden Sea and its possible relations to the mentioned biotic and abiotic environmental factors.

2. Study sites and methods

2.1. Study sites

At present, the *Z. noltii* stands in the Dutch Wadden Sea are located on the tidal flats along the island of Terschelling, viz. at De Keeg-De Ans and off Hoorn, and in the sedimentation fields north of the province of Groningen, viz. at Linthorst Homanpolder and Emmapolder (Fig. 1). In former years, *Z. noltii* was also found at the Balgzand tidal flats in the western Wadden Sea (Fig. 1). This seagrass stand, however, decreased from the 1960s onwards (Polderman and Den Hartog, 1975). The remaining *Z. noltii* population consists now of scattered small (approx. 1 m^2) plots with a summed area of approximately 0.01 km^2 (J.J. Beukema, personal communication, 1991). At present, no other *Z. noltii* stands than the four mentioned above are found in the Dutch Wadden Sea.

The sedimentation fields north of Groningen are part of 60 km^2 of salt-marsh works, where sedimentation and the development of salt-marsh vegetation are artificially stimulated

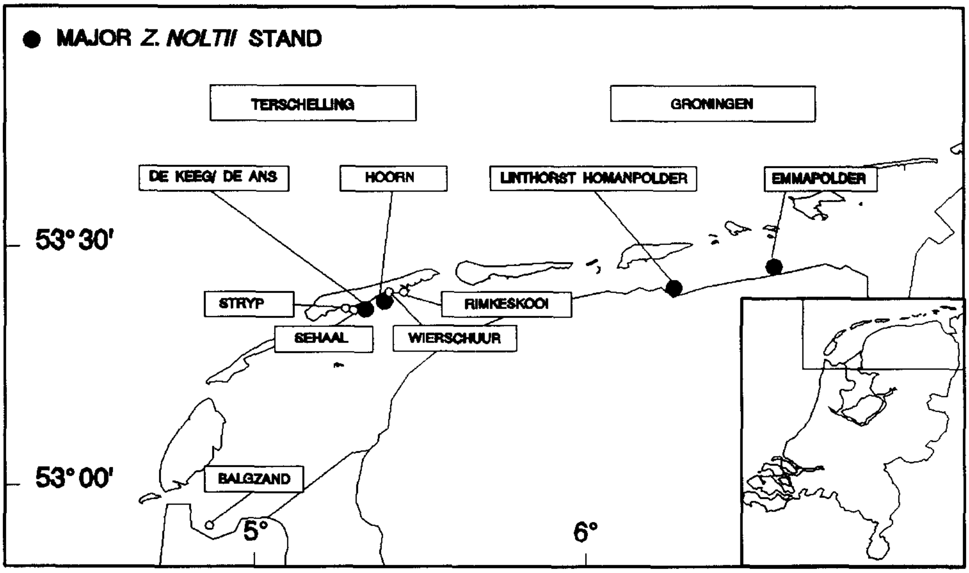


Fig. 1. Overview of study sites of the seagrass *Z. noltii* in 1987/1988 and several other locations in the Dutch Wadden Sea as mentioned in the text.

by means of field drains and brushwood dams (Dijkema, 1983). The fields are separated by brushwood dams perpendicular to the shore, which are 200 or 400 m apart and extend 400 to 1200 m into the Wadden Sea. The dams are numbered by the Ministry of Public Works in such a way that the numbers relate to their mutual distances in steps of 100 m, e.g. the distance between dam numbers 392 and 396 is 400 m. The Linthorst Homanpolder study site is situated between dam numbers 380 and 420, the Emmapolder study site between dam numbers 488 and 520.

