EUTROPHICATION AS A POSSIBLE CAUSE OF DECLINE IN THE SEAGRASS *ZOSTERA NOLTII* OF THE DUTCH WADDEN SEA

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EUTROPHICATION AS A POSSIBLE CAUSE OF DECLINE IN THE SEAGRASS *ZOSTERA NOLTII* OF THE DUTCH WADDEN SEA

C.J.M. Philippart

Proefschrift
ter verkrijging van de graad van
doctor in de landbouw- en milieuwetenschappen,
op gezag van de rector magnificus,
dr. C.M. Karssen,
in het openbaar te verdedigen
op dinsdag 20 december 1994
des namiddags te half twee in de Aula
van de Landbouwuniversiteit te Wageningen.

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STELLINGEN

1. Naar alle waarschijnlijkheid ligt eutrofiëring ten grondslag aan de achteruitgang van Klein Zeegras in de Nederlandse Waddenzee. De hypothese kan echter niet bewezen worden door gebrek aan voldoende gegevens uit het verleden.
   (dit proefschrift)

2. Wadpieren kunnen beschouwd worden als de grenswachters en wadslakjes als de tuinkabouters van Klein Zeegras op het wad bij Terschelling.
   (dit proefschrift)

3. Het geringe voorkomen van Klein en Groot Zeegras in de Nederlandse Waddenzee ten opzichte van de Duitse en Deense Waddenzee kan slechts ten dele verklaard worden uit verschillen in sedimentsamenstelling, sedimentstabiliteit en hoogteligging van de wadplaten. Vermoedelijk spelen verschillen in gebruik en beheer hierbij ook een belangrijke rol.
   (dit proefschrift)

4. Bij het nemen van beheersmaatregelen in het algemeen en het sluiten van gebieden in de Waddenzee voor de visserij in het bijzonder dient men niet alleen rekening te houden met het actuele maar ook met het potentiële voorkomen van zeegrassen.
   (dit proefschrift)

5. In de klimatologie vallen buien soms omhoog.
   (A.M.G. Klein Tank & G.P. Können 1993)

6. Synoniemen als "masochism" voor "mesocosm" en "unfunny" voor "infauna" doen onterecht vermoeden dat het werken met schelpdieren in experimentele ecosystemen een vervelende bezigheid is.
   (Spellingchecker UK WordPerfect 5.1)

7. Het vergelijken van huidige weersomstandigheden met "normale" in plaats van gemiddelde waarden draagt niet bij tot begrip voor de natuurlijke variatie in het weer.
   (NOS weerberichten)

8. Net als in de Nederlandse roddelbladen, leidt in sommige wetenschappelijke tijdschriften het benadrukken van auteursnamen met behulp van hoofdletters af van de inhoud.

9. In de herhaling toont zich de meester.
   (S.H. Hurlbert 1984, S.H. Hurlbert & M.D. White 1993)

10. Het voortdurend veranderen van naam, logo en missie komt het onderzoek en de identiteit van de desbetreffende instituten niet ten goede.

Stellingen behorende bij het proefschrift "Eutrophication as a possible cause of decline in the seagrass *Zostera noltii* of the Dutch Wadden Sea". Katja Philippart, Wageningen, 20 december 1994.

VOORWOORD

Dit onderzoek is uitgevoerd bij de vakgroep Waterkwaliteitsbeheer en Aquatische Ecologie (destijds vakgroep Natuurbeheer) van de Landbouwuniversiteit Wageningen in nauwe samenwerking met de afdeling Aquatische Ecologie te Texel van het Instituut voor Bos- en Natuuronderzoek (destijds Rijksinstituut voor Natuurbeheer). Op deze plaats wil ik graag een aantal mensen bedanken voor hun essentiële bijdragen aan dit proefschrift.

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Katja Philippart, Texel.

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INTRODUCTION
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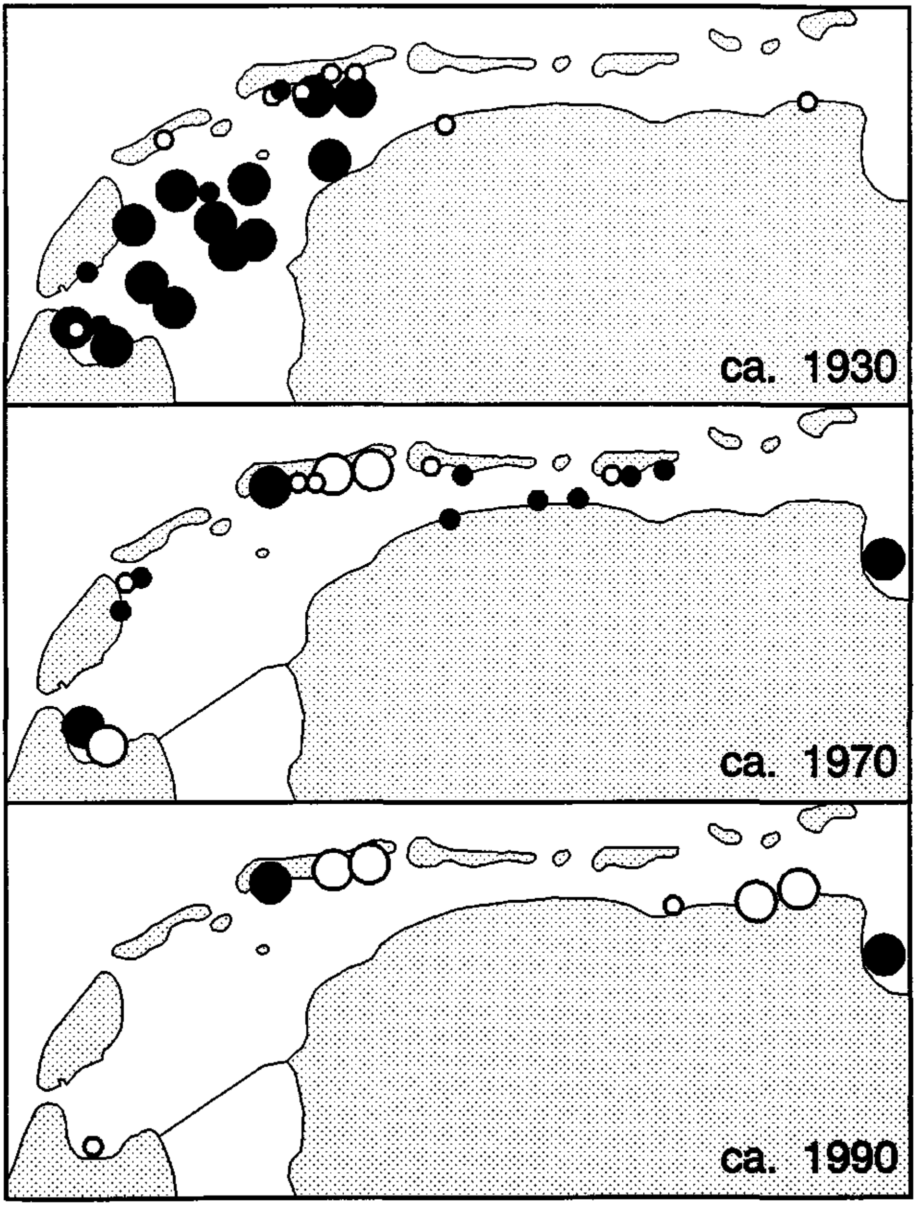

Fig. 1.1 Historical changes in distribution of *Zostera noltii* (○) and *Z. marina* (●) dominated ecosystems in the Dutch Wadden Sea: A. Distribution before 1930 (Oudemans *et al.* 1870, Van Goor 1919, Reigersman *et al.* 1939, Van Eerde 1942, Mörzer Bruijns & Tanis 1955), B. Distribution in 1972/1973 (Polderman & Den Hartog 1975), C. Distribution in 1989 (Dijkema *et al.* 1989, own observations).

INTRODUCTION

Historical changes: the problem

The Wadden Sea is a shallow coastal sea along the northern and western coasts of the Netherlands, Germany and Denmark. The seagrass population is represented by *Zostera noltii* Hornem. and *Zostera marina* L.. Seagrasses are marine vascular plants which are unique in their ability to achieve vegetative and reproductive cycles completely submerged in a saline medium. Seagrass stands form complex ecosystems that function through detritus-based food webs as well as herbivore webs. In the latter, living seagrass plants as well as epiphytes on the plants are grazed. Seagrass meadows are recently recognized as important marine resources (Phillips & Meñez 1988).

The environment may affect the processes involved in the establishment, maintenance and erosion of seagrass stands (Shepherd *et al.* 1989). The fact that the life processes of the plant continue under the numerous and fluctuating factors of the environment bespeaks a considerable breadth of tolerance. But the plasticity of plant growth is not unlimited. Vigour declines when the intensity of any one of the environmental factors begins to tax the plant's ability to cope with it (Daubenmire 1974). Although the Wadden Sea as a whole and in the long run is a rather stable environment, local conditions can fluctuate rapidly with time (Dijkema *et al.* 1983). Fluctuations in coverage and density of Wadden Sea seagrass stands may therefore be considered as natural features of these ecosystems. In former years seagrass abundance as a whole in the Dutch part of the Wadden Sea probably was relatively stable, but seagrass distribution fluctuated as the result of destruction of seagrass stands by strong currents, ice-scouring and sedimentation processes and establishment of stands at former and new habitats (Martinet 1795).

During the last sixty years especially in the Dutch part of the Wadden Sea, a decline of seagrasses has occurred which seems to exceed possible decrease due to natural fluctuations. *Z. marina* disappeared from the subtidal zone of the Wadden Sea in 1932 and the coverage and density of the remaining littoral populations of *Z. noltii* and *Z. marina* started to decrease in the sixties (Fig. 1.1). Before 1932, *Z. marina* occurred in the intertidal as well as in the subtidal zone of the Wadden Sea. Most of subtidal eelgrass stands were found in the western part of the Dutch Wadden Sea, covering an area of approximately 50 to 150 km^2 (Oudemans *et al.* 1870, Van Goor 1919). A subtidal eelgrass stand was also found near Sylt, Germany, covering approximately 0.4 km^2 (Reise *et al.* 1989). In the thirties the subtidal eelgrass disappeared very sudden from the Netherlands and Sylt and failed to return in the Wadden Sea (Michaelis *et al.* 1971, Reigersman *et al.* 1939, Reise 1989, Short *et al.* 1988). After this decline, seagrasses were only found in the intertidal zone of the Wadden Sea.

In the Dutch Wadden Sea during the sixties the intertidal seagrass stands consisted mainly of *Z. noltii*. The main seagrass populations were found on the Balgzand and at the tidal flats south of the island of Terschelling. Although both seagrass populations fluctuated between 1936 and 1965, a marked decrease in coverage and density was found for the period between 1965 and 1973. In 1972 the area covered with seagrasses was estimated at 5 km^2 (Den Hartog & Polderman 1975, Polderman & Den Hartog 1975). Although locally some increase of seagrasses can be found, in general the decrease continued. The seagrass population on the Balgzand has almost completely disappeared (J.J. Beukema, pers. comm. 1991) and the present coverage of remaining seagrass stands in the Dutch Wadden Sea is approximately 2 km^2 and mainly consists of *Z. noltii* (Dijkema *et al.* 1989). Decline of intertidal seagrass stands is not restricted to the Dutch part of the Wadden Sea. In the seventies intertidal seagrasses were found to be decreasing in Niedersachsen, Germany (Lüning & Asmus 1990), and in 1989 a decrease of seagrass stands compared to the situation in 1983 was reported for the area of Schleswig-Holstein (Brunckhorst & Reise 1989).

Environmental factors: possible causes

Although the cause of the disappearance of the subtidal eelgrass population from the entire Wadden Sea is still being discussed, the dominant interpretation is that of an epidemic disease (Short *et al.* 1988). After the first appearance of this disease on the Atlantic coasts of North America, *Z. marina* declined within two years to the point of almost complete disappearance in North America as well as in Europe (Short *et al.* 1988). Since 1938, this seagrass species occurred only in the intertidal areas of the Wadden Sea, and it never recovered in the subtidal zone (Den Hartog 1994). In the Netherlands, the decline of the subtidal eelgrass stands coincided with the completion of the separation between the former Zuiderzee and the Wadden Sea in 1932, which may have affected seagrass habitats and prevented re-establishment (Reigersman *et al.* 1939). *Z. noltii* was less affected by the disease (Vergeer & Den Hartog 1991) and became the more abundant seagrass species in the Dutch Wadden Sea due to the decline of *Z. marina*.

Many theories are provided to explain the decline of the intertidal seagrasses in the Wadden Sea but none of them were proven so far. All suggestions on possible causes are concerned with human activities, effecting abrupt or long-term changes in the Dutch Wadden Sea.

Seagrasses most probably were not affected by toxic substances. Den Hartog & Polderman (1975) did not find a relation between seagrass decrease and the telodrin poisoning of the Wadden Sea in 1965. Measurement of the quantity of several organochloric compounds revealed that contents were higher in seagrasses from the Balgzand than in those from Terschelling, but it was not clear whether these concentrations had any effect on seagrass stands. After 1965, the levels of these toxic substances in Wadden Sea organisms gradually declined as the result of the closure of the telodrin factory in 1965 and purification of effluent of other pesticide industries since 1967 (Koeman 1971).

Polderman & Den Hartog (1975) also suggested an increased occurrence of floating macroalgae due to an increase of nutrients in the Wadden Sea. This theory was acknowledged by Brunckhorst & Reise (1989) for the decline of seagrasses in Schleswig-Holstein. Since 1979 a mass development of macroalgae (*Enteromorpha, Chaetomorpha* and *Ulva*) was reported in this area, which is supposed to be due to a long-term increase of nitrogen (Reise *et al.* 1989, Reise 1989). But Polderman & Den Hartog (1975) did not supply actual data on suffocation of seagrasses by macroalgae during that time. Van den Hoek *et al.* (1983) conclude that available data do not support the presumption that the increasing nutrient load of the Dutch Wadden Sea resulted in an increasingly massive growth of *Ulva* and *Enteromorpha* in the period from 1932 until the 1980s.

Giesen *et al.* (1990) and De Jonge & De Jong (1992) mention an increase of turbidity of the Dutch Wadden Sea to explain the absence of recovery of subtidal eelgrass stands. But high variations in turbidity during the tidal cycle, the season and different years make it difficult to demonstrate long-term trends (Cadée 1982). In addition, the seagrass stands in the Dutch Wadden Sea are generally located in the upper littoral zone (Dijkema *et al.* 1989). These seagrasses are emerged during low tide and it may, therefore, be expected that possible influence of increased turbidity will only affect seagrass growth during high tide.

Seagrass stands are found to be affected by an increase of blue mussel (*Mytilus edulis*) and cockle (*Cerastoderma edule*) densities and subsequent fishery by man. Ruth (pers. comm. 1990) mentioned that a high spat fall and a subsequent mass development of mussels destroyed stands of *Z. noltii* in the area of Schleswig-Holstein, Germany, in 1988. No high abundance of mussels and cockles was, however, mentioned during the period in which the seagrasses were found to decline in the Dutch Wadden Sea (Polderman & Den Hartog 1975). Shellfish fisheries may have direct negative effects on seagrasses because the upper sediment is reworked during these activities. This kind of fishery is held responsible for the decrease of seagrass stands in the Oosterschelde, the Netherlands (De Jong & Meulstee 1989). Although the cockle fishery increased from 1950 to 1980 in the Dutch Wadden Sea, it cannot alone explain the decrease of seagrass stands in this area (J. de Vlas, pers. comm. 1990). Seagrasses and cockles show different optima in the intertidal zone. In general, seagrass stands are located at short distances from the coast (Dijkema *et al.* 1989) and high biomass values of cockles are found at distances from 1 to 6 km from the shore (Beukema 1983). If shellfish fisheries expand to the shallow coastal zones of the Wadden Sea, however, it has devastating effects on seagrass stands (De Jonge & De Jong 1992, Van Katwijk 1993, own observations).

Many authors found a relation between decline of seagrasses and eutrophication (e.g. Cambridge *et al.* 1986, Kemp *et al.* 1983, Shepherd *et al.* 1989). Eutrophication is the one most marked long-term change in the Wadden Sea during the last 25 years. In the Dutch Wadden Sea simultaneous increase of nutrient levels (De Jonge & Postma 1974, Van der Veer *et al.* 1989), primary production (Cadée & Hegeman 1986) and secondary production (Beukema 1989) are found. Eutrophication did occur in all parts of the Wadden Sea for which the decline of littoral seagrasses is reported. Eutrophication is, therefore, the most plausible cause for the decline of seagrasses in the Dutch part of the Wadden Sea.

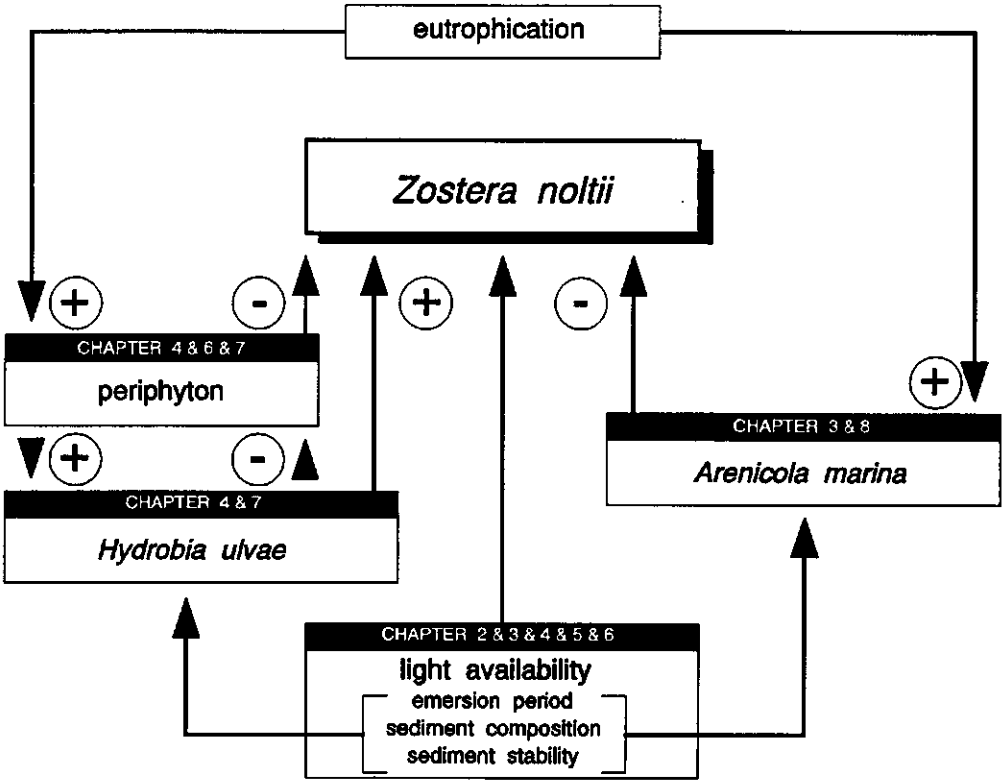

Fig. 1.2 Hypothesis of the limiting factors for the distribution of *Zostera noltii* dominated ecosystems in the Dutch Wadden Sea and possible effects of eutrophication.

Hypothesis

To assess the impact of environmental change on seagrass communities, the relations between environmental variables and the occurrence of the species have to be known. So knowledge has to be acquired on the environmental variables which are believed to be important for seagrasses. The most important environmental factors determining intertidal Wadden Sea habitats for seagrasses are period of emersion and sediment composition (Dijkema 1991). The sediment type reflects, among other factors, the exposure to tidal currents and waves, i.e. stability of the habitat. Therefore, the first environmental variables that have to be tested for their relation with the occurrence of seagrass are period of emersion, sediment composition and stability (Fig. 1.2).

This study was based on the hypothesis that *Zostera noltii* declined because of eutrophication. This hypothesis rests on the premise that seagrass stands in the intertidal zone occur above a lower limit imposed by penetration of light at an intensity which allows photosynthesis to significantly exceed respiration (Shepherd *et al.* 1989). The light availability for the seagrass is not only determined by tidal height and turbidity of the water but also by the density of epiphytes on the leaves of the seagrasses. It may, therefore, be expected that epiphytes play a major role in the determination of light conditions for seagrasses in the intertidal zone.

Seagrasses generally suffer from nutrient stress (Short 1987) and mild nutrient enrichment may, therefore, enhance seagrass growth (Shepherd *et al.* 1989). But nutrient enrichment usually favours as well growth of macroscopic and microscopic algae. Microscopic algae on the leaves (periphyton) cause reduction in growth of macrophytes due to decreasing light conditions (Phillips *et al.* 1978). Since the primary production and chlorophyll-*a* of microphytobenthos on tidal flats in the western Wadden Sea doubled over the period 1968-1981 (Cadée 1984), it may be expected that epiphytes did also increase during this period. Periphyton can have negative effects on seagrass photosynthesis and growth as the result of shading and competition for carbon and nutrient sources (Sand-Jensen 1977, Silberstein *et al.* 1989, Shepherd *et al.* 1989). An increase of the periphyton can, subsequently, cause a decline of the seagrass stand (Fig. 1.2).

Epiphyte biomass may be suppressed by grazing epifauna (Orth & Van Montfrans 1984, Hootsmans & Vermaat 1985). The mudsnail *Hydrobia ulvae* is the potential grazing species on seagrass in the Wadden Sea. The mudsnails seem to have responded to eutrophication. Through erratically fluctuating, the mean density of mudsnails increased during the 1970s and the 1980s in the western half of the Dutch Wadden Sea (Beukema 1989). If this increase of mudsnails resulted in a consumption of the increased load of epiphytes, present *Z. noltii* stands are supposed to be flourishing as in former years. But if the mudsnails were not able to fully counteract the increase in epiphytes, the growth and development of present *Z. noltii* stands could have been suboptimal, possible resulting in a decrease or even complete disappearance of the standing stock (Fig. 1.2).