2.2. Historical changes

Historical data on the distribution of *Z. noltii* in the Dutch Wadden Sea were obtained from earlier surveys, false-colour photographs, literature (Mörzer Bruijns and Tanis, 1955; Polderman and Den Hartog, 1975; Jacobs et al., 1983; Hootsmans et al., 1986), and by interviewing colleagues and local inhabitants. The data on *Z. noltii* as supplied by Polderman and Den Hartog (1975) were corrected for the presence of *Z. marina* by subtracting the relative area covered by this seagrass species from the total area covered by both seagrass species. The coverage of *Z. noltii* at the Linthorst Homanpolder seagrass stand was estimated for October 1975, June 1981 and August 1983, and of the Emmapolder seagrass stand for August 1983. The seagrass coverage at the study sites of Groningen in 1983 was derived from false-colour photographs, and the data in 1975 and 1981 were collected in the field using the same method as in 1987.

2.3. Mapping

The two Terschelling study sites were mapped walking a sawtooth pattern on the tidal flats. The distance between the turning points of the track was 100 m at most. The coverage of seagrass, macroalgae and lugworm faecal castings, and the sediment type were noted regularly, approximately every 20 m. The position of the sample points was determined with a portable Decca location transmitter (Philips A Navigator MK-4). The accuracy of the position in the field was approximately 20 m, after calibration using fixed points on the seadike. The mapping of the Hoorn study site was restricted to the densest part of the seagrass stand. Scattered plants of *Z. noltii* east of the mapped area beyond the Wierschuur but not as far away as the Rimkeskooi (Fig. 1) were not included.

In the sedimentation fields off Groningen, both study sites were divided into hypothetical squares of 100×100 m^2 each. The mean values of the coverage of seagrass, macroalgae, and lugworm faecal castings, and the sediment type were noted for each square.

2.4. Environmental factors

The coverage of seagrass and macroalgae was classified according to a modified scale of Braun–Blanquet (Westhoff and Van der Maarel, 1973). This classification distinguishes eight classes, namely 0%, < 1%, 1–5%, 6–10%, 11–25%, 26–50%, 51–75% and > 75% coverage. The seagrass distribution was mapped during the months in which the maximal above-ground biomass occurs, i.e. August and September (Jacobs et al., 1983; Vermaat et al., 1987). The Linthorst Homanpolder and Emmapolder study sites were mapped in August and September 1987, respectively, and both study sites on Terschelling in September 1988. The coverage of seagrass was noted for each species separately, but no attempt was made to distinguish between the different species of macroalgae.

The bioturbation by the lugworms is related to their faecal production (Cadée, 1976). Therefore, the relative turnover rate of sediment was estimated as the area covered with faecal castings, applying the same classification in coverage as used for seagrass and macroalgae (Westhoff and Van der Maarel, 1973). At the Terschelling study sites, also the number of lugworm castings per square metre was determined.

The classification of the sediment type was based on the rule of thumb that the sediment can be characterized in the field by determining the depth of the footprints of the observer (Sindowski, 1973; Dijkema, 1991). A footprint depth of less than 5 cm corresponds with sand (< 5% clay particles), 5-10 cm with a muddy sand, and the sediment consists of mud (> 8% clay particles) if the footprint is deeper than 10 cm. As the footprint depth at the Groningen study sites ranged from less than 5 cm to more than 10 cm, it was directly translated into sediment type. However, as the depth of the footprint on the tidal flats of Terschelling was seldom more than 5 cm, most of the area of the study sites of Terschelling was considered to consist of sand. Therefore, the footprint depth on Terschelling was not classified as sediment type, but noted in centimetres.

The period of emersion was calculated by combining information on the local tidal curves (Anonymous, 1976; Anonymous, 1977) with data on the height of the tidal flat levels relative to the Netherlands Ordnance Level (NAP), which is approximately equal to Mean Sea Level (Anonymous, 1988a; Anonymous, 1988b).

The sediment stability of the study sites was measured as the net accretional balance, i.e. long-term net sedimentation and erosion rates (Glim et al., 1988; Dijkema et al., 1992). Unfortunately, no data were available on the short-term sediment movements, which are generally much stronger than represented by net sedimentation or erosion per year.

For each study site, relationships between seagrass coverage, macroalgae coverage, lugworm density and sediment type were tested by means of X-square tests. Classes were pooled until the requirements for testing were fulfilled (Elliot, 1983).

3. Results

3.1. Historical changes

In 1987/1988, all four study sites comprised more or less monospecific *Z. noltii* stands. *Z. marina* occurred only as scattered plants at a density of less than one plant per 10 m^2 on the tidal flats of Terschelling and in the Emmapolder study site. The maximum coverage of the seagrass *Z. noltii* was more than 75% at both study sites on the Terschelling tidal flats (Fig. 2) and between 10% and 25% at the Linthorst Homanpolder and Emmapolder sites (Fig. 2).

On the Terschelling tidal flats (Fig. 1), *Z. noltii* occurred in the 1930s in Stryp, Sehaal, De Keeg-De Ans and Hoorn (Mörzer Bruijns and Tanis, 1955). In 1972 (Polderman and Den Hartog, 1975), however, the Stryp and Sehaal seagrass stands had disappeared and did not return during the following 15 years (personal observations). The two remaining stands showed relatively low values in covered area between 1976 and 1986 (Fig. 3), but from 1986 to 1987/1988 a strong increase was noted. The area of the seagrass stand of De Keeg-De Ans increased by more than 50% between 1972/1973 and 1987/1988, whereas the area of the *Z. noltii* stand of Hoorn decreased by almost 30% (Table 1).

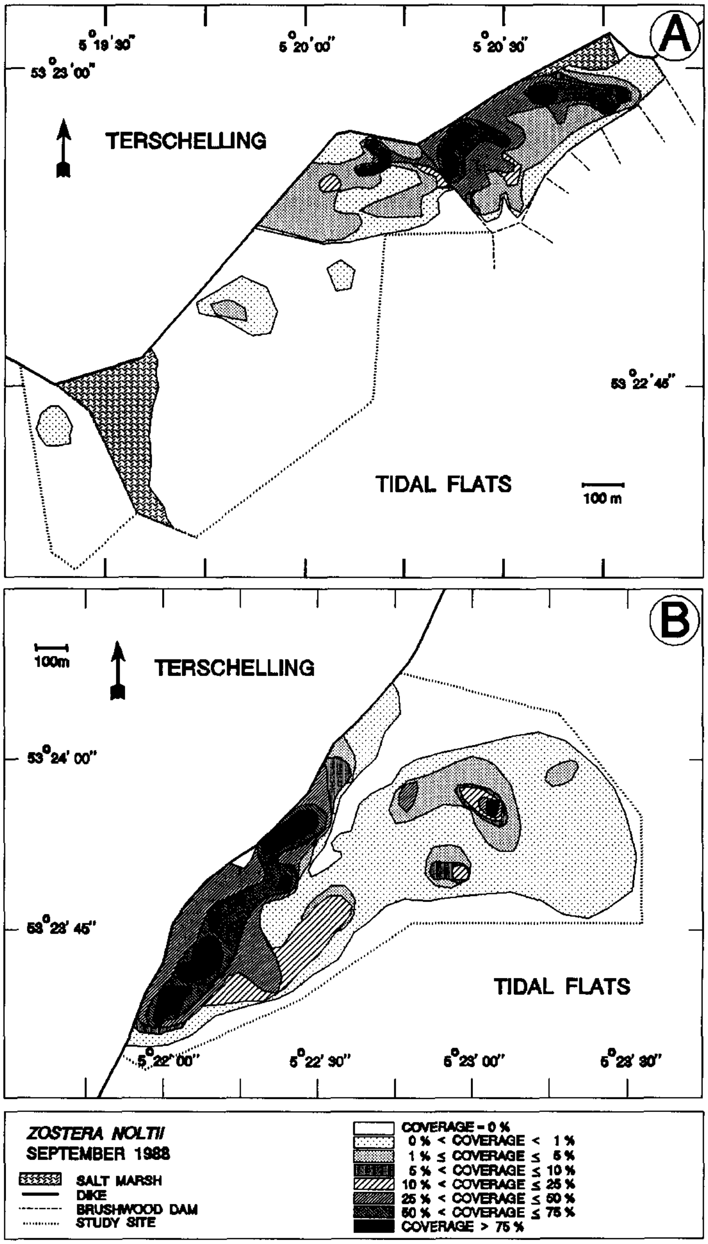
In the sedimentation fields off Groningen, the area of the seagrass stands showed a rapid increase over the past 10 years (Fig. 3). The situation at the beginning of the 1970s is not known exactly. According to P. Bouwsema (personal communication, 1991) no seagrass occurred in or near the salt-marsh works of the Linthorst Homanpolder before 1970, and some seagrass was present in the eastern part of the Emmapolder salt-marsh works from the beginning of the 1970s onwards. Assuming that the seagrass species referred to is *Z. noltii*, it is concluded that the covered area was zero or almost zero in both study sites of Groningen in 1972/1973 (Table 1). After 1975, the seagrass stands increased in a more or less similar way in both study sites (Fig. 3).