In addition to the model of seagrass decline according to Phillips *et al.* (1978), it was observed that the lower limit of intertidal Wadden Sea seagrass stands was bordered by a high abundance of faecal castings of the lugworm *Arenicola marina* on the tidal flats of Terschelling. Since lugworms in high densities ($85 \cdot m^{-2}$) are able to rework an amount of sediment that corresponds with a layer of 33 cm per year (Cadée 1976), it was thought possible that high abundances of lugworms restrict seagrass growth and survival as the result of their feeding behaviour. Because the numerical density and biomass of the lugworms increased in some parts of the Dutch Wadden Sea (Beukema 1989), they may have contributed to further restriction of seagrass habitats (Fig. 1.2).

OUTLINE OF THE THESIS

The present thesis describes the results of research on the distribution and possible causes for the decrease of the seagrass *Z. noltii* in the Wadden Sea, carried out from 1986 to 1990. Chapter 2 examines the relation between the distribution of

Zostera dominated ecosystems in the international Wadden Sea and several possibly limiting environmental factors, i.e. period of emersion, sediment type, sediment stability, mean salinity and geographical region. Chapter 3 describes the former and present distribution of *Z. noltii* dominated ecosystems in the Dutch Wadden Sea in relation with their environment, i.e. period of emersion, sediment type, sediment stability, macroalgae and lugworms. The seasonal dynamics and structures of a *Z. noltii* dominated ecosystem, including periphyton and mudsnails, on the tidal flats of Terschelling in the Dutch Wadden Sea are studied in Chapter 4. Results of a shading experiment on the effects of periphyton on the growth, biomass and survival mechanisms of *Z. noltii* on the tidal flats of Terschelling are discussed in Chapter 5. Chapter 6 describes the effects of the length of light periods on the growth, biomass and photosynthesis-irradiance curves of *Z. noltii*, originating from the Netherlands and Mauritania. Chapter 7 deals with results of an exclosure experiment on the role of the periphyton-grazing mudsnail *H. ulvae* on the growth and biomass of *Z. noltii*. In Chapter 8, the results of a transplantation experiment on the interaction between the seagrass *Z. noltii* and the bioturbating lugworm *A. marina* on the tidal flats of Terschelling is described. Chapter 9 summarizes and discusses the main results of the previous chapters in relation to the hypothesis.

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WADDEN SEA SEAGRASSES: WHERE AND WHY?

ABSTRACT Wadden Sea seagrasses, *Zostera noltii* Hornem. and *Zostera marina* L., are declining in several parts of the Wadden Sea. Knowledge of the factors which determine seagrass distribution is required to manage this specific habitat of the Wadden Sea and to prevent further decline. For this purpose, a habitat map of the Wadden Sea (scale 1:100,000) was divided into squares of 1 cm^2, representing 1 km^2 in the field. Values of several environmental factors (e.g. period of emersion, sediment type, sediment stability, region) and the presence of seagrasses were noted for each square in the intertidal zone. Possible effects of mean salinity on seagrass distribution were assumed to be reflected in regional effects. A logit model was assumed in statistical analysis. All the main individual environmental factors, as well as the interaction between period of emersion and region, were found to contribute significantly to the models for both seagrass species. The models showed that no seagrass is to be expected in the proximity of main river estuaries, even under optimal conditions concerning period of emersion, sediment type and sediment stability. Further research on the effects of river output on seagrass growth is therefore recommended.

INTRODUCTION

The Wadden Sea is a shallow coastal part of the North Sea of approximately 8,000 km^2, situated along the coasts of the Netherlands, Germany and Denmark. Two species of seagrass occur in this area, viz. *Zostera noltii* Hornem. and *Zostera marina* L. (eelgrass). Seagrasses play a specific role in the Wadden Sea. They supply habitats for numerous algae and animal species and form a food source for brent geese and widgeons.

Wadden Sea seagrasses have been declining during the last sixty years. Sublittoral eelgrass used to occur in the westernmost part of the Wadden Sea and in the northern part near Sylt (Harmsen 1936, Reise *et al.* 1989). In both areas the sublittoral eelgrass populations disappeared completely in the 1930s and have not returned. The dominant interpretation of the cause of this decline is that of an epidemic disease (Short *et al.* 1988). In the Netherlands however, the disappearance of sublittoral eelgrass was also thought to be related to the closure of the former Zuiderzee. The enclosing dam caused changes in hydrographical conditions in the western part of the Dutch Wadden Sea, which may have locally affected seagrass habitats and prevented re-establishment (Reigersman *et al.* 1938).

The remaining littoral populations of *Z. noltii* and *Z. marina* started to decrease in the Dutch Wadden Sea in the 1960s (Polderman & Den Hartog 1975) and in Niedersachsen, Germany, in the 1970s (Lüning & Asmus 1990). Only in Köningshafen at the northern end of Sylt do both species seem to have increased since the 1970s (Reise *et al.* 1989). Although there are many theories (e.g. Den Hartog & Polderman 1975), the cause of the decline of littoral seagrasses in some parts of the Wadden Sea since the 1960s is still not clear.

Knowledge of the factors which determine seagrass distribution is necessary to manage this specific ecosystem effectively. It may also give clues to possible causes of decline.

Recently a habitat map (scale 1:100,000) of the Wadden Sea has been published (Dijkema *et al.* 1989). This map presents the distribution of the habitats of the intertidal parts and the salt marshes (Dijkema 1991). The map shows the distribution of several abiotic (e.g. period of emersion, sediment type, mean salinity) and biotic features (e.g. seagrasses, musselbeds) in the littoral zone. The habitat map therefore provides an unique opportunity to analyze relations between the distribution of seagrasses and their environment for entire area.

The present study analyses the occurrence of *Z. noltii* and *Z .marina* in the Wadden Sea in relation to several environmental factors which are expected to be relevant: period of emersion, sediment type, sediment stability, mean salinity and region. Region was considered as a geographical variable. Results are related to the possible causes of decline of littoral seagrass beds.

STUDY AREA AND METHODS

Study area

The study area was restricted to the tidal flats of the Wadden Sea. The area on the habitat map was subdivided into squares of 1 cm^2, representing 1 km^2 in the field. Squares more than half covered by water, saltmarsh, land or musselbeds were removed from the dataset. In each remaining square ($n=4,294$) the following features were classified.

Biotic and abiotic features

Seagrasses. The presence or absence of *Zostera noltii* as well as *Z. marina* were noted as 0 or 1 values respectively in each square. The abundance of each species was not taken into account.
Period of emersion. The main classifications were low (l), high (h) and uppermost (u) tidal flats, depending on period of emersion. This map classification was extended by the introduction of two intermediate types (lh and hu) (Fig. 2.1a). The classification of period of emersion type was dependent on the proportion of different period of emersion types to the square area. If a square was at least two-thirds covered by one of the three main emersion types, it was classified as that particular type, otherwise it was an intermediate type.
Sediment type. A sediment type classification was made into moderately fine sand (r), fine sand (s), muddy sand (x), mud (m) and three intermediate types (rs, sx and xm) (Fig. 2.1b). This distinction was based on the proportion of clay particles in the grainsize distribution (Dijkema 1991) and the presence of megaripples. Megaripples indicate highly dynamic areas, in which sand is coarser than on tidal flats due to wave reworking of the sediment (Reineck 1980). Squares with sandy sediment and containing at least two megaripple marks on the habitat map were classified as moderately fine sand, sandy squares containing one megaripple mark were classified as an intermediate type between moderately fine and fine sand. If a square was at least two-thirds covered by one of the other three main sediment types (s, x, m), it was classified as that particular type, otherwise it was an

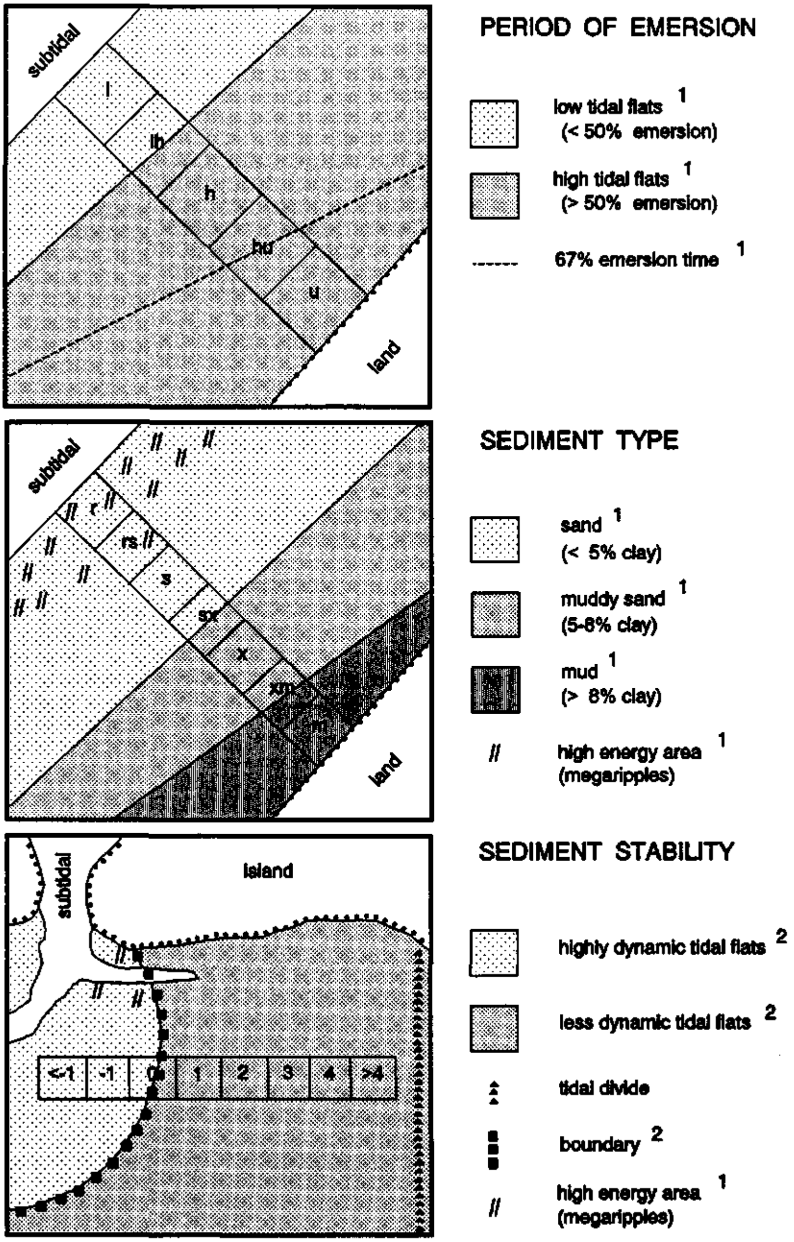

Fig. 2.1 Classification of the environmental factors period of emersion, sediment type and sediment stability of tidal flats of the Wadden Sea ([1] after Dijkema *et al.* 1989, [2] after Ehlers 1988).

intermediate type.

Sediment stability. The environmental factor 'sediment stability' was based on a division into highly dynamic or less dynamic parts of the Wadden Sea. Flood deltas inside tidal inlets are the most dynamic parts of the Wadden Sea. Inner parts of tidal flats towards the mainland coast and tidal divides are more stable (Ehlers 1988). Tidal divides and boundaries between highly dynamic and less dynamic parts of the Wadden Sea were marked by lines (Fig. 2.1c). The positions of these lines were based on the inner boundaries of the flood deltas as roughly indicated by Ehlers (1988) and the next two features on the map. Tidal flats with megaripples and near channels wider than 500 m were considered as highly dynamic areas. The remaining tidal flats are considered as less dynamic parts. Further, it was assumed that sediment stability was highest on the tidal divisions and decreased towards the tidal inlets. An estimate of the sediment stability of a square was obtained by measuring the shortest distance between the centre of the square and the boundary line. The distance was never measured across a tidal divide. When the square was located inside a less dynamic part, this distance was noted as positive, otherwise it was negative. Finally, the measured distances were ranked into eight classes (Fig. 2.1c).

Mean salinity. Mean salinity was divided into four classes (Table 2.1). Temporal variations in salinity were not considered in this study.

Region. The area was divided into 24 regions (Fig. 2.2). A region consisted in general of a tidal flat area confined by main tidal channels. The region parameter is supposed to reflect a combination of effects on a larger scale than 1 km^2, like tidal range, turbidity, climate, fishing, but also salinity.

Associations. All mutual associations between the environmental factors, i.e. period of emersion, sediment type, sediment stability, mean salinity and region, were tested by means of likelihood-ratio chi-square tests.

Statistical modelling

Probability. A logit model was assumed for the analysis of relations between seagrass presence and environmental factors. This model belongs to the class of Generalized Linear Models (Nelder & Wedderburn 1972, McCullagh & Nelder 1989). It describes the relation between the probability (*p*) of occurrence of a seagrass species in a square and the value of a linear predictor (*lp*) as follows:

$$\ln \frac{p}{(1-p)} = lp$$

Linear predictor. The value of the linear predictor (*lp*) is calculated as the sum of a constant α and the effects of independent factors. These factors may be main effects of environmental factors (e.g. β_j as the effect of period of emersion *j*, γ_k as the effect of sediment type *k*) as well as effects due to interactions of environmental factors (e.g. $\beta\gamma_{jk}$ as the effect of interaction between period of emersion *j* and sediment type *k*), e.g.

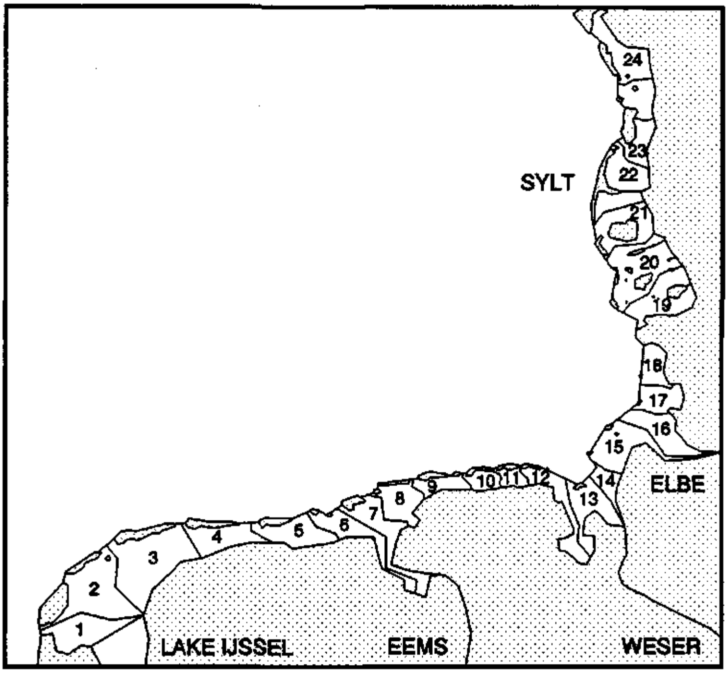

Fig. 2.2 The subdivision of the Dutch, German and Danish Wadden Sea into 24 regions.

$$lp = \alpha + \beta_j + \gamma_k + \dots + \beta\gamma_{jk} + \dots$$

Rewriting the model shows that this model answers to the axiom that the probability (p) should never exceed the range from 0 to 1:

$$p = \frac{\exp(lp)}{1 + \exp(lp)}$$

Likelihood. The data Y_i of the model consist of observations on seagrass absence (0) or presence (1) in the squares. The model gives a probability p_i for each observation i. The discrepancy between data and model results can be expressed by means of the likelihood (L). Roughly the likelihood is equivalent to the probability of the data given the model. Assuming Y_i to be independent Bernoulli variables, the likelihood (L) equals:

$$L = \prod_i p_i^{Y_i} \cdot (1 - p_i)^{(1 - Y_i)}$$

Deviance. The discrepancy or goodness-of-fit of a model can also be expressed by its deviance (D). The deviance (D) is proportional to the log of the ratio of the maximum likelihood achievable for the full model and that achieved by the model under investigation:

$$D = \log \frac{L_{full\ model}}{L_{model\ under\ investigation}}$$

A full model is an exact fit and it contains as many parameters as observations. The deviance of a full model is thus equal to zero. The null model on the other hand is the simplest model and has just one parameter, representing a common *p* for all observations.

An important property of the deviance is that if two models, which can be obtained by imposing constraints on the parameters of the other, are compared the difference in deviance (G^2) is approximately X^2_v, distributed under the hypothesis that the simplest model is true, where v is the difference in the number of degrees-of-freedom (*df*). Likelihood-ratio chi-square tests may therefore be used to test the significance of improvement in a model if a new parameter is added.

The level of significance for each test separately was kept low ($\alpha = 0.01$) to compromise between the experimental error rate growing too small at low significance levels ($\alpha = 0.05$) and the power becoming to high at higher significance levels ($\alpha = 0.001$). Maximum likelihood estimates of the parameters (α, $\beta_{j,}$ etc.) of the logit models were made using the statistical package GENSTAT 5 (Payne *et al.* 1987).

Main and interaction effects. A main effect of an environmental factor (e.g. period of emersion) was tested by comparing the model without that main effect, but with all other main effects included (e.g. model 1), to the model with all main effects included (e.g. model 2):

MODELS 1 and 2.

Model 1:
lp = constant + sediment + stability + salinity + region

Model 2:
lp = constant + sediment + stability + salinity + region + emersion

G^2 = deviance model 1 - deviance model 2
v = df model 1 - df model 2

If X^2_v is significant, than it may be concluded that model 2 shows a significantly better fit than model 1 and therefore that the environmental factor period of emersion contributed significantly to the distribution of the seagrass species under investigation. All main effects were tested in the same way. An

Feature	**Classification**		**Area**	
	Character	Code	km^2	%
Emersion	> 0%	I	2585	60.20
	↓	Ih	797	18.56
		h	591	13.76
		hu	208	4.84
	< 100%	u	113	2.63
Sediment	moderately	r	74	1.72
	fine sand	rs	279	6.50
	↓	s	2692	62.69
		sx	381	8.87
		x	490	11.15
		xm	149	3.47
	mud	m	229	5.33
Stability	low	<-1	160	3.73
		-1	144	3.53
	↓	0	1143	26.62
		1	1230	28.64
		2	790	18.40
		3	441	10.27
		4	214	4.98
	high	>4	172	4.01
Salinity	< 5	I	18	0.42
	5-10	II	78	1.82
	10-18	III	254	5.92
	> 18	IV	3944	91.85
Region	Balgzand	1	81	1.89
	Vlieland	2	239	5.57
	Terschelling	3	374	8.71
	Ameland	4	178	4.15
	Schiermonnikoog	5	176	4.10
	Rottummerplaat	6	190	4.42
	Borkum	7	180	4.19
	Juist	8	149	3.47
	Norderney	9	90	2.10
	Langoog	10	80	1.86
	Spiekeroog	11	61	1.42
	Wangerooge	12	158	3.68
	Mellum	13	272	6.33
	Land Wursten	14	123	2.86
	Neuwerk	15	223	5.19
	Ditmarschen	16	190	4.42
	Trischen	17	156	3.63
	Blauort	18	129	3.00
	Nordstrand	19	220	5.12
	Pellworm	20	301	7.01
	Föhr	21	170	3.96
	Sylt	22	191	4.45
	Rømø	23	224	5.22
	Fanø	24	139	3.24

Table 2.1 Classification and distribution of environmental features of intertidal flats in the Wadden Sea (total area = 4,294 km^2).

interaction effect of environmental factors (e.g. period of emersion x sediment type) was tested in a similar way by comparing the model with the interaction effect and all main effects to the model with only the main effects. All interaction effects were tested in the same way.

Parameter estimates. A logit model supplies maximum likelihood estimates of the parameters, i.e. estimates for the constant and the classes of the main and interaction effects which are included in the model. Each model has its own set of parameters. Only the values of the first classes (e.g. main effects: period of emersion I, sediment type r, sediment stability <-1, mean salinity <5 and region 1) of the parameters of all investigated models were zero by definition. The value of a parameter cannot be estimated when a particular class does not occur in any square in the study area.

RESULTS

Abiotic features. More than half of the tidal flat area of the Wadden Sea is situated below Mean Sea Level (Table 2.1). More than 70% of the area is covered with sand (Table 2.1). The tidal flats of the Wadden Sea are relatively stable because almost 70% of this area is situated inside the boundary between highly and less dynamic tidal flats, and less than 8% is situated outside it (Table 2.1). Mean salinity of the squares generally exceeds 18 (Table 2.1). The area of tidal flats in the regions varies between 61 and 374 km^2 (Table 2.1). All associations between the environmental factors, i.e. period of emersion, sediment type, sediment stability, mean salinity and region, are mutually highly significant ($p<0.001$).

The highest significance of association was found between the environmental factors mean salinity and region. It was expected that including the mean salinity factor as well as the region factor would lead to serious estimation problems in the model due to large standard errors in parameter estimates. Therefore, the mean salinity factor was excluded from the analysis. The effect of the mean salinity, if present, will be reflected in the effect of the region factor. Statistical modelling was therefore restricted to the main effects of the environmental factors period of emersion, sediment type, sediment stability and region, and the interaction effects.

Seagrass models. Even though the environmental factors are mutually associated, the main effects of all environmental factors as well as the interaction effect of period of emersion and region were found to contribute significantly to the models for both *Zostera noltii* (Table 2.2) and *Z. marina* (Table 2.3). The distribution of both species can therefore be explained by the model:

$$lp = \alpha + \beta_j + \gamma_k + \delta_l + \epsilon_m + \beta\epsilon_{jm}$$

where α is a constant, β_j represents the effect of period of emersion j, γ_k the effect

Table 2.2 Deviance (D) and degrees-of-freedom (df) of models of presence of *Zostera noltii* in the Wadden Sea and differences in deviance (G^2), differences in degrees-of-freedom (v) and significance (p) of more complex models compared to more simple models.

Model		D	df	G^2	v	p
Null model	(most simple model)	2759	4293			
Models 1	all main effects minus one					
	minus period of emersion	1864	4257	95	4	<0.001
	minus sediment type	1852	4259	83	6	<0.001
	minus sediment stability	1834	4260	65	7	<0.001
	minus region	2437	4276	668	23	<0.001
Model 2	all main effects	1769	4253	124	88	<0.001
Model 3	all main effects + interaction (emer x region)	1645	4165			
Full model	(most complex model)	0	0			

of sediment type *k*, δ_l the effect of stability *l*, ϵ_m the effect of region *m* and $\beta\epsilon_{jm}$ the effect of interaction between emersion time *j* and region *m*. The maximum likelihood estimates of the parameters of the resulting models of *Z. noltii* and *Z. marina* are listed in table 2.4 and 2.5, respectively.