The total area covered by *Z. noltii* stands in the Dutch Wadden Sea in 1987/1988 was approximately 2.6 km^2 (Table 1), which is almost twice as much as in 1972/1973. This increase is mainly due to the occurrence of relatively new seagrass stands in the salt-marsh works of Groningen. However, the seagrass in the largest and densest stand of the Dutch Wadden Sea, viz. Hoorn, was severely reduced during this period.

3.2. Environmental factors

The macroalgae coverage was generally less than 1% at the study sites (Fig. 4). Densities of more than 25% coverage only occurred in the De Keeg-De Ans study site, which was due to the presence of two accumulations of macroalgae outside the seagrass stand. No significant relationships between the coverage of *Z. noltii* and macroalgae were found at the other study sites (Table 2).

Lugworms were present inside as well as outside the seagrass stands in all four study sites (Fig. 4). The coverage by faecal castings was highest at the Hoorn study site outside the seagrass stand. The faecal casting coverage in the other three study sites was lower (Fig. 4). On the tidal flats of Terschelling, the distribution of seagrass was negatively correlated with the lugworm faecal castings, i.e. *Z. noltii* was more abundant in areas with a low



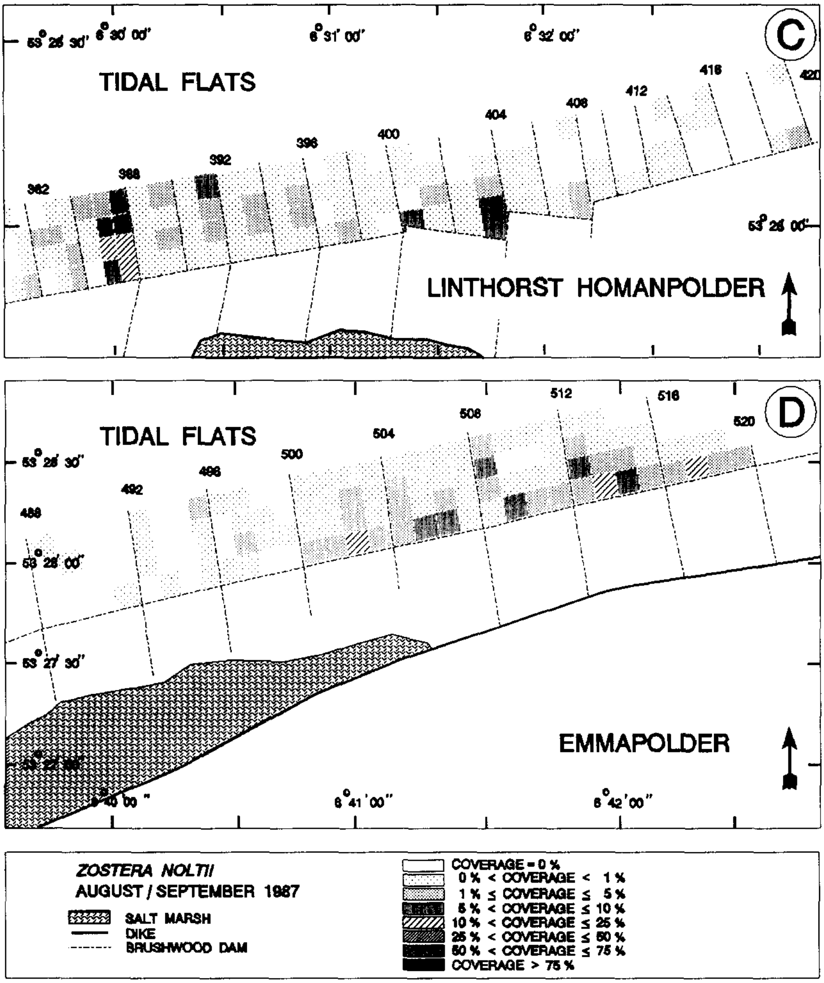


Fig. 2. Coverage of *Z. noltii* in the study sites (A) De Keeg-De Ans and (B) Hoorn on the tidal flats off Terschelling in September 1988. (C) Linthorst Homanpolder and (D) Emmapolder in the outer sedimentation fields of the salt-marsh works off Groningen in August and September 1987, respectively.

coverage of castings than in areas with high casting coverage (Table 2). In the Linthorst Homanpolder study site, however, a positive relationship was found between the coverage of *Z. noltii* and that of the *A. marina* faecal castings (Table 2). The mean density of lugworm faecal castings in the De Keeg-De Ans study site was eight castings per square metre inside and 59 castings per square metre outside the seagrass stand. At the Hoorn study site, these densities measured 24 castings per square metre inside and 54 castings per square metre outside the seagrass stands. If all lugworms present were adults, they should be able (Cadée, 1976) to rework an amount of sediment that is comparable to a layer of approximately 3 cm year^{-1} inside the seagrass stand at De Keeg-De Ans and 9 cm year^{-1} inside the seagrass stand at Hoorn. The sediment reworking capacity of the lugworms on the tidal flats of Terschelling outside these seagrass stands would be approximately 20 cm year^{-1}.

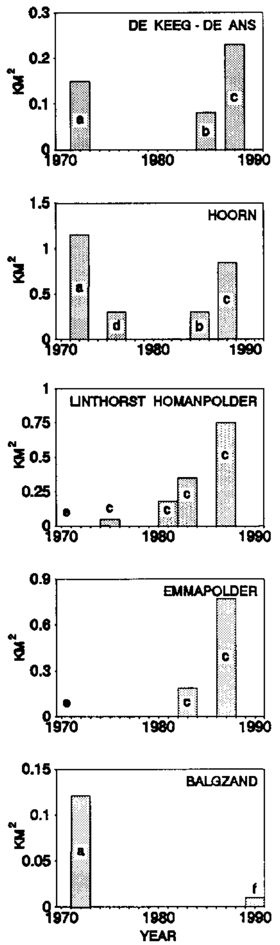


Fig. 3. Historical changes of the area of the main stands of the seagrass *Z. noltii* in the Dutch Wadden Sea from 1970 to 1988 (a) after Polderman and den Hartog, 1975; (b) Hootsmans et al., 1986; (c) present paper; (d) Jacobs et al., 1983; (e) after P. Bouwsema, personal communication, 1991; (f) J.J. Beukema, personal communication, 1991). See also Table 1.

The footprint depth and the coverage of seagrass were positively correlated in both study sites on the tidal flats of Terschelling (Table 2): *Z. noltii* generally occurred in the parts of the tidal flats of Terschelling where the sandy sediment was less coarse than in its surroundings (Fig. 4). Hardly any seagrass occurred in squares classified as mud in the sedimentation fields off the coast of Groningen (Fig. 4). However, the distribution of *Z. noltii* was not significantly related to the sediment type in these areas (Table 2). Footprint depth and the coverage by *A. marina* faecal castings were negatively correlated in both study sites of Terschelling (Table 2): the highest coverage by castings was generally found in the areas with relatively coarse sand (Fig. 4). The relation between sediment type and the coverage by *Z. noltii* and *A. marina* faecal castings could not be tested for the Emmapolder study site because here the testing requirements could not be fulfilled.