Sediment type. For both models the maximum parameter value of the sediment type factor was found in class m (Tables 4 and 5). Therefore in all distinguished regions of the Wadden Sea the probability of occurrence of both *Z. noltii* as *Z. marina* is maximal in squares covered with mud. The ranges (differences between maximum and minimum values) of the parameter estimates of sediment of *Z. noltii* and *Z. marina* are 2.77 and 6.08, respectively. This difference indicates that *Z. marina* is more sensitive to the type of sediment than *Z. noltii*.

Sediment stability. For both models the maximum parameter value of the sediment stability factor was found in class 2 (Tables 2.4 and 2.5). Therefore in all the distinct regions of the Wadden Sea the probability of occurrence of *Z. noltii* and *Z. marina* is maximal in squares which are situated in relatively stable areas at a distance of 2 km from the boundary between highly and less dynamic tidal flats. The ranges of the parameter estimates of sediment stability of *Z. noltii* and *Z. marina* are of the same order of magnitude, 6.13 and 6.79 respectively, which indicates that the seagrass species are equally sensitive towards the effects of this sediment stability.

Period of emersion and region. The contribution of the effect of the interaction between the environmental factors period of emersion and region to both models indicates that the effects of period of emersion on the presence of both seagrass differs for different regions. In other words, the optimum period of emersion of

Table 2.3 Deviance (D) and degrees-of-freedom (df) of models of presence of *Zostera marina* in the Wadden Sea and differences in deviance (G^2), differences in degrees-of freedom (v) and significance (p) of more complex models compared to more simple models.

Model		D	df	G^2	v	p
Null model	(most simple model)	2357	4293			
Models 1	all main effects minus one					
	minus period of emersion	1735	4257	25	4	<0.001
	minus sediment type	1733	4259	23	6	<0.001
	minus sediment stability	1815	4260	105	7	<0.001
	minus region	2148	4276	438	23	<0.001
Model 2	all main effects	1710	4253	141	88	<0.001
Model 3	all main effects + interaction (emer x region)	1569	4165			
Full model	(most complex model)	0	0			

both seagrass species was found to be dependent on their geographical position in the Wadden Sea. The effect of period of emersion on the probability of seagrasses occurring can therefore only be considered for each region separately and not, contrary to the effects of the sediment type and sediment stability factors, for the Wadden Sea as a whole.

The effect of period of emersion per region can be calculated as the sum of the main effect of period of emersion and the interaction effect of period of emersion and the particular region. Maximum probabilities of *Z. noltii* were more frequently found for longer periods of emersion than those of *Z. marina* (Table 2.6). The optimum period of emersion of *Z. noltii* seems to be related to that of *Z. marina* per region (Table 2.6). Region 7 was excluded from this analysis because it showed two optima for period of emersion for *Z. noltii*.

Minimum and maximum probability in regions. In order to study the probabilities of occurrence of seagrasses in all regions, the minimum and maximum values of the linear predictor of both seagrass species in every region was calculated. The minimum value of the linear predictor for a region can be found by adding the value of the constant and the specific region parameter to the minimum values of the parameters for sediment type and sediment stability and the minimum value of the sum of period emersion and interaction between period of emersion and region. The maximal linear predictor for a region can be calculated as the sum of the constant and the value for the specific region parameter and maximum values of the other parameters. The sum of ranges of parameters of sediment type, sediment stability and the combination of period of emersion and the interaction between period of emersion and region equals the difference between minimum and

Table 2.4 Maximum likelihood estimates of parameters of the logit model for presence of *Zostera noltii* in the Wadden Sea.

Constant		**Sediment type**			**Sediment stability**	
-11.52		r	0.00		<-1	0.00
		rs	-0.01		-1	3.24
		s	1.70		0	5.18
		sx	2.10		1	5.83
		x	2.62		2	6.13
		xm	2.30		3	5.75
		m	2.76		4	5.68
					>4	4.97
Period of emersion		l	lh	h	hu	u
		0.00	4.08	5.35	0.47	0.00
Region						
1	0.00	0.00	0.00	0.00	0.00	0.00
2	-4.29	0.00	-4.00	-5.40	-0.50	0.30
3	-0.18	0.00	-2.08	-9.70	-4.80	-4.40
4	-4.68	0.00	-4.14	-5.20	-0.40	1.10
5	-4.45	0.00	0.59	0.90	-0.20	9.09
6	-0.04	0.00	-3.80	-10.44	-4.90	-4.60
7	0.91	0.00	-10.01	-11.37	-6.80	0.69
8	-4.74	0.00	1.19	1.41	7.39	9.15
9	1.69	0.00	-2.10	-3.12	2.12	(0.0)
10	2.46	0.00	-2.95	-3.93	0.40	(0.0)
11	-4.60	0.00	3.01	1.92	2.60	0.10
12	0.75	0.00	-3.69	-4.51	-0.24	-5.40
13	-0.18	0.00	-1.90	-3.86	2.31	-4.10
14	-4.54	0.00	-4.32	-5.80	-1.00	-0.50
15	-4.26	0.00	-4.34	-5.60	-0.80	-0.50
16	-4.13	0.00	-4.46	-6.09	-1.40	-0.80
17	-4.34	0.00	-4.38	-5.61	-0.60	-0.50
18	-4.29	0.00	-4.16	-5.40	-0.60	0.50
19	2.46	0.00	-2.82	-4.12	2.65	0.71
20	3.21	0.00	-3.40	-3.70	0.56	-1.83
21	1.92	0.00	-2.57	-4.86	-0.16	-7.30
22	2.46	0.00	-3.11	-4.73	2.19	-0.35
23	0.90	0.00	-3.10	-3.29	2.52	-5.00
24	2.51	0.00	-3.56	-5.70	(0.0)	(0.0)

maximum values of the linear predictor per region (Fig. 2.3). The differences in minimum and maximum probabilities of seagrasses occurring in the various regions illustrate the difference in the size of the effects of period of emersion for different regions: for both seagrass species regions 11 to 13 are more affected by the period of emersion factor than regions 16 to 18 (Fig. 2.3). The results also show that the probability of occurrence of both seagrass species is affected by the period of

Table 2.5 Maximum likelihood estimates of parameters of the logit model for presence of *Zostera marina* in the Wadden Sea.

Constant		**Sediment type**			**Sediment stability**	
-19.17		r	0.00		<-1	0.00
		rs	3.92		-1	-0.45
		s	5.15		0	4.88
		sx	5.44		1	5.80
		x	5.16		2	6.34
		xm	5.39		3	6.11
		m	6.08		4	5.88
					>4	4.51
Period of emersion		l	lh	h	hu	u
		0.00	7.53	0.10	-0.12	-0.63
Region						
1	0.00	0.00	0.00	0.00	0.00	0.00
2	-0.09	0.00	-7.50	0.00	0.10	1.10
3	3.30	0.00	-4.18	-3.60	2.96	-3.10
4	3.24	0.00	-11.20	2.10	-3.50	-1.10
5	-0.32	0.00	-2.80	0.00	0.60	1.50
6	-0.24	0.00	-7.62	-0.70	-0.10	0.50
7	6.32	0.00	-8.86	-7.00	-7.40	-6.90
8	5.74	0.00	-6.55	0.40	1.22	3.35
9	6.30	0.00	-6.89	1.20	0.62	(0.0)
10	6.10	0.00	-6.37	-0.70	-5.90	(0.0)
11	-0.35	0.00	-0.95	7.30	3.20	0.70
12	4.18	0.00	-6.36	0.30	1.16	-3.70
13	5.39	0.00	-8.80	0.20	0.01	-5.10
14	5.11	0.00	-6.35	-5.80	-5.40	-4.90
15	4.61	0.00	-6.09	1.00	-4.80	-4.60
16	0.36	0.00	-8.15	-1.00	-0.80	-0.10
17	-0.12	0.00	-7.84	-0.40	-0.10	-0.10
18	-0.10	0.00	-7.60	-0.10	-0.20	1.10
19	6.21	0.00	-6.26	0.60	3.11	1.03
20	7.56	0.00	-7.03	0.60	-0.18	-7.50
21	6.60	0.00	-6.43	-7.50	-7.90	-6.60
22	4.86	0.00	-6.58	1.40	2.12	-5.20
23	5.53	0.00	-7.66	1.70	2.46	-4.70
24	7.38	0.00	-7.83	-0.60	(0.0)	(0.0)

emersion factor to the same extent.

Subsequently minimum and maximum probabilities of occurrences of seagrasses per region can be calculated from the values of the linear predictors according to the logit function. The results show that no seagrass is expected to occur under the most unfavourable conditions for period of emersion, sediment type and sediment stability, since probabilities coinciding with minimum values of

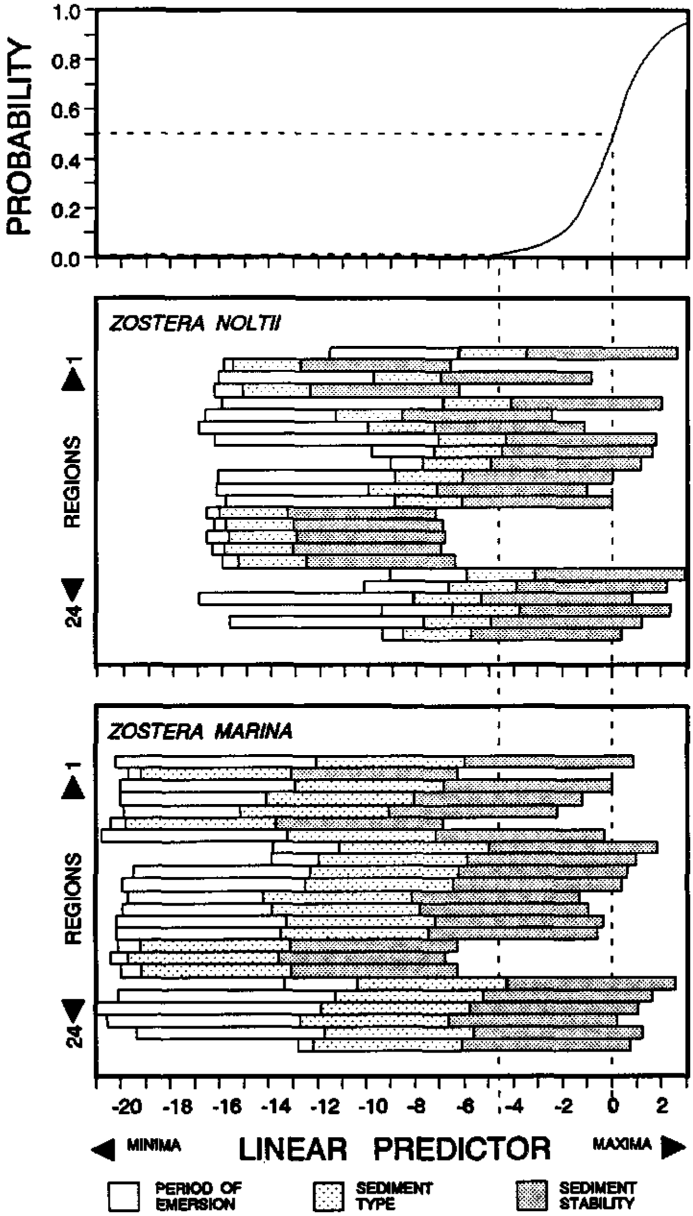

Fig. 2.3 Minimum and maximum values of linear predictors and probabilities of *Zostera noltii* and *Z. marina* per region. The ranges are calculated as the differences in minimum and maximum values of parameter estimates of the environmental factors period of emersion, sediment type and sediment stability.

Table 2.6 Occurrence of optimum periods of emersion of *Zostera noltii* and *Z. marina* in 23 Wadden Sea regions (region 7 excluded). The table shows the number of times a particular combination of optimum periods of emersion of both seagrass species is found.

Zostera noltii	l	lh	h	hu	u	
Zostera marina						*total Zm*
l	2	2	0	0	0	4
lh	2	2	3	0	1	8
h	0	0	2	2	1	5
hu	0	0	0	3	0	3
u	0	0	0	0	3	3
total *Zn*	4	4	5	5	5	23

the linear predictor do not exceed 1% in any region (Fig. 2.3). And even under optimum conditions for period of emersion, sediment type and sediment stability, seagrasses are not likely to occur in regions 2, 16, 17 and 18, because the probability of occurrence of both *Z. noltii* as *Z. marina* is less than 1% (Fig. 2.4). The probability of occurrence of both seagrass species exceeds 50% under optimal environmental conditions in regions 1, 8 to 11, and 19 to 24.

DISCUSSION

Statistical modelling. The kind of data and the way of data gathering make it questionable that the observations Y_i are in fact Bernoulli variables. The results of significance tests must therefore be interpreted with caution. Moreover, the resulting models belong to a class of exploratory models and should not be overinterpreted. Furthermore, some results (e.g. period of emersion, sediment type) are based on features which are specific to the habitat map of the Wadden Sea, and therefore they should not be directly extrapolated to other maps or to other areas.

In spite of these limits, modelling results on the distribution of Wadden Sea seagrasses give new insights into relations between Wadden Sea seagrasses and several environmental factors. Until now, relations between Wadden Sea seagrasses and their environment have only described by one factor at the time. The main advantage of the use of using Generalized Linear Models for the analysis of relations between seagrass and environment is the possibility of describing the effects of each environmental factor in combination with other environmental factors and their interactions.

The results can be used for management purposes. The probability of occurrence of seagrass species in a square may be considered as a measure of the species specific suitability to that square. Modelling results can be used to create

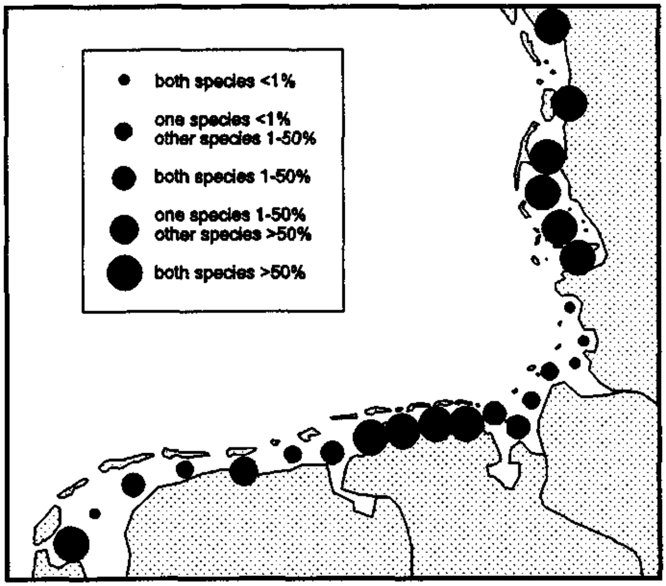

Fig. 2.4 Probability of occurrence of *Zostera noltii* and *Z. marina* in Wadden Sea regions under optimum conditions for period of emersion, sediment type and sediment stability.

maps of the suitable areas for seagrasses in the Wadden Sea (Fig. 2.5).

Sediment type. Both *Zostera noltii* as *Z. marina* show a low probability of occurrence on moderately fine sand (r). Seagrasses depend directly on the soil for nutrients and anchorage. Experimental studies have revealed that eelgrass growth, abundance and leaf size was higher on mud than on sand, which was assigned to limitation of nitrogen in sand (Short 1987). These results agree with former findings on the relation between sediment type and morphology and abundance of sublittoral eelgrass in Danish waters and the Dutch Wadden Sea: 'mud-Zostera' had broader and longer leaves and therefore more luxurious growth than 'sand-Zostera' (Ostenfeld 1908, Van Goor 1919).

Sediment stability. The present results show that both *Z. noltii* as *Z. marina* prefer lowly dynamic areas, per definition characterized by low tidal current velocities and low wave action. The findings on seagrass distribution in the Wadden Sea confirm those in Chesapeake Bay (USA) in which the distribution of *Z. marina* was found to be negatively affected by wave action (Orth & Moore 1988).

At a larger time-scale, the stability of the western part of the Dutch Wadden Sea may still be affected by the closure of the former Zuiderzee in 1932. It will probably take another few decennia until the slow adjustment of the tidal channels towards the new situation is complete (Philippart 1989). In this area the on-going change towards a new status quo may be unfavourable for the establishment of seagrass due to local sedimentation and erosion processes.

Period of emersion and region. The environmental factors period of emersion and region seem to play the most important role in the occurrence of *Z. noltii* and *Z. marina* in the Wadden Sea. The association between optimum position in the littoral zone of both seagrass species indicates that they are affected in the same way.

The optimum position of seagrass in an intertidal zone is considered to be a compromise between desiccation and light conditions (Keller & Harris 1966). Seagrasses are found to be sensitive to desiccation (Ogata & Matsui 1965). This is confirmed by observations in the Wadden Sea on desiccation and the subsequent decline of *Z. noltii* beds as the result of ditching of reclamation areas (Wohlenberg 1936, Anonymous 1987). Light intensities on a tidal flat are strongly affected by tidal fluctuations. Hence light conditions become more favourable higher up in the intertidal zone. Seagrass productivity is related to light intensity and is species specific. *Z. marina* shows lower values for light compensation and saturation points than *Z. noltii* (Jimenéz *et al.* 1987) and therefore is better equipped to occur at lower light intensities. The combination of general species-specific characteristics towards desiccation and productivity may therefore explain the field observations of the vertical distribution of *Z. noltii* and *Z. marina* in the intertidal zone of the Wadden Sea.

Regions with low probability of occurrence of seagrass under optimum conditions (Fig. 2.5) are generally situated near freshwater inputs from the main rivers. The regions Balgzand (region 1) and Vlieland (region 2) are affected by discharge water from the River Rhine, the Dollard and Borkum areas (regions 6 and 7) by discharge from the River Eems, the Wurster Wadden Sea area (regions 13 to 15) by discharge from the River Weser, and the area between Cuxhaven and the Eiderstedt peninsula (regions 15 to 18) by discharge from the River Elbe (Wellershaus 1978). These observations indicate that the presence of seagrass is strongly and negatively influenced by water from the main rivers. This might be explained by relatively low salinities and/or strongly fluctuating salinities, high turbidity and high concentrations of nutrients and toxic substances, e.g. ammonia, sulphides, some heavy metals, synthetic detergents and herbicides (Bloemendaal & Roelofs 1988), in river estuaries.

Production of both *Z. noltii* and *Z. marina* is negatively affected by long periods of low salinities (Ogata & Matsui 1965, Pinnerup 1980). In all regions, except the Ditmarschen region, mean salinity is more than 18 in at least 75% of the area. And since intertidal seagrasses are exposed to fresh water during rain at low tide, it may be expected that salinity fluctuations with short periods of low salinity do not affect seagrass growth. Apparently the impact of river water discharges exceeds the possible effects of salinity.

Light conditions for intertidal seagrasses are not only affected by the period of emersion and tidal height, but also by water column turbidity and periphyton load on leaves of seagrasses (Orth & Moore 1988). Wadden Sea river estuaries are generally more turbid than their surroundings (Postma 1982). Turbidity in estuaries is strongly correlated with suspended matter, whereas phytoplankton plays an insignificant role (Colijn 1982). Light conditions in river estuaries may therefore be

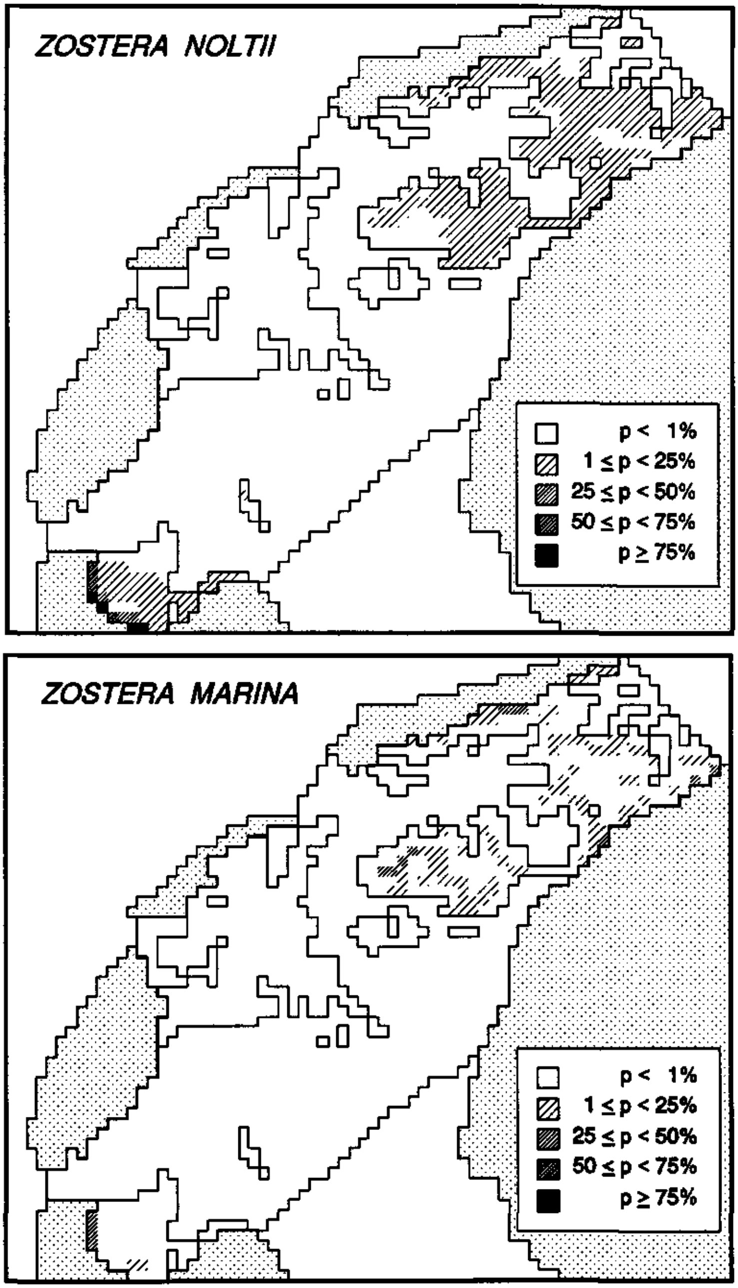

Fig. 2.5 Probability of occurrence of *Zostera noltii* and *Z. marina* per km^2 on tidal flats in the western part of the Dutch Wadden Sea.

unfavourable for seagrass growth, even under pristine conditions.