Table 1
Area of the stands of the intertidal seagrass *Zostera noltii* in the Dutch Wadden Sea in 1970/1972 and 1987/1988

	Area (km^2) 1972/1973	Area (km^2) 1987/1988
De Keeg-De Ans	0.15[a]	0.23[b]
Hoorn	1.15[a]	0.84[b]
Linthorst Homanpolder	±0[c]	0.75[b]
Emmapolder	±0[c]	0.77[b]
Balgzand	0.12[a]	0.01[d]
Total	1.42	2.60

[a] After Polderman and Den Hartog (1975; corrected for the presence of *Z. marina*.
[b]The present paper.
[c] After P. Bouwsema, personal communication, 1991.
[d] J.J. Beukema, personal communication, 1991.

The long-term accretional balance in the study sites ranged from −0.01 m year^{-1} to +0.02 m year^{-1} on the tidal flats of Terschelling between 1977 and 1983 (Glim et al., 1988), and from −0.02 m year^{-1} to +0.05 m year^{-1} in the Groningen sedimentation fields between 1961 and 1989 (Dijkema et al., 1992). The accretional balance of the western

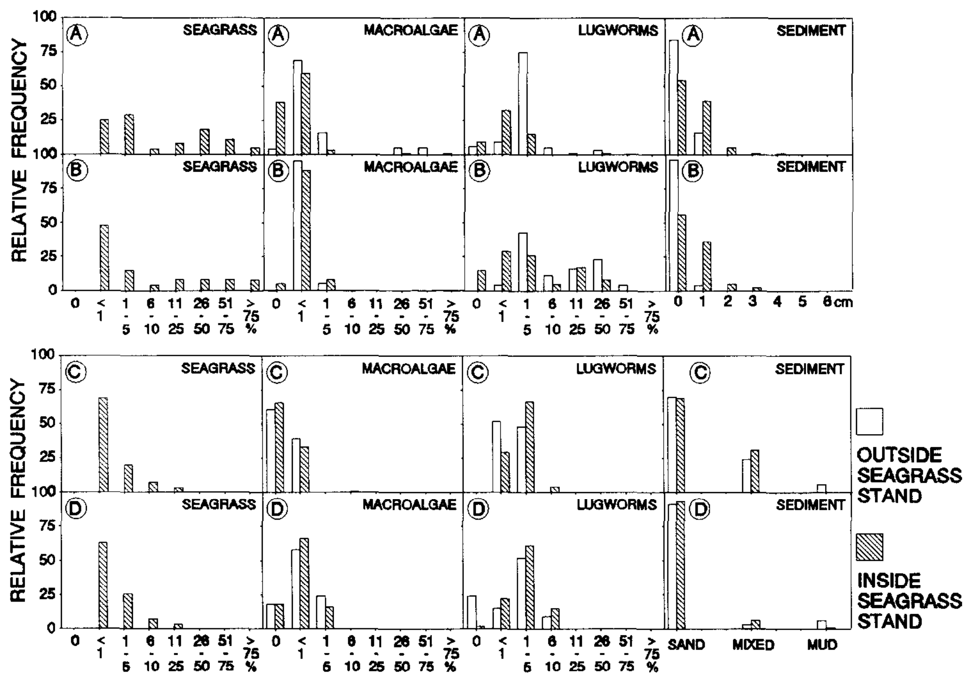


Fig. 4. Relative frequency of the coverage (%) of the seagrass *Z. noltii*, the coverage (%) of macroalgae, the coverage (%) of the faecal castings of the lugworm *A. marina* and sediment type (see text) in the close surroundings of (white bars) and inside (hatched bars) the seagrass stands in the sampling points at (A) De Keeg-De Ans ($n=191$), (B) Hoorn ($n=361$), (C) Linthorst Homanpolder ($n=152$) and (D) Emmapolder ($n=120$) study sites in 1987/1988.

Table 2
Significance of relationships between the coverage (%) of *Z. noltii*, the coverage (%) by faecal castings of *A. marina*, the coverage (%) by macroalgae and sediment type (see text) in the De Keeg – De Ans ($n = 191$), Hoorn ($n = 361$), Linthorst Homanpolder ($n = 152$) and Emmapolder ($n = 120$) study sites in 1987/1988

Study site	Correlation	χ^2	d.f.	*P*
De Keeg-De Ans				
Z. noltii vs. macroalgae	–	63.46	6	***
Z. noltii vs. *A. marina*	–	131.30	6	***
Z. noltii vs. sediment	+	31.48	3	***
A. marina vs. sediment	–	22.29	3	***
Hoorn				
Z. noltii vs. macroalgae	None	5.97	4	ns
Z. noltii vs. *A. marina*	–	142.78	15	***
Z. noltii vs. sediment	+	58.59	7	***
A. marina vs. sediment	–	107.69	6	***
Linthorst Homanpolder				
Z. noltii vs. macroalgae	None	1.58	3	ns
Z. noltii vs. *A. marina*	+	17.10	3	***
Z. noltii vs. sediment	None	2.31	3	ns
A. marina vs. sediment	None	2.20	1	ns
Emmapolder				
Z. noltii vs. macroalgae	None	7.84	4	ns
Z. noltii vs. *A. marina*	None	1.31	1	ns

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; ns, not significant.

part of the salt-marsh works of Groningen, including Linthorst Homanpolder, was generally higher than that of the eastern part which includes Emmapolder. For example, the squares in the Linthorst Homanpolder salt-marsh works which have contained seagrass since 1975 experienced a generally positive accretional balance of $+0.003$ to $+0.03$ m year^{-1}, whereas the accretional balance of the squares in the Emmapolder study site containing seagrass since 1975 was zero or even negative up to a rate of -0.015 m year^{-1} (Dijkema et al., 1992).

The limits of the period of emersion of the seagrass stands in the study sites ranged from approximately 40–55% at De Keeg-De Ans, 40–75% at Hoorn, 50–60% at Linthorst Homanpolder, and 50–75% at Emmapolder, with maximum densities of *Z. noltii* occurring at 40%, 50%, 60–75% and 60% emersion time, respectively.

4. Discussion

4.1. Historical changes

The interpretation of the historical changes in the abundance of *Z. noltii* stands in the Dutch Wadden Sea must be performed with caution, owing to the different ways in which the data on the distribution of seagrass were obtained. Some stands were never mapped at all, e.g. Stryp and Sehaal, and other stands were mapped for different parts of the total area. Furthermore, sampling did not always take place at the same time of the year. As the seagrass coverage is generally low at the borders of the seagrass stand, the total area of the seagrass stand will easily be underestimated if it is not mapped during the period at which maximum biomass occurs. The Hoorn study site was mapped previously at an unknown date in 1971 (Polderman and Den Hartog, 1975) and in July 1975 (Jacobs et al., 1983). Hootsmans et al. (1986) mapped the seagrass at both study sites at the Terschelling tidal flats in June 1985. The corresponding low values for the total area of these seagrass stands were, therefore, probably not the result of a temporary decrease of the seagrass in these years but due to differences in the periods of sampling.

In former years, seagrass flourished on the tidal flats off Groningen where later on the Linthorst Homanpolder and the Emmapolder salt-marsh works were located (Anonymous, 1941; A. Ploegman and T.G. van Hoorn, personal communication, 1991). The outer sedimentation fields of these salt-marsh works were constructed between 1950 and 1953, and subsequently ditched yearly until 1966/1969 (Dijkema et al., 1989a). The absence of seagrass in the 1950s and the 1960s may have been caused by the resulting drainage of the sediment and burying of seagrass material under the excavated material. Drainage is known to be fatal to *Z. noltii*: this seagrass species was deliberately diminished by means of ditching and subsequent desiccation in German salt-marsh works (Wohlenberg, 1938). *Z. noltii* reappeared in the salt-marsh works of Groningen approximately 10 years after the last ditching was carried out. The increase of *Z. noltii* in the Groningen study sites is, therefore, most probably a recolonization of original habitats in the Dutch Wadden Sea as the result of a change in the management of the salt-marsh works.