Nowadays Wadden Sea rivers generally discharge large amounts of nutrients. Increase of nutrients may result in an increase of the growth of, and shading by, epiphytic algae attached to seagrass leaves (Phillips *et al.* 1978). In Cockburn Sound (western Australia) a marked increase of nitrogen loading was found to coincide with seagrass decline, probably due to an enhanced epiphyte growth (Cambridge *et al.* 1986). Seagrasses may have been forced up the intertidal zone to receive enough light, if nutrient increase in the Wadden Sea also resulted in an increased periphyton load. If the higher intertidal zone was unfavourable due to desiccation, eutrophication may have been the cause of the decline of seagrass beds.

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CHAPTER 3

WAX AND WANE OF *ZOSTERA NOLTII* IN THE DUTCH WADDEN SEA

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 to 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 with the clay content of the sediment and negatively with the density of lugworms. The presence of macroalgae, however, seem 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 due to the fact that these seagrass stands are still expanding.

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 are the habitat of two seagrass species, viz. *Zostera noltii* Hornem. and *Z. marina* L. (eelgrass). Eelgrass 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 & 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 at 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. 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.

STUDY SITES AND METHODS

Study sites

At present, the *Zostera 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. 3.1). In former years, *Z. noltii* was also found at the Balgzand tidal flats in the western Wadden Sea (Fig. 3.1). This seagrass stand, however, decreased from the 1960s onwards (Polderman & Den Hartog 1975). The remaining *Z. noltii* population consists now of scattered small (approx. 1m^2) plots with a summed area of approximately 0.01 km^2 (J.J. Beukema pers. comm. 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 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.

Historical changes

Historical data on the distribution of *Zostera noltii* in the Dutch Wadden Sea were obtained from earlier surveys, false-colour photographs, literature (Hootsmans *et al.* 1986, Jacobs *et al.* 1983, Mörzer Bruijns & Tanis 1955, Polderman & Den Hartog 1975), 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

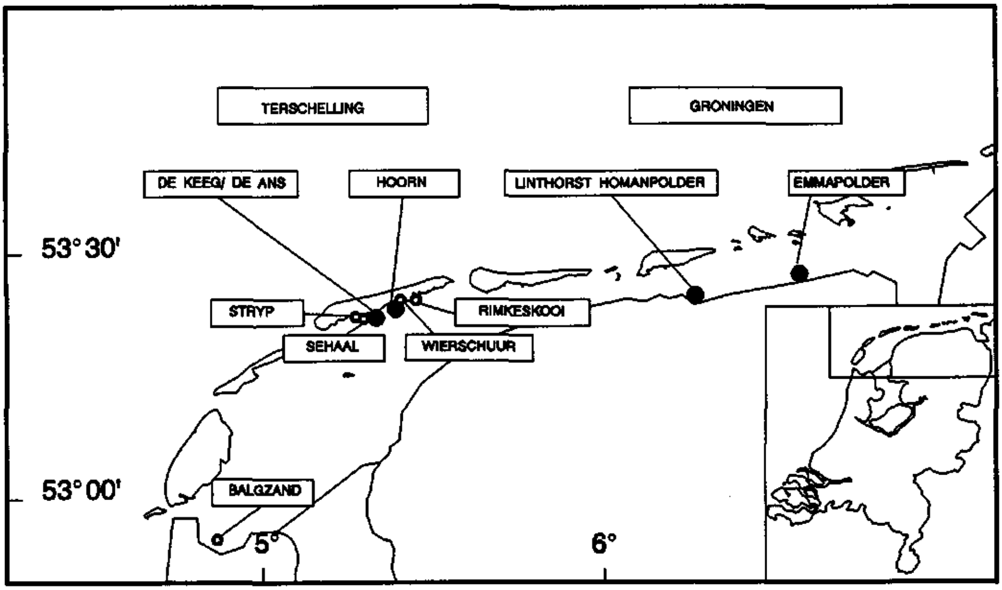

Fig. 3.1 Overview of study sites of the seagrass *Z. noltii* in 1987/88 and several other locations in the Dutch Wadden Sea as mentioned in the text.

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.

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 *Zostera noltii* east of the mapped area beyond the Wierschuur but not as far away as the Rimkeskooi (Fig. 3.1) were not included.

In the sedimentation fields off Groningen, both study sites were divided into hypothetical squares of 100 by 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.

Environmental factors

The coverage of seagrass and macroalgae was classified according to a modified scale of Braun-Blanquet (Westhoff & 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 & Van der Maarel 1973). At the Terschelling study sites, also the number of lugworm castings per m^2 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 to 10 cm with a muddy sand, and the sediment consists of mud (> 8% clay particles) if the footprint is deeper than 10 cm. Since 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, since the depth of the footprint on the tidal flats of Terschelling was seldom more than 5 cm, most of the area of these study sites 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, 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, 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·$year^{-1}$.

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

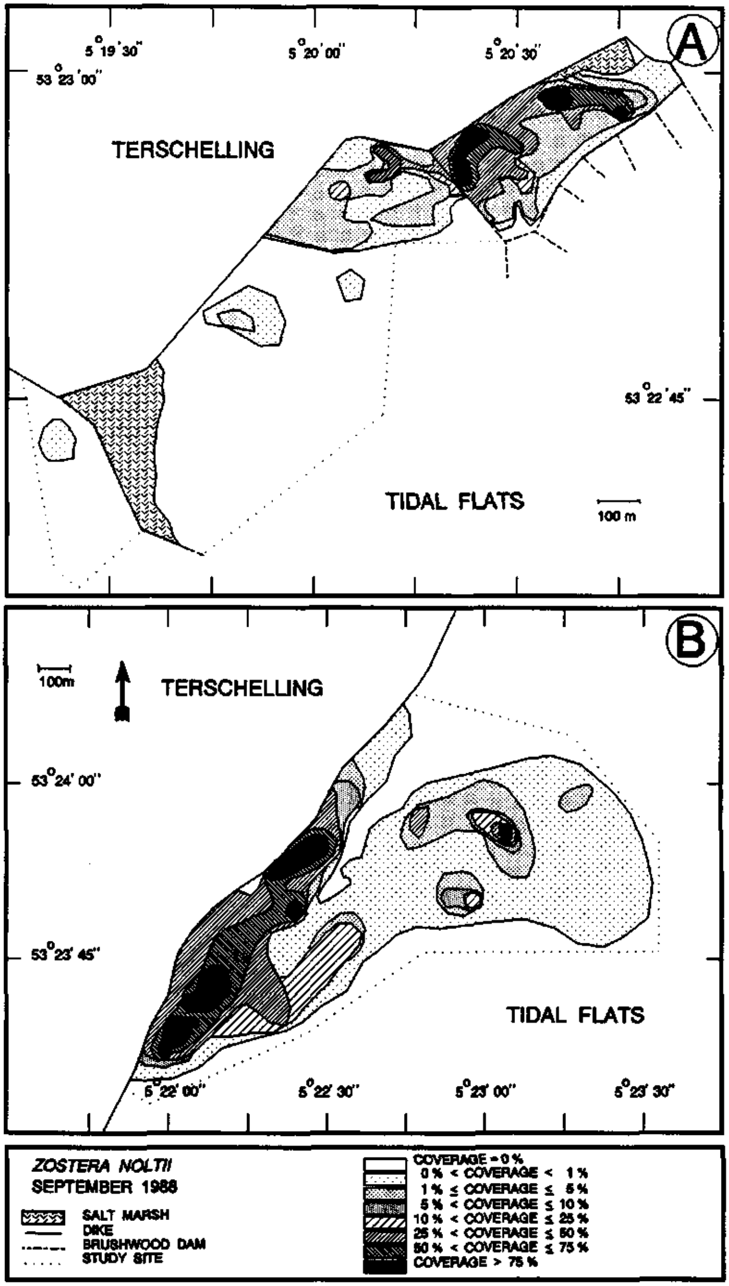

Fig. 3.2 Coverage of *Zostera noltii* in the study sites De Keeg-De Ans (A) and Hoorn (B) on the tidal flats off Terschelling in September 1988.

Table 3.1 Area of the stands of the intertidal seagrass *Zostera noltii* in the Dutch Wadden Sea in 1970/72 and 1987/88.

	Area (km^2) 1972/73	Area (km^2) 1987/88
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 & Den Hartog 1975 (corrected for presence of *Z. marina*)
[b] present paper
[c] after P. Bouwsema pers. comm. 1991.
[d] J.J. Beukema pers. comm. 1991.

RESULTS

Historical changes

In 1987/88, all four study sites comprised more or less monospecific *Zostera noltii* stands. The eelgrass *Z. marina* occurred only as scattered plants at a density of less than 1 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. 3.2) and between 10% and 25% at the Linthorst Homanpolder and Emmapolder sites (Fig. 3.3).

On the Terschelling tidal flats (Fig. 3.1), seagrass occurred in the 1930s in Stryp, Sehaal, De Keeg-De Ans and Hoorn (Mörzer Bruijns & Tanis 1955). In 1972 (Polderman & Den Hartog 1975), however, the Stryp and Sehaal seagrass stands had disappeared and did not return during the following 15 years (pers. obs.). The two remaining stands showed relatively low values in covered area between 1976 and 1986 (Fig. 3.4), but from 1986 to 1987/88 a strong increase was noted. The area of the seagrass stand of De Keeg-De Ans increased by more than 50% between 1972/73 and 1987/88, whereas the area of the seagrass stand of Hoorn decreased by almost 30% (Table 3.1).

In the sedimentation fields off Groningen, the area of the seagrass stands showed a rapid increase over the past 10 years (Fig. 3.4). The situation at the beginning of the 1970s is not known exactly. According to P. Bouwsema (pers. comm. 1991) no seagrass occurred in or near the salt-marsh works of the Linthorst

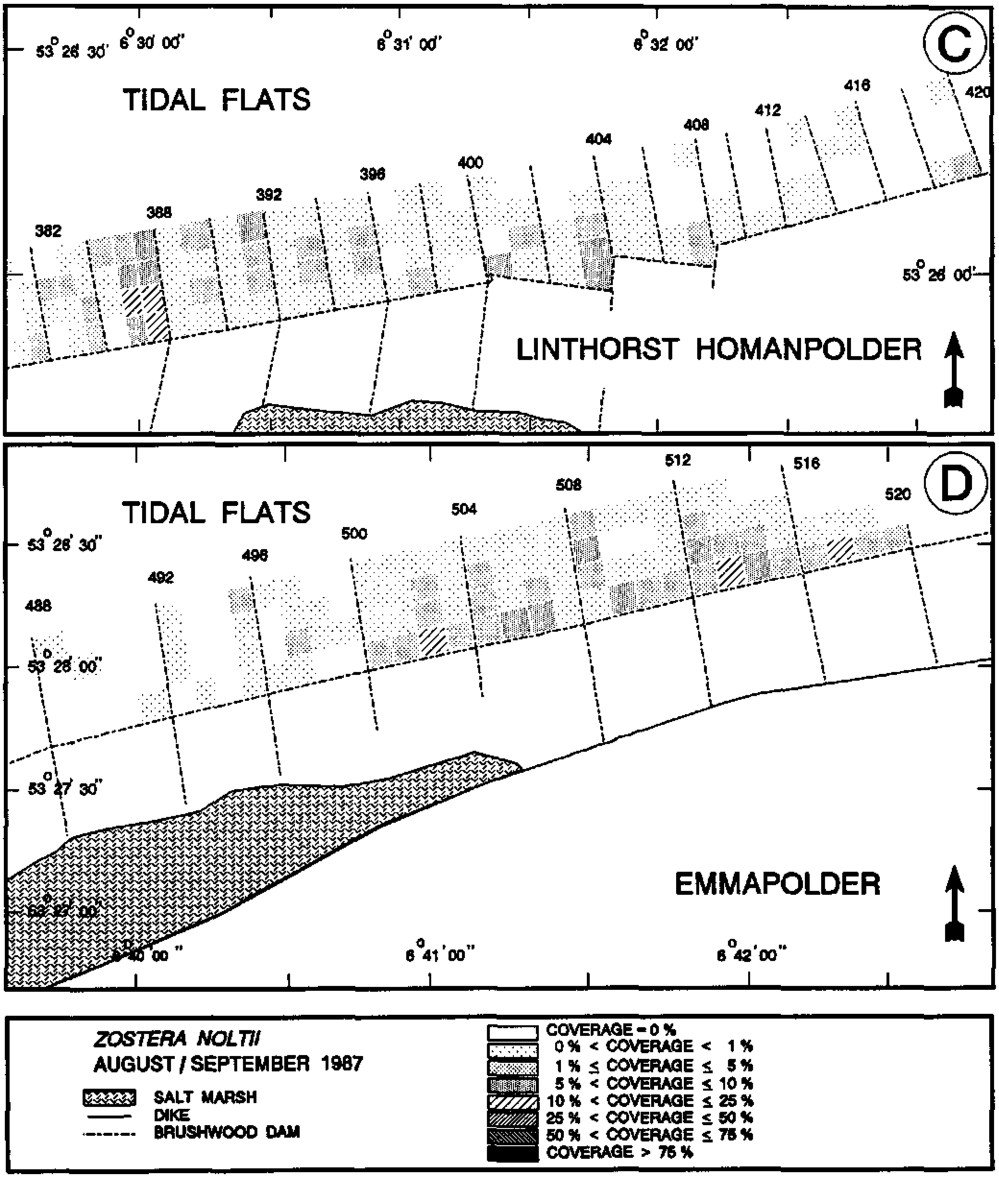

Fig. 3.3 Coverage of *Zostera noltii* in the study sites Linthorst Homanpolder (C) and Emmapolder (D) in the outer sedimentation fields of the salt-marsh works off Groningen in August and September 1987, respectively.

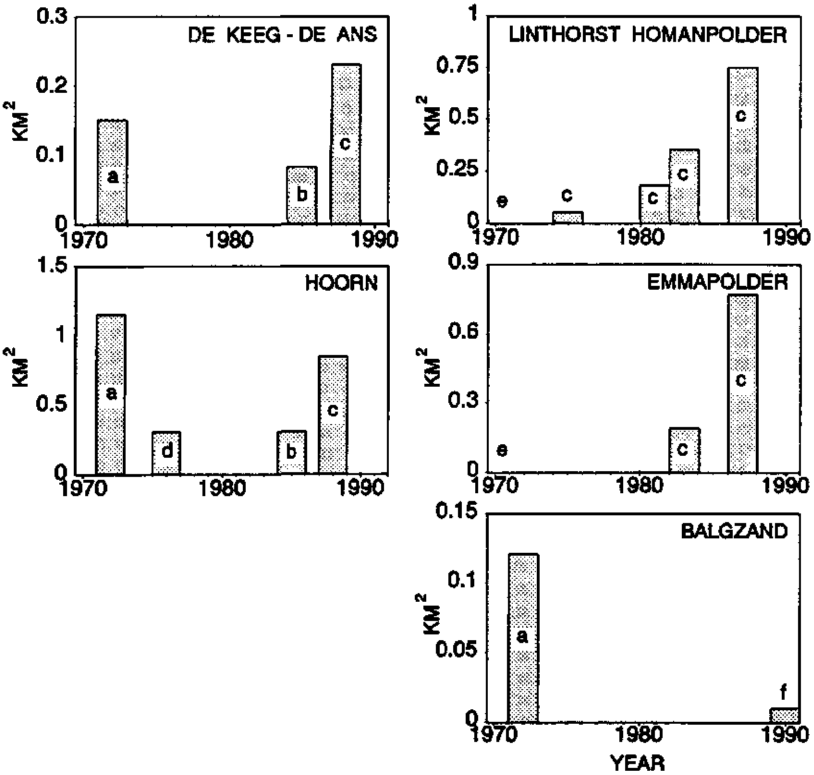

Fig. 3.4 Historical changes of the area of the main stands of the seagrass *Zostera noltii* in the Dutch Wadden Sea from 1970 to 1988 ([a] after Polderman & Den Hartog 1975, [b] Hootsmans *et al.* 1986, [c] present paper, [d] Jacobs *et al.* 1983, [e] after P. Bouwsema pers. comm. 1991, [f] J.J. Beukema pers. comm. 1991). See also table 3.1.

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 1972/73 (Table 3.1). After 1975, the seagrass stands increased in a more or less similar way in both study sites (Fig. 3.4).

The total area covered by *Z. noltii* stands in the Dutch Wadden Sea in 1987/88 was approximately 2.6 km^2 (Table 3.1), which is almost twice as much as in 1972/73. 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.

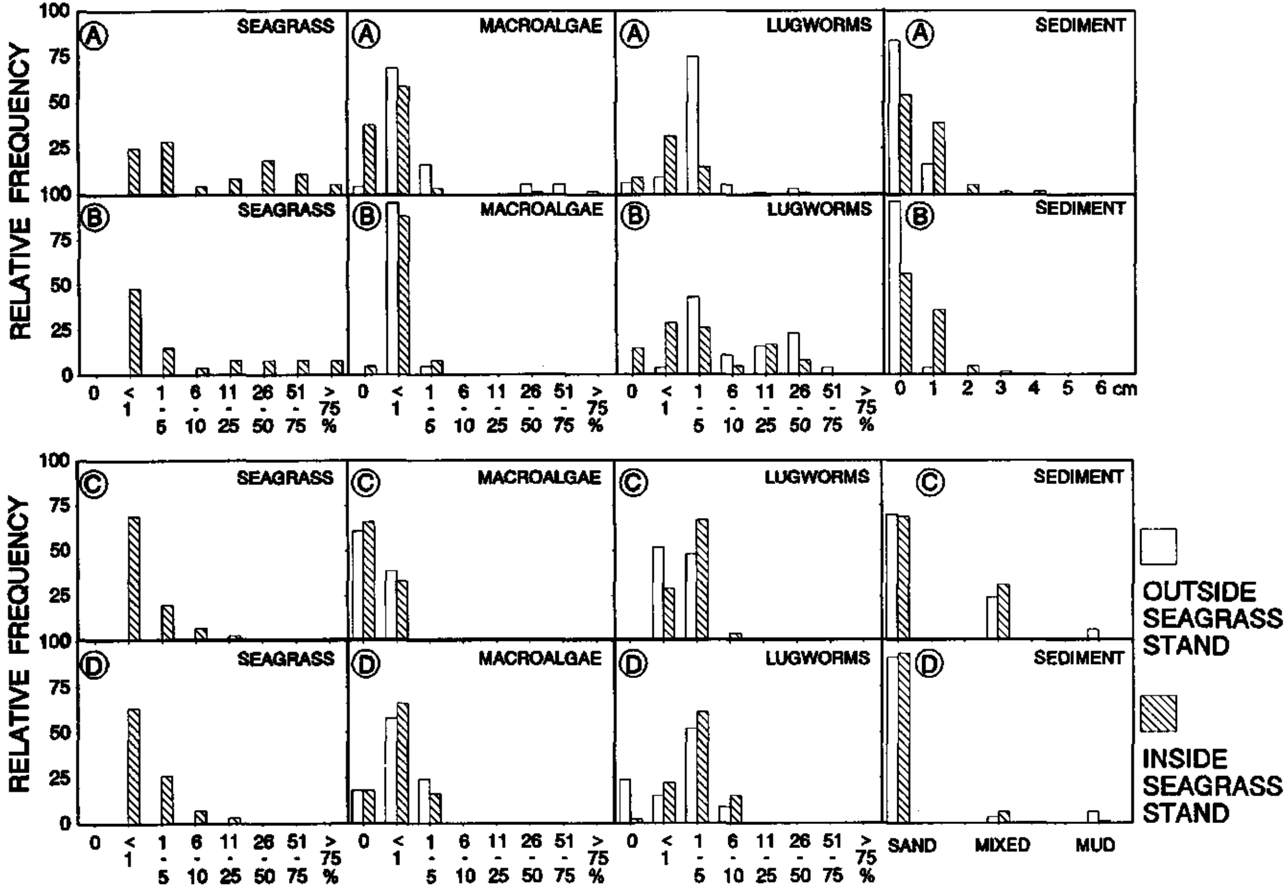

Fig. 3.5 Relative frequency of the coverage (%) of the seagrass *Zostera noltii*, the coverage (%) of macroalgae, the coverage (%) of the faecal castings of the lugworm *A. marina* and sediment type (see text) in the close surroundings of (white bars) and inside (hatched bars) the seagrass stands in the sampling points at De Keeg-De Ans (A: n = 191), Hoorn (B: n = 361), Linthorst Homanpolder (C: n = 152) and Emmapolder (D: n = 120) study sites in 1987/88.

Environmental factors

The macroalgae coverage was generally less than 1% at the study sites (Fig. 3.5). 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 *Zostera noltii* and macroalgae were found at the other study sites (Table 3.2).

Lugworms were present inside as well as outside the seagrass stands in all four study sites (Fig. 3.5). 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. 3.5). 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 coverage of castings than in areas with high casting coverage (Table 3.2). 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 3.2). The mean density of lugworm faecal castings in the De Keeg-De Ans study site was 8 castings$\cdot$m^{-2} inside and 59 castings$\cdot$m^{-2} outside the seagrass stand. At the Hoorn study site, these densities measured 24 castings$\cdot$m^{-2} inside and 54 castings$\cdot$m^{-2} 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$\cdot$year^{-1} inside the seagrass stand at De Keeg-De Ans and 9 cm$\cdot$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$\cdot$year^{-1}.

The footprint depth and the coverage of seagrass were positively correlated in both study sites on the tidal flats of Terschelling (Table 3.2): *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. 3.5). Hardly any seagrass occurred in squares classified as mud in the sedimentation fields off the coast of Groningen (Fig. 3.5). However, the distribution of *Z. noltii* was not significantly related to the sediment type in these areas (Table 3.2). Footprint depth and the coverage by *A. marina* faecal castings were negatively correlated in both study sites of Terschelling (Table 3.2): the highest coverage by castings was generally found in the areas with relatively coarse sand (Fig. 3.5). 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.

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

Table 3.2 Significance of relationships between the coverage (%) of *Zostera noltii*, the coverage (%) by faecal castings of *Arenicola 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 1987/88 ($^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$, ns: not significant).