4.2. *Environmental factors*

The increase of *Z. noltii* in the Groningen salt-marsh works, doubling in area every 3 years, indicates that this seagrass species is capable of a fast colonization of suitable areas. The seagrass stands on the Terschelling tidal flats, however, did not extend at this rate during the last 15 years and the Hoorn stand severely decreased. Obviously, expansion of the seagrass off Terschelling is restricted by one or more environmental factors, in particular at the Hoorn study site. Knowledge of these factors may give clues to possible causes of historical changes in seagrass stands.

In the Groningen salt-marsh works, the annual sedimentation and erosion rates in the seagrass stands are higher than those found at the Terschelling tidal flats. Assuming that the short-term sediment dynamics are proportional to these long-term sedimentation and erosion rates, it may be concluded that sediment stability is not the most likely environmental factor which determines the borders of *Z. noltii* stands off Terschelling.

At the Terschelling study sites, seagrass coverage was significantly related with sediment composition. Seagrasses depend directly on the soil for nutrients and anchorage. In the sedimentation fields of the salt-marsh works off Groningen, no seagrass was found on muddy sediment with a high water content. This kind of sediment is most probably too soft for the seagrass plants to anchor. The sediment composition in all study sites lies well within the range suitable for seagrass growth in the Wadden Sea (Philippart et al., 1992). Therefore, it is concluded that the small differences in sediment composition as observed at tidal flats off Terschelling are not likely to restrict expansion of the local seagrass stands.

Although macroalgae were able to severely affect seagrass stands in the German Wadden Sea, the densities of the macroalgae in the Dutch Wadden Sea were at the time of mapping too low to cause any negative effects on *Z. noltii*. Also during other visits of the study sites, no high densities of macroalgae or traces of effects on seagrass by macroalgae, i.e. blackened plants and sediment, were found (personal observations). It is, therefore, not to be expected that macroalgae play a significant role in the abundance of this seagrass species at the study sites.

The relative position of seagrass in an intertidal zone is considered to be a compromise between the negative effects of desiccation and the positive effects of better light conditions (Keller and Harris, 1966). The upper boundaries of the *Z. noltii* stands at the Terschelling study sites are not restricted by a natural physical strain but by dikes and dams which separate land from tidal flats. Light conditions are influenced by the height and period of emersion, the turbidity of the water and the periphyton load on the seagrass leaves (Phillips et al., 1978; Orth and Moore, 1988; Giesen et al., 1990). During the last decades, the biomass of phytoplankton and microphytobenthos in the western Wadden Sea doubled (Cadée, 1984; Cadée and Hegeman, 1986). Although no data are available on historical changes in epiphytes during this period, the observed changes in the abundance of other small algae in the Wadden Sea suggest that a likewise increase in epiphyte load occurred.

For the Hoorn study site, the expansion of the seagrass stands was found to be restricted by the high bioturbation rate of the adult lugworms in their close surroundings (Philippart, 1994). From 1970 to 1990, the biomass of *A. marina* significantly increased on the Balgzand tidal flats (Beukema, 1992). A simultaneous increase in density of the lugworms at the Hoorn study site may have resulted in an extension of the area of the lugworms in the direction of the seagrass stand.

The observed historical changes in the abundance of the seagrass *Z. noltii* in the Dutch Wadden Sea seem, therefore, to be related with changes in the estuarine environment. Revival and subsequent expansion of the seagrass stands off Groningen was most probably the result of a decrease in desiccation rates of the sedimentation fields. The decrease of the seagrass stand at the Hoorn study site may be caused by an increase in water turbidity, periphyton load or lugworm densities.

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