Study site				Correlation	X^2	df	p
De Keeg-De Ans	*Z. noltii*	vs.	Macroalgae	-	63.46	6	***
		vs.	*A. marina*	-	131.30	6	***
		vs.	Sediment	+	31.48	3	***
	A. marina	vs.	Sediment	-	22.29	3	***
Hoorn	*Z. noltii*	vs.	Macroalgae	None	5.97	4	ns
		vs.	*A. marina*	-	142.78	15	***
		vs.	Sediment	+	58.59	7	***
	A. marina	vs.	Sediment	-	107.69	6	***
Linthorst Homanpolder	*Z. noltii*	vs.	Macroalgae	None	1.58	3	ns
		vs.	*A. marina*	+	17.10	3	***
		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
		vs.	*A. marina*	None	1.31	1	ns

polder salt-marsh works which have contained seagrass since 1975 experienced a generally positive accretional balance of +0.003 to +0.03 $m \cdot year^{-1}$ year, 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 $m \cdot year^{-1}$ (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.

DISCUSSION

Historical changes

The interpretation of the historical changes in the abundance of *Zostera noltii* stands in the Dutch Wadden Sea must be performed with caution, due 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. Since 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 a unknown date in 1971 (Polderman & 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 & T.G. van Hoorn pers. comm. 1991). The outer sedimentation fields of these salt-marsh works were constructed between 1950 and 1953, and subsequently ditched yearly until 1966/69 (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.

Environmental factors

The increase of *Zostera noltii* in the Groningen salt-marsh works, doubling in area every three 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 (pers. obs.). 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 & 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 hight and period of emersion, the turbidity of the water and the periphyton load on the seagrass leaves (Phillips *et al.* 1978, Giesen *et al.* 1990, Orth & Moore 1988). During the last decades, the biomass of phytoplankton and microphytobenthos in the western Wadden Sea doubled (Cadée 1984, Cadée & 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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CHAPTER 4

SEASONAL VARIATION OF AN INTERTIDAL *ZOSTERA NOLTII* DOMINATED COMMUNITY IN THE DUTCH WADDEN SEA

ABSTRACT The seasonal dynamics of a seagrass dominated community on the tidal flats of Terschelling, consisting of the seagrass *Zostera noltii*, periphyton and the periphyton grazing mudsnail *Hydrobia ulvae*, was studied to asses the relationships between the life cycle of the seagrass and the light conditions in its habitat. The total biomass of the seagrass showed an unimodal curve with a maximum of more than 110 gADW$\cdot$m^{-2} in August and a minimum of less than 10 gADW$\cdot$m^{-2} in January. Leaf growth rates and biomass development appeared to be related with light conditions in the seagrass habitat. The periphyton chlorophyll density on the seagrass leaves followed a more or less similar pattern as the seagrass, ranging from 0.3 μg chlorophyll$\cdot$cm^{-2} in May to almost 2.5 μg chlorophyll$\cdot$cm^{-2} at the end of August. The periphyton biomass was, however, almost 1.6 mgADW$\cdot$cm^{-2} in May and subsequently decreased to less than 0.6 mgADW$\cdot$cm^{-2} in August. The total weight of *H. ulvae* was more or less stable, varying between more than 150 and less than 400 gDW$\cdot$m^{-2}, although significant time effects were observed within different size-classes of mudsnails.

The light conditions of seagrass were influenced by periphyton and mudsnails. Mean shading caused by periphyton during the growing season was estimated at 10% to 90%, resulting in a reduction of about 2 to 80% of the yearly period at which the light compensation point of the seagrass is exceeded. The mudsnails were found to be theoretically able of ingesting daily 25% to 100% of the standing stock of periphyton and microphytobenthos. It is concluded that grazing by mudsnails and subsequent shading by periphyton determine the biomass development and survival of *Z. noltii* in the seagrass dominated community on the tidal flats off Terschelling.

INTRODUCTION

The seagrass *Zostera noltii* Hornem. is widely distributed along the north-eastern coasts of the Atlantic, extending from temperate Norway to tropical Mauritania (Phillips & Meñez 1988). The populations of this seagrass species obviously experience a broad range in local habitat conditions, e.g. temperature and light, which do not only vary at different latitudes but also during the season.

The biomass variation of seagrasses appears to be related with these seasonal variations in the environment and the extent of variation tends to be greater for populations in higher latitudes (Duarte 1989). In temperate climate zones, winters can be too dark and too cold to sustain seagrass photosynthesis. *Z. noltii* survives this unfavourable growth periods by means of whole plants (Pérez & Camp 1986, Wyer *et al.* 1977) or rhizomes (Jacobs *et al.* 1983). Although inflorescences of *Z. noltii* have been found throughout the area of occurrence, seedlings do not seem to play an important role in year-to-year survival of this seagrass species (Jacobs *et al.* 1983, Vermaat *et al.* 1987, Loques *et al.* 1988).

From the beginning of the 1970s towards the end of the 1980s, the intertidal stands of *Zostera noltii* at the tidal flats of the western Wadden Sea in the Netherlands showed a continuous decline. The seagrass stand on the Balgzand tidal flat (Fig. 4.1) almost completely disappeared and the total area of *Z. noltii* stands on the tidal flats of Terschelling (Fig. 4.1) decreased on average about 20% within 15 years (Chapter 3). This decline is thought to be related to a change in local light conditions.

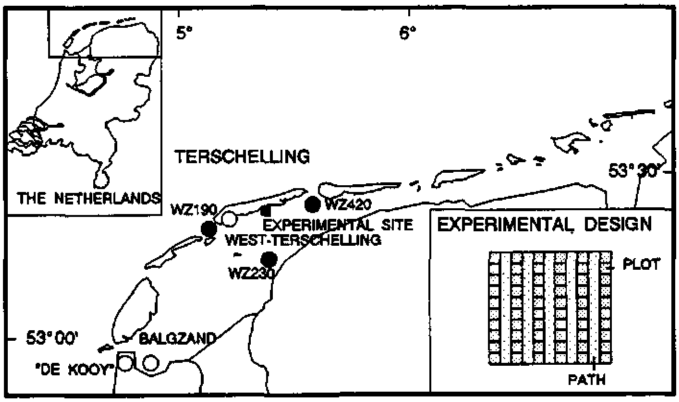

Fig. 4.1 Location of the experimental site on the tidal flats off Terschelling, WORSRO sampling stations of suspended matter (WZ190, WZ230, WZ420) and other locations in the Dutch Wadden Sea as mentioned in the text.

The hypothesis for the decline rests on the premise that light availability is often the primary limiting factor for seagrass growth (Dennison & Alberte 1985). If so, then intertidal seagrass stands occur only above a lower limit imposed by penetration of light at an intensity which allows gross photosynthesis to exceed respiration (Shepherd *et al.* 1989). The light availability for intertidal seagrass stands is not determined by the fluctuations in tidal height and the turbidity of the water alone, but also by the density of the periphyton on seagrass leaves (Orth & Moore 1985). An increase of the turbidity of the water (Giesen *et al.* 1990) or of the density of the periphyton will subsequently result in an decrease of the area of the seagrass stand (Phillips *et al.* 1978, Philippart *et al.* 1992).

The epiphyte biomass is not only determined by the seasonal fluctuations in epiphyte and seagrass growth, but also by grazing epifauna (Orth & Van Montfrans 1984, Van Montfrans *et al.* 1984, Brönmark 1985, Hootsmans & Vermaat 1985, Howard & Short 1986). The potential grazer of periphyton on *Zostera noltii* in the Wadden Sea is *Hydrobia ulvae*. This mudsnail is one of the most abundant epibenthic faunal species living in the Wadden Sea (Dekker 1989). It feeds on diatoms present in microphytobenthos (Cadée 1980) and the periphyton on seagrass leaves (Hootsmans & Vermaat 1985).

This paper aims at assessing the relationships between the life cycle of *Zostera noltii* and the light conditions in its habitat. Firstly, the seasonal cycle of an intertidal seagrass dominated ecosystem including periphyton and mudsnails off Terschelling is described. Secondly, the seasonal cycle of this seagrass species is related to the annual fluctuations in the light conditions in the seagrass habitat and its determining factors, e.g. daily irradiation, tidal cycles and turbidity of the water. Thirdly, this cycle is related to the seasonal abundance patterns of periphyton and *Hydrobia ulvae*.

MATERIALS AND METHODS

Experimental design

The experiment was performed on a tidal flat off Terschelling (Fig. 4.1), the Netherlands. The experimental area covered a relatively dense stand of *Zostera noltii*. This area measured 20 by 22 m and was divided into 11 rows of 2 x 20 m. Six rows were subdivided into experimental plots of 2 by 2 m. The remaining 5 rows were used as paths (Fig. 4.1).

Seagrass

From May 1988 to January 1989, the experimental plots were sampled 8 times at more or less regular intervals. Four randomly chosen plots were sampled during each sampling period. In each selected plot, the leaf growth rate (LGR), leaf loss rate (LLR) and leaf net-growth rate (LNR) of vegetative shoots of *Zostera noltii* were determined according to an adjusted leaf marking technique, assuming linear growth in time (Vermaat *et al.* 1987).

Seagrass, periphyton and mudsnails were sampled by means of a sediment core with diameter of 30 cm (sampling period 1 to 7) and 7 cm (sampling period 8) to a depth of approximately 10 cm. At the first sampling date, the samples were analyzed immediately after collection. During all other sampling dates, the samples were stored in plastic bags at -20°C until further analysis. The samples were washed through a 1-mm sieve and divided into seagrass material and mudsnails.

The seagrass material was divided into vegetative shoots, generative shoots and rhizome internodes. All roots were removed from the samples because it was impossible to separate living from dead root material. Rhizomes were considered alive when crispy and coloured light brown or ivory white. Detached green leaves and shoots in the samples were added to the shoot subsample. The number of shoots and internodes was counted. The biomass of all seagrass samples (ADW) was determined as the difference between dry weight (24 hours 105°C) and ash weight (2 hours 520°C).

Earlier investigations on *Z. noltii* on the tidal flats of Terschelling indicated that this seagrass species shows the same seasonal change in morphology of the rhizomes as *Z. japonica* (Bigley & Harrison 1986), with the length of the latest rhizome internodes being longer in spring than in autumn (Fig. 4.2). The rhizomes of *Z. noltii* were thus divided into four classes, viz. rhizomes which were formed in the previous year (1987) with long (LONG87) and short internodes (SHORT87), and more recently formed rhizomes with long (LONG88) and short internodes (SHORT88).

Periphyton

Eight shoots from each biomass sample of *Zostera noltii* were collected randomly, and subsequently divided into two groups of four shoots each. The number of

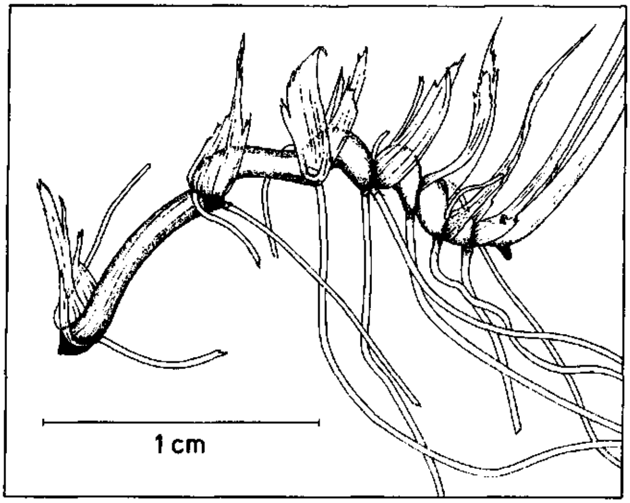

Fig. 4.2 Morphology of *Zostera noltii* rhizomes. Note the difference in length of the internodes formed in summer (close to the apical shoot on the right) and in spring (more distant from the shoot).

leaves and the morphology of all leaves was determined. The leaves were put in a petri-dish filled with Whatman GF/C filtered seawater and cleaned of periphyton by carefully scraping them with a scalpel until they were visually clean.

From one sample of four shoots, the periphyton was collected on Whatman GF/C filters. The periphyton as well as the periphyton-free seagrass leaves were deep frozen until analysis of chlorophyll-*a* and chlorophyll-*b* contents according to the method of Wellburn & Lichtenthaler (1984) in 80% acetone.

From the other sample, the periphyton was collected on pre-treated Whatman GF/C filters (previously rinsed with demineralized water, dried at 450°C and weighted). The biomass of these periphyton samples (ADW), was determined as the difference in dry weight (24 hours at 105°C) and ash weight (2 hours at 450°C). Determination of the biomass of the seagrass leaves (ADW) was performed in the same way as for the other seagrass samples.

Mudsnails

The mudsnails were divided into 5 classes of different shell-size by means of sieves with 1, 1.4, 1.8, 2.24 and 2.5 mm mesh-widths. A distinction was made between dead mudsnails with whitish coloured shells and, at the moment of sampling, living mudsnails with green-brownish coloured shells. The dead mudsnails were removed from small samples. For larger samples, the fraction of dead snails was estimated by means of subsampling. The number and dry weight (24 hours 105°C) of the mudsnails was determined for each size class.

Table 4.1 The environmental circumstances used as input for modelling the light conditions at the habitat of *Zostera noltii* on the tidal flats off Terschelling, the Netherlands.

	Symbol	Value, range or period	Unit
Latitude	Φ	53°24′	degrees, minutes
Daily insolation	I_{daily}	1 Jan - 31 Dec 1988 Airport "De Kooy"[a]	$J \cdot cm^{-2} \cdot day^{-1}$
Levels Low & High Water	z_{lP}	1 Jan - 31 Dec 1988 "West-Terschelling"[b]	cm
Times Low & High Water	t_{lP}	1 Jan - 31 Dec 1988 "West-Terschelling"[b]	hours; minutes
Position in tidal zone	p_z	+50 / 0 / -50[c]	cm ± Mean Sea Level
Attenuation coefficient	k	1 Jan 1984 - 31 Dec 1992[d]	m^{-1}
Light Compensation Point	LCP	59[e]	$\mu E \cdot m^{-2} \cdot s^{-1}$

[a] Royal Netherlands Meteorological Institute (KNMI)
[b] Rijkswaterstaat
[c] Philippart & Dijkema (unpublished)
[d] Rijkswaterstaat, WORSRO database
[e] Philippart (unpublished)

Statistics

All statistical analyses were performed using GENSTAT. Data were tested for normality and homogeneity prior to analysis of variance (ANOVA) of the effects of seasonality. Differences between means were compared by means of Scheffé tests (Sokal & Rohlf 1981).

Light conditions

The light conditions of the habitat of *Zostera noltii* on the tidal flats off Terschelling were estimated according to the equations as described in the appendix and using parameter values as described in table 4.1. The daily insolation was measured at the airport of "De Kooy", located on the mainland and approximately 50 kilometres west of the seagrass stand studied (Fig. 4.1). Tidal heights of the seagrass stand were based on the tidal heights as predicted for the harbour of West-Terschelling for 1988 (Fig. 4.1). Thirty minutes were added to the times of high and low water in order to correct for the difference in timing of the tide between West-Terschelling and the actual seagrass habitat.

The seagrass stand at the tidal flats of Terschelling is located between +50 and -30 cm relative to NAP, i.e. Netherlands Ordnance Level, approximately equal to Mean Sea Level (Chapter 3). It is suggested that the lower limit of this seagrass stand is not determined by light conditions, but by the presence of lugworms (Philippart 1994). The light conditions were, therefore, estimated for positions in the intertidal zone at +50, 0 and -50 cm relative to NAP.

The light attenuation coefficients k of the tidal flat area off Terschelling were estimated from average concentrations of suspended matter concentrations at surrounding sampling stations, viz. WZ190, WZ230 and WZ420 (Fig. 4.1) for the period 1984-1992, i.e. 1988 ± 4 years, as measured and stored in the WORSRO database by Rijkswaterstaat. The k values based on suspended matter concentrations in the Wadden Sea were calculated from the equation supplied by De Jonge & De Jong (1992):

$$k = E_0 + 0.04 \cdot SPM$$

in which SPM is the concentration of the suspended particulate matter ($g \cdot m^{-3}$) and E_0, the background light attenuation coefficient, is assumed to be 0.5 m^{-1}. The observed seasonal trend in light attenuation coefficients was assumed to be cyclic and described by means of a periodic regression equation (Roberts 1992).

The light conditions were expressed as the number of hours per day at which the irradiance was equal to or exceeded the light compensation point (LCP) of this seagrass species. Laboratory experiments showed that the light compensation point of *Zostera noltii* was approximately 59 $\mu E \cdot m^{-2} \cdot s^{-1}$, based on the Michaelis-Menten model (Chapter 6).

RESULTS

Seagrass

All growth rates of vegetative shoots of *Zostera noltii* showed a significant seasonality (Table 4.2). The leaf growth rates (LGR) were approximately 0.04 $mm^2 \cdot mm^{-2} \cdot day^{-1}$ from May to the beginning of August, followed by a significant decrease of more than 50% (Fig. 4.3). The leaf loss rate (LLR) was practically zero in spring and averaged up to more than 0.06 $mm^2 \cdot mm^{-2} \cdot day^{-1}$ in September. Autumn values were, however, not significantly different from spring values due to the large variation in leaf loss rates (Fig. 4.3). The net leaf growth rate (LNR) averaged approximately 0.03 $mm^2 \cdot mm^{-2} \cdot day^{-1}$ from May to the beginning of August and decreased significantly to negative values hereafter (Fig. 4.3).

The total biomass of *Z. noltii* showed a significant effect of time (Table 4.2). The total biomass increased from May to August, reaching a maximum of more than 110 $gADW \cdot m^{-2}$ at the end of August (Fig. 4.4). The total biomass in May 1988 was almost equal to the biomass in January 1989, and approximately 10% of the maximum biomass found in August 1988 (Fig. 4.4). The seasonality of shoots and rhizomes corresponded with another, the maximum biomass of shoots coincided with the maximum biomass of rhizomes at the end of August (Fig. 4.4).

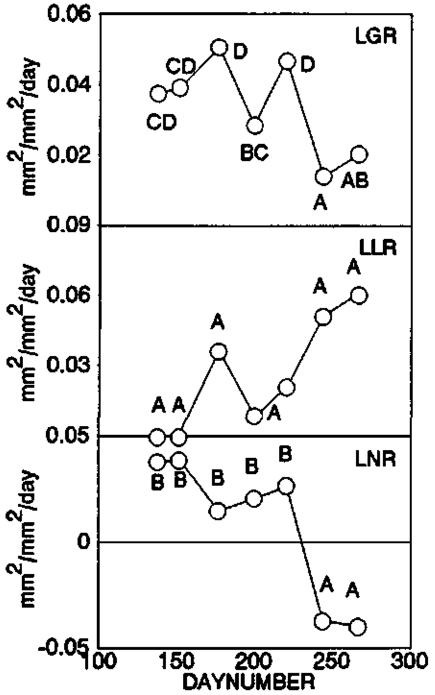

Fig. 4.3 Seasonal variation in mean leaf growth rate (LGR), mean leaf loss rate (LLR) and mean leaf nett-growth rate (LNR) of leaves of *Zostera noltii* on the tidal flats off Terschelling from 17 May to 22 September 1988. Values indicated with similar lettering are not significantly different per group of measurements. Number of replicates is 20.

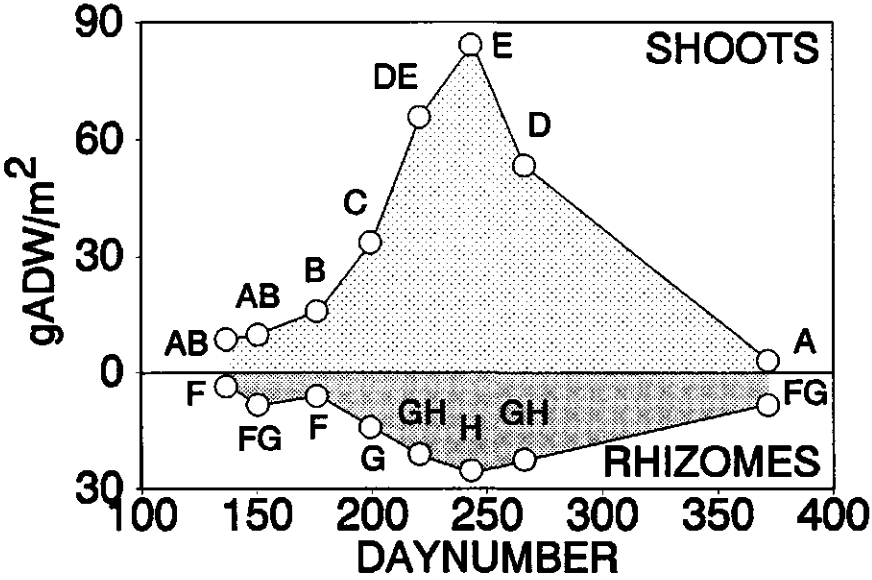

Fig. 4.4 Seasonal variation in mean biomass (gADW·m^{-2}) of shoots and rhizomes of *Zostera noltii* on the tidal flats off Terschelling from 17 May 1988 to 6 January 1989. Number of replicates is 4.

Table 4.2 Degrees of freedom (df), number of replicates (n), deviance ratio (F_s) and level of significance (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, ns = not significant) of seasonal effects on biomass, densities, leaf growth rates and chlorophyll contents of *Zostera noltii* on the tidal flats off Terschelling from 17 May 1988 to 22 September 1988 (period I), from 30 May to 22 September 1988 (period II), or from 17 May 1988 to 6 January 1989 (period III).

		Period	n	df	F_s	p
Biomass	Total (shoots & rhizomes)[b]	III	4	7	22.43	***
(gADW·m^{-2})	Aboveground (shoots)[b]	III	4	7	25.14	***
	Vegetative shoots[b]	III	4	7	27.35	***
	Generative shoots[b]	III	4	7	6.68	***
	Underground (rhizomes)[b]	III	4	7	8.72	***
	Rhizomes LONG87[b]	III	4	7	5.85	***
	Rhizomes SHORT87[b]	III	4	7	5.20	**
	Rhizomes LONG88[b]	III	4	7	9.25	***
	Rhizomes SHORT88[b]	III	4	7	26.30	***
	Shoots/(shoots + rhizomes)[c]	III	4	7	13.65	***
	Gen.sh./(gen.sh. + SHORT88)[c]	III	4	7	13.48	***
Density	Vegetative shoots[c]	III	4	7	9.45	***
(m^{-2})	Generative shoots[b]	III	4	7	6.87	***
	Internodes LONG87[b]	III	4	7	4.52	**
	Internodes SHORT87[b]	III	4	7	3.14	*
	Internodes LONG88[b]	III	4	7	9.83	***
	Internodes SHORT88[b]	III	4	7	1.99	ns
Leaf growth rates	Leaf Growth Rate[c]	I	20	6	8.06	***
(mm^2·mm^{-2}·day^{-1})	Leaf Loss Rate[b]	I	20	6	7.47	***
	Leaf Nett-growth Rate[a]	I	20	6	3.70	**
Chlorophyll	Chlorophyll-*a*[c]	II	4	6	7.49	***
(μgCHL·cm^{-2})	Chlorophyll-*b*[c]	II	4	6	8.93	***
	Chlorophyll-(*a* + *b*)[c]	II	4	6	7.78	***
	Chlorophyll-(*a*/(*a* + *b*))[c]	II	4	6	6.29	***

[a] ANOVA (not transformed)

[b] ANOVA with logarithmic link function

[c] ANOVA with logit link function

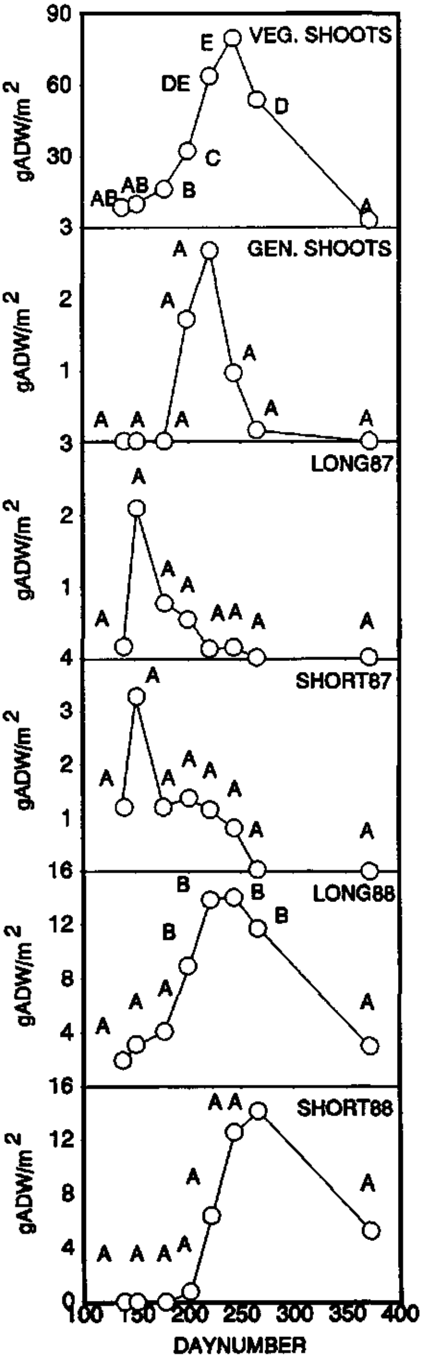

Fig. 4.5 Seasonal variation in mean biomass (gADW·m^{-2}) of vegetative shoots, generative shoots, rhizomes formed in 1987 with long internodes (LONG87), rhizomes formed in 1987 with short internodes (SHORT87), rhizomes formed in 1988 with long internodes (LONG88) and rhizomes formed in 1988 with short internodes (SHORT88) of *Zostera noltii* on the tidal flats off Terschelling from 17 May 1988 to 6 January 1989. Number of replicates is 4. Note the difference in vertical scales.

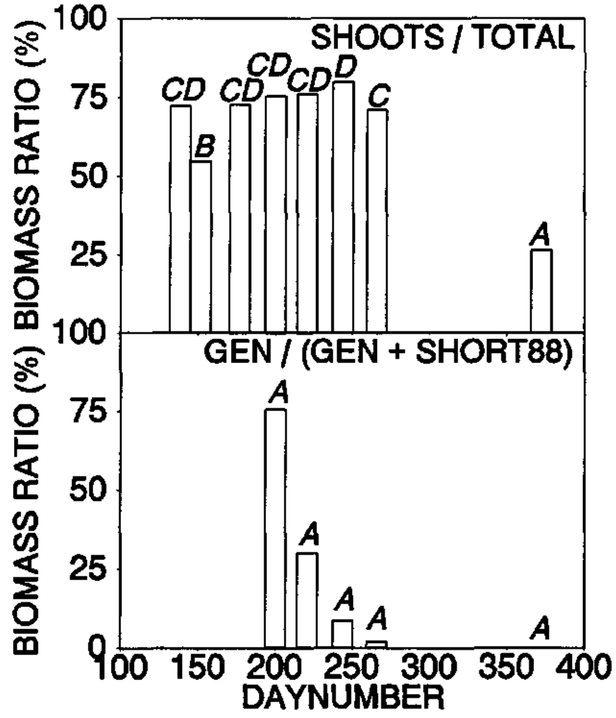

Fig. 4.6 Seasonal variation in the contribution of shoots to the total biomass (shoots and rhizomes), and in the contribution of generative shoots to the total biomass of generative shoots and SHORT88 rhizomes of *Zostera noltii* on the tidal flats off Terschelling from 17 May 1988 to 6 January 1989. Number of replicates is 4.

The aboveground biomass of *Z. noltii* consisted mainly of vegetative shoots (Fig.4.5). Generative shoots were found from July onwards. Flowering lasted at least until September, inflorescences were absent in January (Fig. 4.5). The generative shoots reached their maximum biomass at the beginning of August, the maximum biomass of vegetative shoots was found at the end of August. Rhizomes with long and short internodes produced in 1987, respectively LONG87 and SHORT87, were still present in May 1988. The LONG87 were disappeared in September 1988 and the SHORT87 in January 1989 (Fig. 4.5). Newly formed rhizomes with long internodes (LONG88) were already present in May and reached maximum biomass values in August (Fig. 4.5). Newly formed rhizomes with short internodes (SHORT88) were found from July onwards and reached maximum biomass at the end of summer, i.e. August and September (Fig. 4.5). In August, the biomass of the newly formed rhizomes with long internodes (LONG88) was almost equal to that of the rhizomes with short internodes (SHORT88). In January 1989, the biomass of SHORT88 rhizomes was almost twice as high as that of LONG88 rhizomes (Fig. 4.5). During the fieldwork it was noticed that all rhizomes

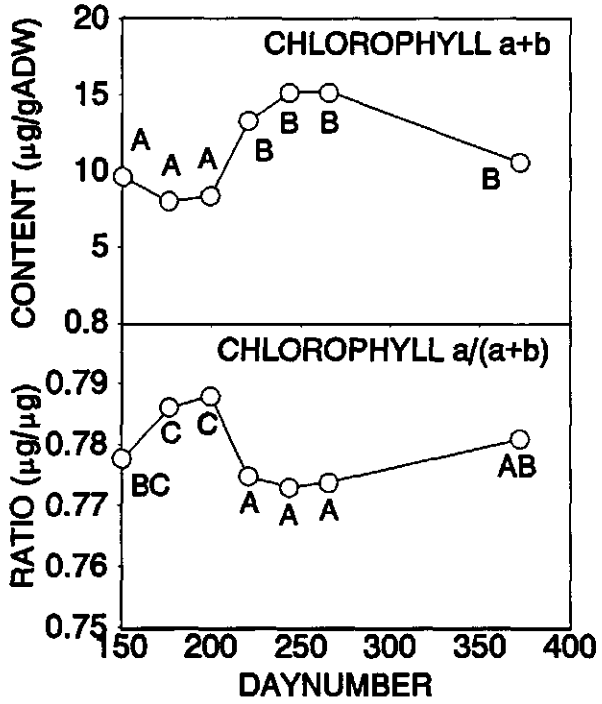

Fig. 4.7 Seasonal variation in mean chlorophyll content (μgCHL($a+b$)·gADW^{-1}) and in the contribution of chlorophyll-a to the total chlorophyll content (μgCHL(a)·μgCHL($a+b$))$^{-1}$ of periphyton-free leaves of *Zostera noltii* on the tidal flats off Terschelling from 30 May to 22 September 1988. Number of replicates is 4.

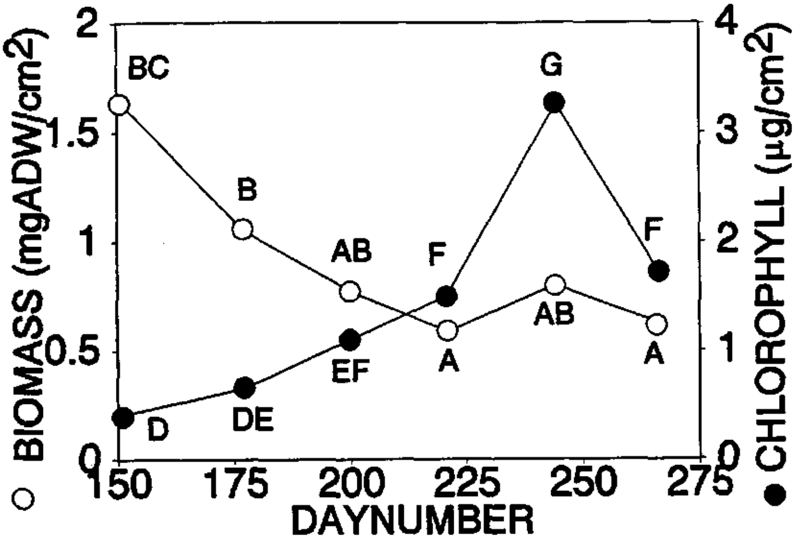

Fig. 4.8 Seasonal variation in mean periphyton dry-weight (gDW·cm^{-2}) and periphyton chlorophyll (μgCHL($a+b$)·cm^{-2}) on the leaves of *Zostera noltii* on the tidal flats off Terschelling from 30 May to 22 September 1988. Number of replicates is 4.

Table 4.3 Degrees of freedom (df), number of replicates (n), deviance ratio (F_s) and level of significance (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, ns = not significant) of seasonal effects on periphyton weight, biomass, ash-content and chlorophyll-content on leaves of *Zostera noltii* on the tidal flats off Terschelling from 30 May to 22 September 1988 (period II).

		Unit	Period	n	df	F_s	p
Per leaf area	Biomass^{b}	mgADW·cm^{-2}	II	4	5	3.66	*
	Ash-content^{c}	gAW·gDW^{-1}	II	4	5	1.04	ns
	Chlorophyll a^{b}	µgCHLa·cm^{-1}	II	4	5	13.03	***
	Chlorophyll b^{b}	µgCHLb·cm^{-2}	II	4	5	3.94	*
	Chlorophyll (a+b)^{b}	µgCHL(a+b)·cm^{-2}	II	4	5	11.06	***
	Chl (a/(a+b)) ratio^{c}	µgCHL(a)·µgCHL(a+b)$^{-1}$	II	4	5	1.20	ns
Per ground area	Biomass^{b}	gADW·m^{-2}	II	4	5	2.62	ns
	Chlorophyll (a+b)^{b}	µgCHL(a+b)·cm^{-2}	II	4	5	13.52	***

[a] ANOVA (not transformed)
[b] ANOVA with logarithmic link function
[c] ANOVA with logit link function

started to fragment from August 1988 onwards, and only rhizome parts were found in January 1989. Quantification of this fragmentation process was not possible because the rhizomes became very fragile in autumn which made it impossible to distinguish between natural fragmentation and fragmentation as the result of sampling.

The biomass ratio of shoots and rhizomes showed a significant seasonality (Table 4.2). The shoot biomass was two to three times as high as rhizome biomass from May to September, hereafter the shoot/rhizome ratio decreased significantly until the shoot biomass was less than half of the rhizome biomass in January 1989 (Fig. 4.6). The biomass ratio of generative shoots and newly formed rhizomes with short internodes (SHORT88) showed also a significant effect of time (Table 4.2). The mean biomass of the generative shoots was three times as high as the mean biomass of SHORT88 rhizomes at the beginning of the flowering season in July and means decreased hereafter. This high biomass ratio in July 1988 did, however, not significantly differ from the low ratio in January 1989, probably due to the high variability in the presence of generative shoots in the seagrass stand.

Chlorophyll-*a* and chlorophyll-*b* contents and the chlorophyll-*a*/(*a*+*b*) ratio of periphyton-free leaves of *Z. noltii* showed significant seasonality (Table 4.2). The content of chlorophyll-*a*+*b* was relatively low between May and July and increased significantly between July and the beginning of August (Fig. 4.7). The chlorophyll-*a*/(*a*+*b*) ratio was highest at the beginning of the growing season and significantly decreased between July and the beginning of August (Fig. 4.7).

Table 4.4 Degrees of freedom (df), number of replicates (n), deviance ratio (F_s) and level of significance (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, ns = not significant) of seasonal effects on *Hydrobia ulvae* on the tidal flats off Terschelling from 17 May 1988 to 6 January 1989 (period III).

	Size	Period	n	df	F_s	p
Biomass[a]	$1.00 \leq s < 1.40$ mm	III	4	7	7.80	***
($gDW \cdot m^{-2}$)	$1.40 \leq s < 1.80$ mm	III	4	7	1.38	ns
	$1.80 \leq s < 2.24$ mm	III	4	7	5.96	***
	$2.24 \leq s < 2.50$ mm	III	4	7	12.56	***
	$s \geq 2.50$ mm	III	4	7	4.84	**
	TOTAL	III	4	7	1.97	ns
Density[a]	$1.00 \leq s < 1.40$ mm	III	4	7	8.08	***
(m^{-2})	$1.40 \leq s < 1.80$ mm	III	4	7	0.70	ns
	$1.80 \leq s < 2.24$ mm	III	4	7	4.36	**
	$2.24 \leq s < 2.50$ mm	III	4	7	11.92	***
	$s \geq 2.50$ mm	III	4	7	4.85	**
	TOTAL	III	4	7	1.25	ns

[a] ANOVA with logarithmic link function

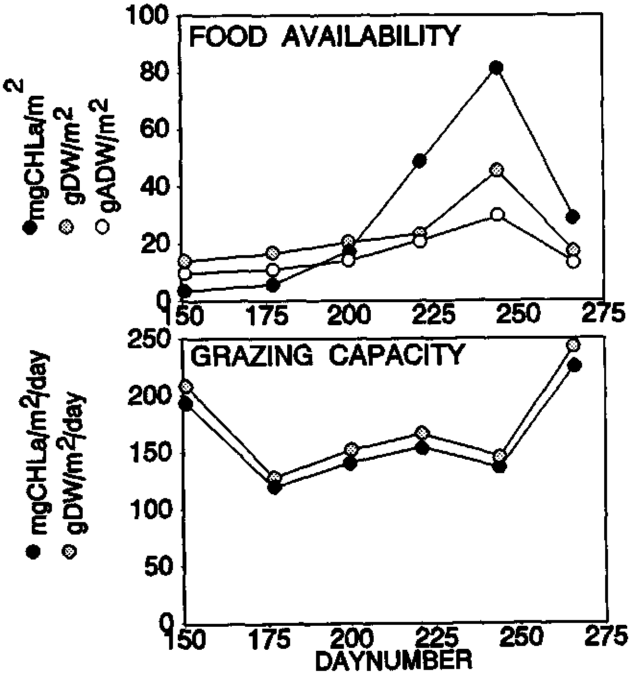

Fig. 4.9 Seasonal variation in periphyton standing stock, expressed in weight ($gDW \cdot m^{-2}$), biomass ($gADW \cdot m^{-2}$) and chlorophyll ($mgCHLa \cdot m^{-2}$), and in grazing capacity of *Hydrobia ulvae*, expressed in weight ($gDW \cdot m^{-2} \cdot d^{-1}$) and chlorophyll ($mgCHLa \cdot m^{-2} \cdot d^{-1}$), in the *Zostera noltii* stand on the tidal flats off Terschelling from 30 May 1988 to 22 September 1988.

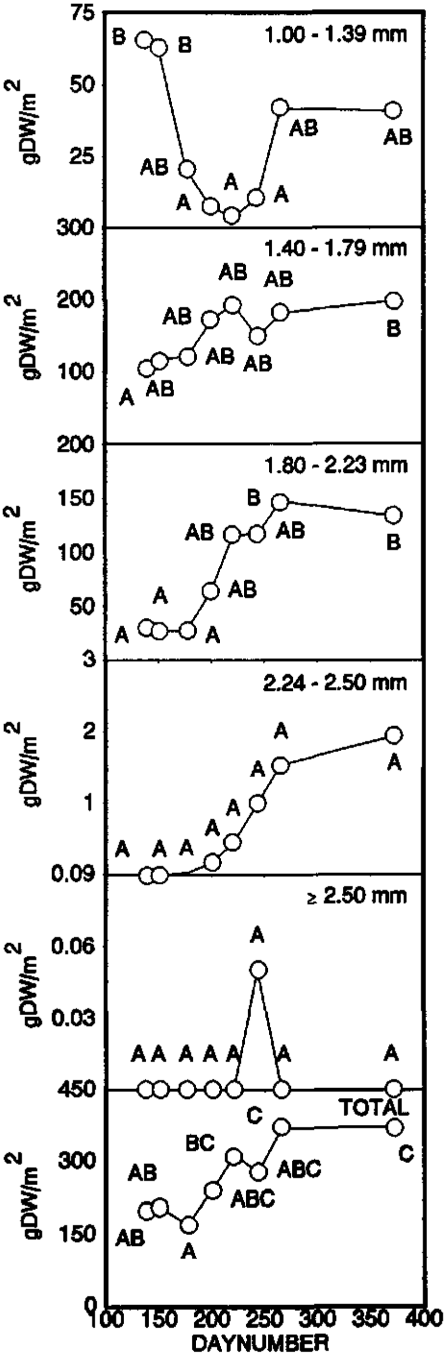

Fig. 4.10 Seasonal variation in mean biomass (gDW·m^{-2}) of *Hydrobia ulvae* of different size classes on the tidal flats off Terschelling from 17 May 1988 to 6 January 1989. Number of replicates is 4.

Periphyton

The periphyton density per leaf area showed a significant effect of time in biomass and chlorophyll (Table 4.3). From the end of May to the end of August, the periphyton biomass decreased from more than 1.6 mgADW·cm^{-2} in May to less than 0.6 mgADW·cm^{-2} at the end of August, whilst the periphyton chlorophyll levels increased almost eight times from 0.3 μg chlorophyll·cm^{-2} to almost 2.5 μg chlorophyll·cm^{-2} (Fig. 4.8). The ash-content of the periphyton showed no significant effect of time (Table 4.3) and was approximately 0.7 from the end of May until September 1988.

Although the mean periphyton biomass per bottom area ranged from almost 10 gADW·m^{-2} at the end of May to almost 30 gADW·m^{-2} at the end of August (Fig. 4.9), the seasonality in biomass was not significant (Table 4.3). The periodicity in periphyton chlorophyll, however, was found to be significant (Table 4.3). The chlorophyll-*a* density of periphyton per bottom area ranged from less than 3 mg·m^{-2} at the end of spring to more than 80 mg·m^{-2} at the end of summer (Fig. 4.9).

Mudsnails

Although the total biomass and density of *H. ulvae* were relatively stable throughout the experimental period, significant time effects were observed for the mudsnails for all size-classes except for snails with a size between 1.4 and 1.8 mm (Table 4.4). The biomass of the smallest mudsnails measured, with a size between 1 and 1.4 mm, significantly decreased more than tenfold from May to August (Fig. 4.10). The mudsnails with a size between 1.4 and 1.8 mm contributed on average for more than half to the total biomass of *H. ulvae*, and their biomass almost doubled during the experimental period from May 1988 to January 1989 (Fig. 4.10). The biomass of the mudsnails with a size between 1.8 and 2.24 mm increased more than five times from June to September (Fig. 4.10). Some mudsnails larger than 2.24 mm appeared from June onwards and mudsnails larger than 2.5 mm were only found at the end of August (Fig. 4.10).

Light conditions

The mean attenuation coefficients of the waters near the seagrass habitat of Terschelling (Fig. 4.1) ranged between almost 4 m^{-1} in January and less than 2 m^{-1} in July (Fig. 4.11). The change in estimated hours in which light conditions equalled or exceeded the light compensation point (LCP) of *Zostera noltii* showed an unimodal pattern (Fig. 4.12). Without shading by periphyton, maximum values of more than 16 hours·day^{-1} occurred at summer solstice for all three positions in the intertidal zone. The length of the period in which the LCP is exceeded decreased on average with lowering the position in the tidal zone (Fig. 4.12).

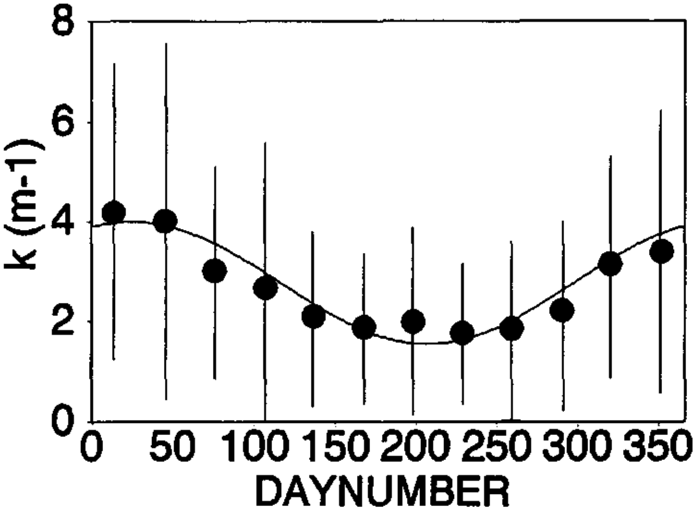

Fig. 4.11 Monthly means (●) ± SD and daily estimates (-) of the light attenuation coefficients *k* (m^{-1}) of the water at the tidal flats off Terschelling from 1 January to 31 December, derived from suspended matter concentrations at three sampling stations in the Wadden Sea between 1984 and 1992. See text for further explanation.

DISCUSSION AND CONCLUSIONS

Seasonality of seagrass

The seasonality in biomass of *Zostera noltii* on the tidal flats of Terschelling showed an unimodal pattern with highest values in summer and lowest in winter. This seagrass stand is considered to be perennial, because all vegetative shoots in May were connected to old rhizome parts which were produced in the former year. These findings are in agreement with observations on this seagrass species at other locations in the Netherlands (Vermaat *et al.* 1987, Duarte *et al.* 1993), Great Britain (Tubbs & Tubbs 1983), France (Loques *et al.* 1988), Spain (Pérez & Camp 1986) and Mauritania (Wolff & Smit 1990).

The winter survival of *Z. noltii* must be mainly through vegetative parts, seedlings are seldom found in temperate stands (Vermaat *et al.* 1987, Duarte *et al.* 1993, this paper). Seedlings may still play an important role if the conditions in winter are too severe for the rhizomes to survive, e.g. due to ice-scouring. In addition, these propagules may form new seagrass stands at other suitable locations in the Wadden Sea. The presence of rhizome fragments alone does not seem sufficient enough to survive winter. Laboratory experiments showed that the spring growth of temperate seagrass material is determined by the presence and related to the leaf area of the shoot which is connected to the rhizome (Duarte *et al.* 1993).

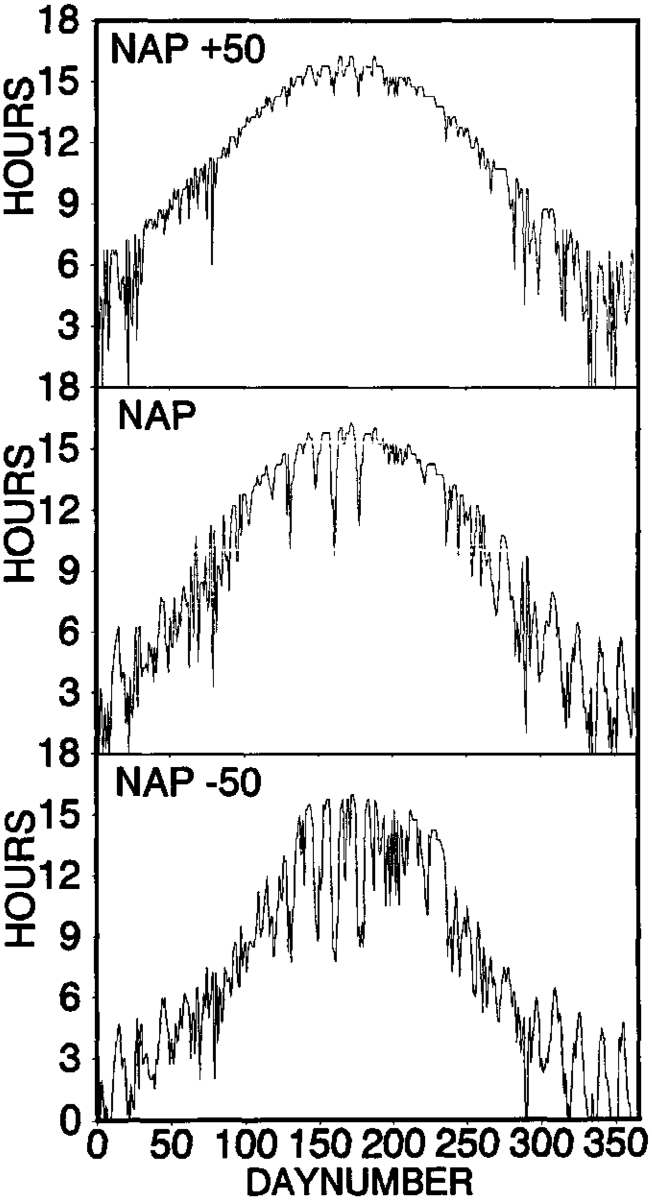

Fig. 4.12. Number of hours per day at which the irradiation (μE·m^{-2}·s^{-1}) at the *Zostera noltii* stand equals or exceeds the light compensation point (59 μE·m^{-2}·s^{-1}) of *Zostera noltii* on the tidal flats off Terschelling at the position in the tidal zone of +50 cm, 0 cm and -50 cm relative to Mean Sea Level (NAP) from 1 January to 31 December 1988 without shading by periphyton.

Since young vegetative shoots are sinks for photosynthetic material (Harrison 1978, Libes & Boudouresque 1978), reserves have be re-allocated from the rhizomes if the old shoots alone cannot support the extensive spring growth (Bulthuis 1983, Pirc 1983, Pangallo & Bell 1988). These reserves must have previously been build up. Indeed, several seagrass species are thought (Bulthuis 1983, Pangallo & Bell 1988, Roberston & Mann 1984) or known (Kuo & Cambridge 1978, Pirc 1983, Pellikaan & Nienhuis 1988, Duarte *et al.* 1993) to accumulate material in the rhizomes. The allocated biomass of submerged macrophytes is estimated to be on average 30% of its maximum biomass (Madsen 1991). The biomass of newly formed rhizomes of *Z. noltii* at the end of the growing season was more than 25 gADW·m^{-2}, which is approximately 20% of the maximum total biomass. The rhizomes with short internodes are the most likely parts in which most of this material is stored, because they are the last rhizomes being produced before winter and most directly connected to their sources, the vegetative shoots (Fig. 4.2).

The seasonality of *Z. noltii* on the tidal flats off Terschelling strongly resembled that of *Z. japonica* in Canada as described by Bigley & Harrison (1986). They distinguished five dominant growth phases in the annual cycle of this seagrass species, starting off with rhizome growth from seedlings. Since seedlings rarely occur in most *Z. noltii* stands, only four growth phases are distinguished for this seagrass species, viz. (1) resumption of growth by overwintering rhizomes in May, (2) horizontal branching of rhizomes with long internodes in May and June, (3) production of generative and vegetative propagules in July, and (4) degeneration and fragmentation of old rhizomes leaving physically independent clones from August onwards.

Seasonality of periphyton

The seasonality of the periphyton chlorophyll on the seagrass leaves coincided with the seasonality of the seagrass with low values at the beginning of the growing season and maximum values at the end of August. The seasonality of the periphyton biomass showed, however, a different pattern with highest values at the beginning of the growing season, followed by a gradual decrease. Apparently, the chlorophyll content of the organic part of the periphyton increased significantly during this period.

The periphyton biomass contributes significantly to the total plant biomass. At the end of May, the periphyton biomass equals the biomass of the seagrass shoots. The contribution decreases during the growing season. Periphyton contributed less than 20% to the total aboveground biomass, i.e. periphyton and seagrass shoots, at the end of September. These densities were relatively high compared to periphyton densities at an intertidal stands of *Zostera noltii* near Köningshafen in the German Wadden Sea. Here, the epiphytes contributed on average less than 5% to the annual mean biomass of epiphytes and seagrass (Asmus & Asmus 1985).

Seasonality of mudsnails

The mudsnail *Hydrobia ulvae* reached a peak density of almost 100,000 m^{-2} at the end of August, which is similar to high densities found at other locations in the Wadden Sea (Cadée 1980). Maximum total biomass was found at the end of the growing season and during winter. The biomass of the smallest mudsnails decreased from May to August, which was at least partly the effect of growth resulting in a shift of snails towards larger size-classes. The biomass of the smallest mudsnails increased from August onwards, which was most probably the result of the spat fall in June/July. These juveniles are expected to be found in 1-mm sieves from August onwards (R. Dekker pers. comm. 1994). Mudsnails bigger than 2.24 mm were seldom found. The total weight of the mudsnails with shell-sizes between 1.40 and 2.23 mm was significantly higher in January 1989 than in May 1988.

The observed variation in mudsnail densities may be partly caused by migratory activities. The evidence for the migration and mobility of *H. ulvae* are, however, contradictory. Mudsnails do migrate during their planktonic larval stage, but it is not clear if this movement is passive or active (McLusky & Elliot 1981). Adult mudsnails are not only able to crawl but also to float for long distances during extremely calm weather (Barnes 1981). This behaviour has also been observed on the tidal flats of Terschelling at rising tide on summer days without wind. The mudsnail was found to be fairly sedentary, however, on the tidal flats of the Grevelingen estuary in the south-western part of the Netherlands (Wolff & De Wolf 1977).

Light conditions

The seasonality of *Zostera noltii* on the tidal flats off Terschelling seems strongly related to the light conditions. The leaf growth rate (LGR) showed highest values around and after summer solstice. The significant drawback in LGR in midsummer was possibly caused by high temperatures and light levels which depressed the photosynthesis of seagrass (Short 1980). Since the maximum seagrass biomass is reached at the end of August, the subsequent decrease of the LGR can be the result of decreased light conditions at the seagrass habitat due to a decrease in insolation and to self-shading. In addition, the LGR can have been reduced due to increased allocation of material to the rhizomes.

If the seasonality of *Z. noltii* is determined by the light conditions in its habitat, the length of the growing season is determined by the position of the seagrass in the intertidal zone. In general, the light conditions improved with a higher position in the intertidal zone. The optimal position of a seagrass stand in an intertidal zone is not only determined by light conditions but also by desiccation (Keller & Harris 1966). The optimal intertidal position of *Z. noltii* was found to be at 50% emersion time for the tidal flats near Terschelling (Philippart *et al.* 1993), i.e. at mean sea level (NAP).

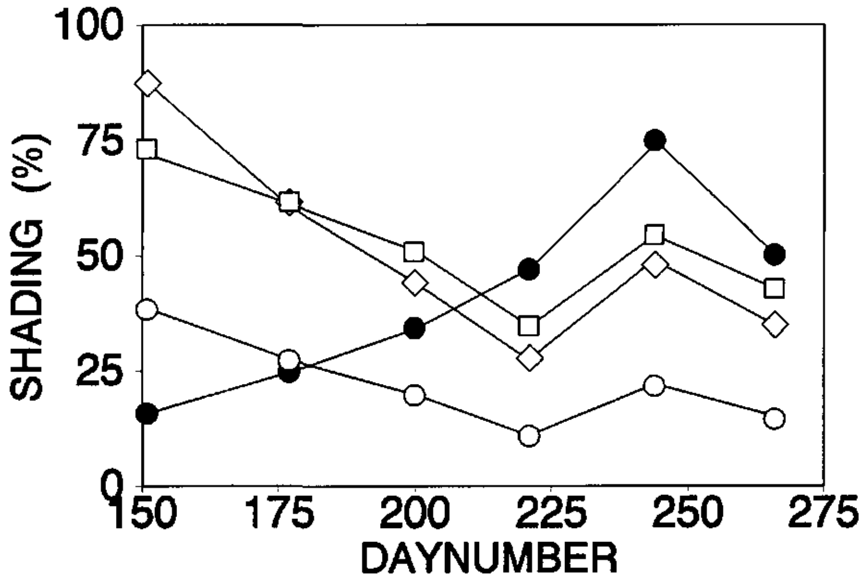

Fig. 4.13 Seasonal variation in light reduction (%) by periphyton on leaves of *Zostera noltii* on the tidal flats off Terschelling from 30 May to 22 September 1988, according to different light reduction equations based on chlorophyll-a (● Silberstein *et al.* 1986) and dry-weight (◇ Bulthuis & Woekerling 1983, □ Van Dijk 1991, ○ Silberstein *et al.* 1986).

Effects of shading by periphyton on seagrass

Periphyton may be a significant determinant of seagrass dynamics on the tidal flats off Terschelling. The shading caused by the periphyton varied between 10% and 90%, depending on the time of the year and of the relationship between periphyton and light reduction applied (Fig. 4.13). The number of hours·year^{-1} at which the insolation equalled or exceeded the LCP generally decreased with increasing shading levels and lower positions in the tidal zone (Fig. 4.14). This amount of shading results in a reduction of approximately 2% to 80% of the period at which the light compensation point (LCP period) of *Zostera noltii* is exceeded. In addition to shading, periphyton also has negative effects on seagrass photosynthesis and growth through competition for carbon and nutrient sources (Sand-Jensen 1977).

It must be noted that these estimates of shading were based on mean values of periphyton density and that the differences in age of the leaves was not taken into account. Especially in April and May, old leaves were thickly wrapped up and young leaves seemed free of periphyton (own observations). Therefore, the distribution of periphyton over the leaves has to be included if the effect of shading on seagrass by periphyton is calculated. Unfortunately, no such measurements were done during this survey.

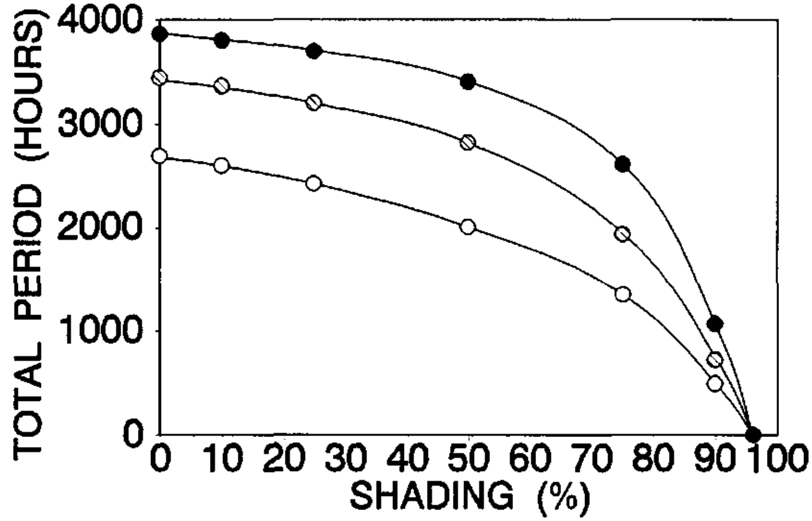

Fig. 4.14 Period per year (hours) at which the irradiation ($\mu E \cdot m^{-2} \cdot s^{-1}$) at the *Zostera noltii* stand equals or exceeds the light compensation point (59 $\mu E \cdot m^{-2} \cdot s^{-1}$) of this seagrass species on the tidal flats off Terschelling at the position in the tidal zone of +50 cm (top), 0 cm (middle) and -50 cm (bottom) relative to Mean Sea Level (NAP) from 1 January to 31 December 1988 at different levels of shading by periphyton.

Effects of grazing by mudsnails on seagrass

The mudsnail *Hydrobia ulvae* must be a significant determinant of periphyton dynamics on the tidal flats off Terschelling. The grazing capacity of the mudsnails at the seagrass habitat of Terschelling can be estimated assuming that each mudsnail is able to ingest 103 μg DW$\cdot$hour^{-1} of food, which contains 930.1 μg chlorophyll-*a*$\cdot$gDW^{-1} (Jensen & Siegismund 1980). Under these conditions, the grazing capacity of the mudsnails averaged 170 gDW$\cdot m^{-2} \cdot$day^{-1} and 160 mg chlorophyll-*a*$\cdot m^{-2} \cdot$day^{-1} between May and September 1988 (Fig. 4.9).

The estimated grazing capacity of mudsnails per day exceeds easily the standing stock of periphyton. The dry-weight of the material available in the seagrass stand can be estimated by multiplying the ash-free dry weight of the periphyton with its ash-content (Fig. 4.9). Even when assumed that additional food like microphytobenthos is present at a density of 80 mg chlorophyll-*a*$\cdot m^{-2}$ (Vermaat *et al.* 1987), the potential daily ingestion rate of *H. ulvae* would still be 25% to 100% of the total standing stock. This ingestion rate is, however, probably an overestimation of actual ingestion rate. Intraspecific competition between mudsnails, which can significantly reduce the actual grazing rate (Lopez-Figueroa & Xavier Niell 1987) was neglected in the estimations.

If the periphyton growth rate is approximately 0.10 day^{-1} (Vermaat & Hootsmans 1991), the mudsnails have to ingest roughly 20 mg chlorophyll-*a*$\cdot m^{-2}$ at maximum to keep the periphyton and the microphytobenthos at a constant level.

The results indicate that grazing cannot keep the seagrass leaves free from periphyton. Considering their potential grazing capacity, however, it may be expected that the mudsnails still significantly determine the periphyton standing stock and therefore the light conditions for *Zostera noltii.* An exclosure experiment on the tidal flats showed that grazing by mudsnails significantly influenced the density and biomass of this seagrass species (Chapter 7). The biomass development and survival of *Z. noltii* stand on the tidal flats of Terschelling seems, therefore, highly dependent on the presence and grazing capacity of *H. ulvae* living in the seagrass dominated community.

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APPENDIX

The daylength is related to the earth's orbit around the sun. The calculation of the day angle **Γ** [radians] is based on the daynumber of the year (Iqbal 1983). The daynumber d_n [-] ranges from 1 for 1 January to 365 for 31 December. Its is assumed that February has 28 days in every year. Because of the leap year cycle, there is a slight variation in accuracy of the calculation of the day angle, according to:

$$\Gamma = (2 \cdot \pi \cdot (d_n - 1)) \; / \; 365$$

The solar declination **δ** [degrees] is the angle between a line joining the sun and the earth to the equatorial plane (Iqbal 1983). It is zero at the vernal and autumnal equinoxes and has a value of approximately +23½° at the summer solstice and about -23½° at the winter solstice in the northern hemisphere. The solar declination can be calculated based on the day angle [radians], according to:

$$\delta = (0.006918 - 0.399912 \cdot \cos\Gamma + 0.070257 \cdot \sin\Gamma$$

$$-0.006758 \cdot \cos 2\Gamma + 0.000907 \cdot \sin 2\Gamma$$

$$-0.002697 \cdot \cos 3\Gamma + 0.00148 \cdot \sin 3\Gamma) \cdot (180/\pi)$$

The daylength N_d [hours] is a function of the solar declination [degrees] and the geographic latitude **Φ** [degrees] (Kirk, 1986). The geographic latitude is positive in the northern hemisphere and negative in the southern one. The daylength can be calculated based on the previous two equations according to:

$$N_d = \frac{2}{15} \cdot \cos^{-1} (-\tan\phi \cdot \tan\delta)$$

The daily insolation as supplied by the weather station $I_{weather\ station}$ is often expressed in energy, viz. J·cm^{-2}·day^{-1} (Netherlands) or in Cal·cm^{-2}·day^{-1} (France, Italy). These values can be conversed to each other according to 1 Cal = 4.1868 Joule. The daily insolation as supplied by the weather stations include the entire spectrum of visible light. Photosynthesis is however only related to the daily insolation of photosynthetic available radiation (PAR), ranging from 400 to 700 nm. The daily insolation including the entire visible light spectrum and expressed as [J·cm^{2}·day^{-1}] can be converted to the daily insolation restricted to PAR I_{daily} and expressed in number of quanta [μE·cm^{-2}·day^{-1}] according to:

$$I_{daily} = 2.05 \cdot I_{weather\ station}$$

The conversion factor 2.05 (± 0.23, n=730) in eqn. (4b) is based on the daily totals of energy in the spectrum ranging from 300 to 3000 nm and the number of quanta in the visible spectrum ranging from 400 to 700 nm as measured by K. Kersting (pers. comm., 1992) on the mainland of the Netherlands during two years. The estimation of the irradiance at solar noon $\mathbf{I}_{\mathbf{solar\ noon}}$ $[\mu E \cdot m^{-2} \cdot s^{-1}]$ can be estimated from the daily irradiance $\mathbf{I}_{\mathbf{daily}}$ $[\mu E \cdot cm^{-2} \cdot day^{-1}]$, assuming that under all weather conditions the light intensity during the day is distributed in the same way as under a perfectly clear sky with a maximum light intensity at solar noon, according to:

$$I_{solar\ noon} = (10^{+4} \cdot \pi \cdot I_{daily}) \ / \ (3600 \cdot 2 \cdot N_d)$$

The irradiance at time t $\mathbf{I}_t$ $[\mu E \cdot m^{-2} \cdot s^{-1}]$ can be subsequently estimated from the daylength [hours] and the irradiance at solar noon $[\mu E \cdot m^{-2} \cdot s^{-1}]$. If the period between time t and solar noon $\mathbf{t}_n$ [hours] is larger than the half of the daylength, the point in time is located before sunrise or after sunset and irradiance therefore zero. Otherwise the irradiance can be estimated according to:

$$I_t = I_{solar\ noon} \cdot \cos \frac{(90 \cdot t_n)}{(N_d \ / \ 2)}$$

The calculation of the water level at time t $\mathbf{z}_t$ [m] is based on the sinusoidal pattern of variation in tidal height. If the time [hours] and waterlevel [m] at the previous and next inflection points of the sine are known, respectively $\mathbf{t}_{\mathbf{PrevIP}}$, $\mathbf{t}_{\mathbf{NextIP}}$ and $\mathbf{z}_{\mathbf{PrevIP}}$, $\mathbf{z}_{\mathbf{NextIP}}$ the water level above seagrass in subtidal habitats can be calculated for any time after Ferreira & Ramos (1989) according to:

$$z_t = \frac{z_{NextIP} + z_{PrevIP}}{2} + \frac{z_{NextIP} - z_{PrevIP}}{2} \cdot \cos \frac{\pi \cdot (t_{NextIP} - t)}{(t_{NextIP} - t_{PrevIP})}$$

The depth of immersion at time t $\mathbf{d}_t$ [m] of seagrasses in intertidal habitats depends on the water level at time t [m] and the position of the stand in the tidal zone $\mathbf{p}_z$ [m]. If the water level is lower than the position of the macrophyte in the tidal zone, the plant is emerged and the depth of immersion is zero. Otherwise, the depth of immersion can be calculated according to:

$$d_t = x_t - p_z$$

Daylight is partly reflected by the surface of the water. Daylight reflection is a matter of high complexity, because it is dependent on the state of the sea surface and the spectral distribution in air, which in turn depends on cloud cover, solar elevation, etc. A fixed correction term for the daylight reflection equal to 7% is recommended as being the best compromise (Højerslev 1978). It is assumed that reflection always occurs; even when the seagrass is emerged it is covered by a thin layer of water. The irradiance just under the water surface $\mathbf{I}_{0-}$ $[\mu E \cdot m^{-2} \cdot s]$ can therefore be estimated using the irradiance just above the water surface $\mathbf{I}_{0+}$ $[\mu E \cdot m^{-2} \cdot s^{-1}]$, according to:

The irradiance at the seagrass habitat at time t $\mathbf{I}_{d,t}$ $[\mu E \cdot m^{-2} \cdot s^{-1}]$ is dependent on the

$$I_{0-} = 0.93 \cdot I_{0+}$$

irradiance just above the water surface [μE$\cdot$m$^{-2}\cdot$s^{-1}], the height of the waterlayer $\mathbf{d}_t$ [m] and the attenuation coefficient of the water **k** [m^{-1}], which is the result of the water itself and of the absorbing and scattering elements present in the water, according to the Lambert-Beer law:

$$I_{d_t} = I_{0_t} \cdot \exp^{(-k \cdot d_t)}$$

The irradiance reaching the leaves of the seagrass at time t $\mathbf{I}_{seagrass,t}$ [μE$\cdot$m$^{-2}\cdot$s^{-1}] is among other things dependent on the irradiance at the seagrass habitat at time t $\mathbf{I}_{d,t}$ [μE$\cdot$m$^{-2}\cdot$s^{-1}] and the shading by periphyton $\mathbf{k}_{shading}$ [%], according to:

$$I_{seagrass_t} = \frac{(100 - k_{shading})}{100} \cdot I_{d_t}$$

CHAPTER 5

EFFECTS OF SHADING ON THE GROWTH, BIOMASS AND SURVIVAL MECHANISMS OF THE INTERTIDAL SEAGRASS *ZOSTERA NOLTII* IN THE DUTCH WADDEN SEA

ABSTRACT The decrease of *Zostera noltii* in the Dutch Wadden Sea may be attributed to cultural eutrophication, resulting in an enhancement of the growth of epiphytes and subsequent shading of the seagrass. Shading affects not only photosynthesis and biomass, but also the survival during periods unsuitable for vegetative growth. The effect of low light levels on the leaf growth rates, the biomass and the survival mechanisms of *Z. noltii* was examined on tidal flats off the island of Terschelling in the Dutch Wadden Sea. Various levels of periphyton density were simulated by placing nets of different mesh width above the seagrass vegetation from May to October 1989. Shading effected a decrease in the leaf growth rate and an increase in the leaf loss rate, resulting in a decrease of the leaf net growth rate and the total biomass of *Z. noltii*. Generative and vegetative propagules were lower in biomass under shaded conditions than propagules developed in the controls. Most changes in growth, biomass and survival of *Z. noltii* were linearly related with artificial shading. It is concluded that improvement of light conditions may restore the seagrass stand, but only if the propagules are still of sufficient quality to support the extensive spring growth.

INTRODUCTION

The seagrass communities of *Zostera noltii* on the tidal flats of the island of Terschelling in the Dutch Wadden Sea started to decrease in area and density in the sixties and decreased further during the following two decades (Den Hartog & Polderman 1975, Chapter 3). The decrease of the *Z. noltii* stands may be attributed to cultural eutrophication according to the mechanism described for freshwater macrophytes by Phillips *et al.* (1978). Nutrient enrichment enhances the growth of epiphytes (Borum 1985, Silberstein *et al.* 1986). An abundant epiphytic community can affect the growth of seagrasses by obstructing the gas exchange between the leaves of the plants and the ambient water (Sand-Jensen 1977). Epiphytes can also significantly reduce the photon flux density reaching the seagrass leaves, since light attenuation by epiphytes increases with biomass (Bulthuis & Woekerling 1983, Silberstein *et al.* 1986). The increase of nutrient concentrations in the Wadden Sea coincided with a doubling of the primary production and chlorophyll-a of microphytobenthos on tidal flats over the period 1968-1981 (Cadée 1984). Although no data are available on the long-term changes in biomass of epiphytes on seagrass in the Wadden Sea, it is hypothesized that these algae also increased during this period and subsequently caused unfavourable growth conditions in the Dutch Wadden Sea.

Seagrasses often experience light limitation in their habitats (Dennison & Alberte 1982). Limiting light conditions may not only affect the net growth of macrophytes, but also the survival during the periods which are unsuitable for vegetative growth (Van Dijk & Van Vierssen 1991). In temperate climate zones, the annual regeneration of biomass largely depends on the number and quality of the generative (seeds) or vegetative (turions) propagules produced before winter (Van Vierssen 1990). When studying the effects of eutrophication as a possible cause of the decline of *Z. noltii* in the Dutch Wadden Sea, one has therefore not only to consider the effects of shading on leaf growth rates and total biomass but also the production and biomass of the generative and vegetative propagules.

The present paper discusses the leaf growth rates, the biomass and the survival mechanisms of a *Z. noltii* population under various light conditions on the tidal flats off Terschelling in the Dutch Wadden Sea.

MATERIAL AND METHODS

Experimental design

The experiment was performed in a monospecific *Zostera noltii* stand in the Dutch Wadden Sea, located on the tidal flats south of the island of Terschelling (Fig. 5.1). Four light conditions were created by artificially shading the seagrass community, thus simulating various levels of periphyton density.

The experimental area was located on an intertidal slope, with an average emersion period of 3 hours per tide. The maximum difference in length of the emersion period between the northwest and southeast side of this area was 30 minutes per tide. The experimental area was divided into two blocks to additionally examine the effects of the emersion period on seagrass growth, biomass and survival mechanisms under the various light conditions. Each block was divided into 32 plots (2x2 m^2) marked by poles. On 23 May 1989, per block 24 nets (Agroflor) of different mesh-widths (levels B, C and D) were positioned above the plots, reducing the incident light by 55%, 70% and 85%, respectively. The remaining plots served as controls (level A, no shading). The treatments were randomly distributed over the plots in each block (Fig. 5.2).

Sampling methods

The plots were sampled every four weeks from May to October 1989. During each sampling period, eight plots were sampled; two plots per light level, one in each block. In each selected plot, the leaf growth rate (LGR), the leaf loss rate (LLR) and the leaf net growth rate (LNR) were determined by a leaf-marking technique (Vermaat *et al.* 1987). The plants in the centre of the plot were collected using a sediment core (19 cm diameter) to a depth of 0.2 m. The samples were deep-frozen at -20 °C until further analysis.

In the laboratory, the samples were carefully sieved (mesh-width 1 mm) and the plant material was collected. The plants were separated in aboveground parts (vegetative and generative shoots) and rhizomes (rhizomes with long internodes formed in 1988, rhizomes with short internodes formed in 1988, rhizomes with long internodes formed in 1989 and rhizomes with short internodes formed in 1989). It was assumed that the rhizomes with short internodes formed in 1989 would function as turions during the winter of 1989/1990. Roots were excluded from the analysis because it was impossible to distinguish correctly between dead and living root material. Detached shoots and leaves in the samples were supposed to be attached during sampling and therefore included in the samples.

The numbers of the vegetative shoots, the generative shoots and the internodes of the different rhizome fractions were counted. The biomass of these

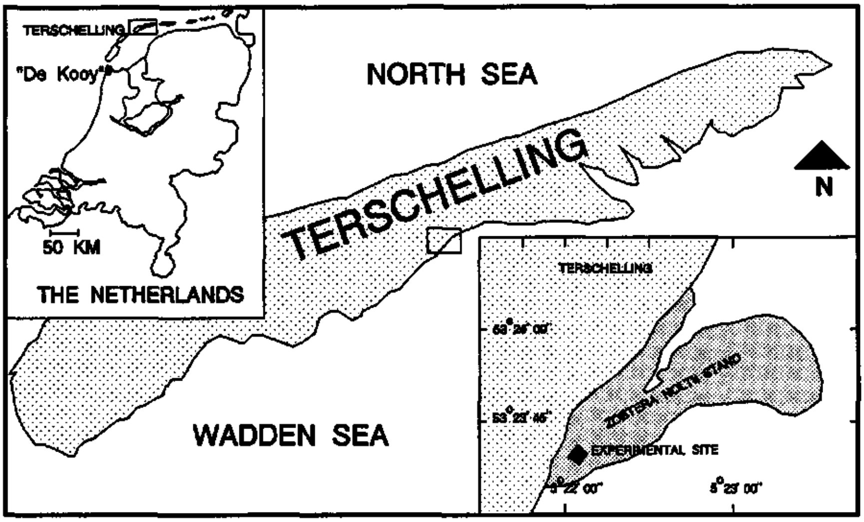

Fig. 5.1 The location of the experimental plot on the tidal flats off Terschelling.

fractions was determined as ash-free dry weight (ADW), being the difference between dry-weight (DW: 24 hours at 105 °C) and ash-weight (AW: 2 hours at 550 °C).

Statistical analysis

The effect of shading on growth and biomass of *Zostera noltii* was examined by means of analysis of variance (ANOVA). To perform ANOVAs, observations have to be normally distributed, independent and the variance has to be constant for all observations. It was suspected that the observations on the leaf growth rates did not agree with these conditions, possibly not even approximately. In addition, the ANOVAs were non-orthogonal, and unbalanced due to missing values. The effects of time and shading on the growth rates were, therefore, examined by comparing the results of the following three ANOVAs.

ANOVA 1: The data on leaf growth rates (LGR, LLR and LNR) were analyzed for main effects (time, shading and block) and all interaction effects (time·shading, time·block, shading·block and time·shading·block). The missing values were, when possible, estimated (Healy & Westmacott 1956, Preece 1971). In addition, the effect of shading was examined for a linear and a quadratic relation with the leaf growth rates.

ANOVA 2: This ANOVA is performed with the means of time as observations. Time effects were taken as stochastic blocks. Subsequently, the data were analyzed for main effects of shading and blocks and for the interaction effects (shading·block). Missing values were estimated by the same method as for ANOVA

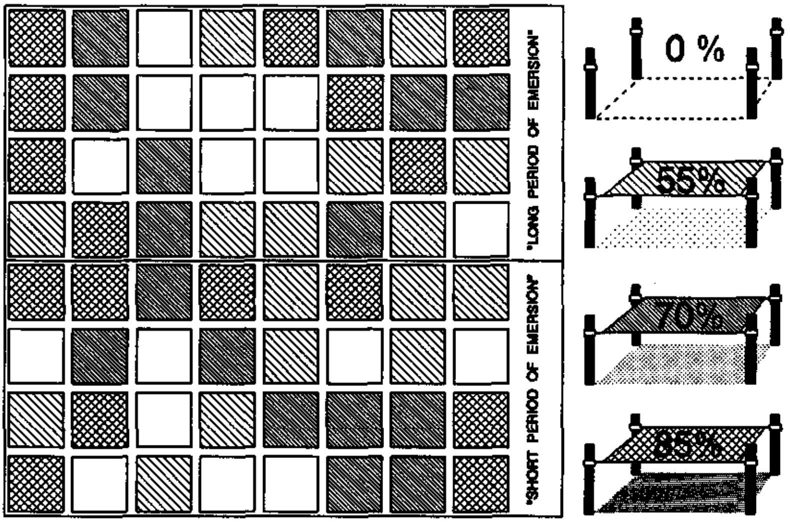

Fig. 5.2 The experimental design with two blocks and four light intensities (A = 0%, B = 55%, C = 70%, D = 85%).

1. ANOVA 2 is an ANOVA for shading, block and shading·block using the means of observations on time as observations, if there were no missing values. Given a small number of missing values, however, this analysis is a small modification of it. As for ANOVA 1, the effect of shading was additionally examined for a linear and a quadratic relation with the leaf growth rates.

ANOVA 3: The data were analyzed by a non-orthogonal (and unbalanced) analysis of variance using the original data, i.e. without estimating the missing values. A main effect was estimated under the assumption that the other two main effects could exist and that interaction effects were absent. The first order interactions (time·shading, time·block and shading·block) were estimated assuming that all other effects existed and the higher order interaction (time·shading·emersion) was absent. The interaction time·shading·block was estimated assuming that all other effects existed. Testing uses the residual sum of squares assuming the existence of all interactions.

Using ANOVA 2 has the advantage that the means of time are probably asymptotically normally distributed. ANOVA 2 is, however, less powerful for testing than the other two ANOVAs and it is not able to test the effects of time. ANOVA 3 has the advantage over ANOVA 1 (and 2) that it is based on the original values only and does not include estimates for missing values. In contrast to ANOVA 2 and 3, ANOVA 1 is balanced and orthogonal, making it possible to estimate levels of effects without the influence of other effects.

The data on the biomass and biomass rates of *Z. noltii* were analyzed by an ANOVA which included all main effects (time, shading and block) and the first

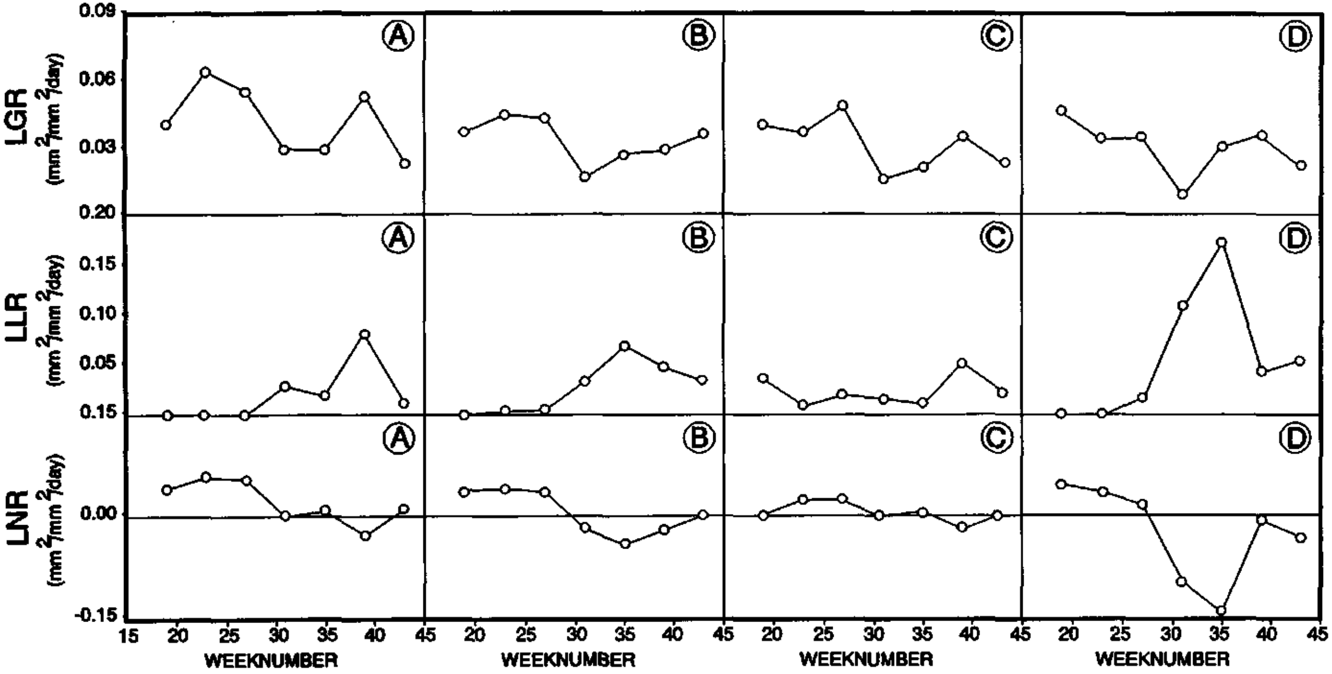

Fig. 5.3 The relative leaf growth rate (LGR), the relative leaf loss rate (LLR) and the relative leaf net growth rate (LNR) of *Zostera noltii* ($mm^2 \cdot mm^{-2} \cdot day^{-1}$) under four light intensities (A = 0%, B = 55%, C = 70%, D = 85%) on the tidal flats of Terschelling from May to October 1989 as based on the results of ANOVA 1.

Table 5.1 Degrees of freedom (df), sum of squares (SS) and level of significance (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$) of the effects of time, shading and block the relative leaf growth rate (LGR) of *Zostera noltii* in the Dutch Wadden Sea from May to October 1989, as tested by three different ANOVAs. See text for further explanation of the statistical analyses.

	ANOVA 1			ANOVA 2			ANOVA 3		
	df	SS	p	df	SS	p	df	SS	p
Time	6	0.043	***	6	0.047		6	0.022	***
Shading	3	0.009	***	3	0.010	***	3	0.005	*
Linear	1	0.009	***	1	0.010	***			
Quadratic	1	0.000		1	0.000				
Deviations	1	0.000		1	0.000				
Block	1	0.000		1	0.000		1	0.000	
Time x Shading	16	0.014	*				16	0.007	
Time x Block	6	0.002		3	0.005	*	6	0.001	
Shading x Block	3	0.004	*				3	0.002	
Time x Shad x Block	14	0.010					14	0.005	
Error	184	0.087		220	0.100		184	0.087	

order interactions (time·shading, time·block and shading·block). The second order interaction (time·shading·block) was assumed to be absent. The data sets on total biomass, the biomass ratio of aboveground and belowground material and the individual biomass of generative shoots and of rhizome internodes each contained one missing value. The presence of missing values in these biomass data sets was corrected in the same way as was done for the leaf growth rates. The effect of shading was also examined for linear and quadratic relations with biomass and biomass rates.

RESULTS

Leaf growth rates

The leaf growth rate (LGR) varied significantly in time and was obviously affected by shading (Table 5.1, Fig. 5.3). There may be an effect of several interactions (time·shading and shading·emersion) on LGR. The ANOVAs which included the estimates for the missing values showed a significant contribution of these interactions to the explaining model. Yet, the ANOVA which used the original values only did not show any significant interactions. The contribution of estimated values to the data set of the first two ANOVAs was high, approximately 50%. It is therefore most accurate to derive conclusions on significance of effects and interactions on the results of ANOVA 3 and state that the effects of interaction on

Table 5.2. Degrees of freedom (df), sum of squares (SS) and level of significance (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$) of the effects of time, shading and block the relative leaf loss rate (LLR) of *Zostera noltii* in the Dutch Wadden Sea from May to October 1989, as tested by three different ANOVAs. See text for further explanation of the statistical analyses.

	ANOVA 1			ANOVA 2			ANOVA 3		
	df	SS	p	df	SS	p	df	SS	p
Time	6	0.241	***	6	0.183		6	0.110	**
Shading	3	0.093	***	3	0.033		3	0.019	
Linear	1	0.045	**	1	0.022	*			
Quadratic	1	0.030	*	1	0.009				
Deviations	1	0.018		1	0.003				
Block	1	0.001		1	0.003		1	0.001	
Time x Shading	16	0.298	***				16	0.121	
Time x Block	6	0.040		3	0.045	*	6	0.022	
Shading x Block	3	0.024					3	0.008	
Time x Shad x Block	14	0.142	*				14	0.080	
Error	184	0.967		220	1.190		184	0.967	

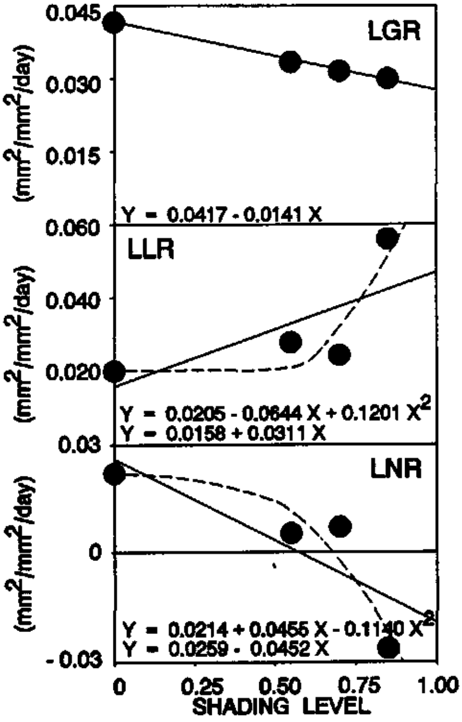

Fig. 5.4 The effect of shading on the mean relative leaf growth rate (LGR), the relative leaf loss rate (LLR) and the relative leaf net growth rate (LNR) of *Zostera noltii* on the tidal flats of Terschelling from May to October 1989 (straight lines show significant linear relations and curved lines significant quadratic relations as based on ANOVA 1).

Table 5.3 Degrees of freedom (df), sum of squares (SS) and level of significance (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$) of the effects of time, shading and block the leaf net growth rate (LNR) of *Zostera noltii* in the Dutch Wadden Sea from May to October 1989, as tested by three ANOVAs. See text for further explanation of the statistical analyses.

	ANOVA 1			ANOVA 2			ANOVA 3		
	df	SS	p	df	SS	p	df	SS	p
Time	6	0.419	***	6	0.341		6	0.194	***
Shading	3	0.139	***	3	0.071	**	3	0.039	
Linear	1	0.094	***	1	0.061	***			
Quadratic	1	0.027	*	1	0.006				
Deviations	1	0.017		1	0.005				
Block	1	0.000		1	0.003		1	0.001	
Time x Shading	16	0.271	***				16	0.114	
Time x Block	6	0.040		3	0.037		6	0.020	
Shading x Block	3	0.016					3	0.006	
Time x Shad x Block	14	0.106					14	0.061	
Error	184	1.017		220	1.210		184	1.017	

LGR were insignificant. Both ANOVAs 1 and 2 showed a significant linear relation between shading and LGR (Table 5.1, Fig. 5.4).

The leaf loss rate (LLR) was strongly affected by time and probably by shading (Table 5.2, Fig. 5.3). ANOVA 3 showed no significant effect of shading on LLR at all. No significant interactions were found for ANOVA 3. ANOVA 1 showed both a significant linear and quadratic relation between shading and LLR, and ANOVA 2 showed only a significant linear relation (Table 5.2, Fig. 5.4).

The leaf net growth rate (LNR) was strongly affected by time and most probably by shading (Table 5.3, Fig. 5.3). ANOVA 3 showed no significant effect of shading on LNR at all. No significant interactions were found for ANOVA 3. ANOVA 1 showed both a significant linear and quadratic relation between shading and LNR, and ANOVA 2 showed only a significant linear relation (Table 5.3, Fig. 5.4).

Biomass

The total biomass of *Zostera noltii* (gADW·m^{-2}) was affected by time and shading and the interaction between time and shading was significant (Table 5.4, Fig. 5.5). Total biomass was found to be linearly related with shading (Table 5.4, Fig. 5.6).

The ratio of aboveground and belowground biomass of *Z. noltii* (gADW·gADW^{-1}) was affected by time and shading and no significant interactions were found (Table 5.4, Fig. 5.5). This biomass ratio was linearly related with shading (Table 5.4, Fig. 5.6).

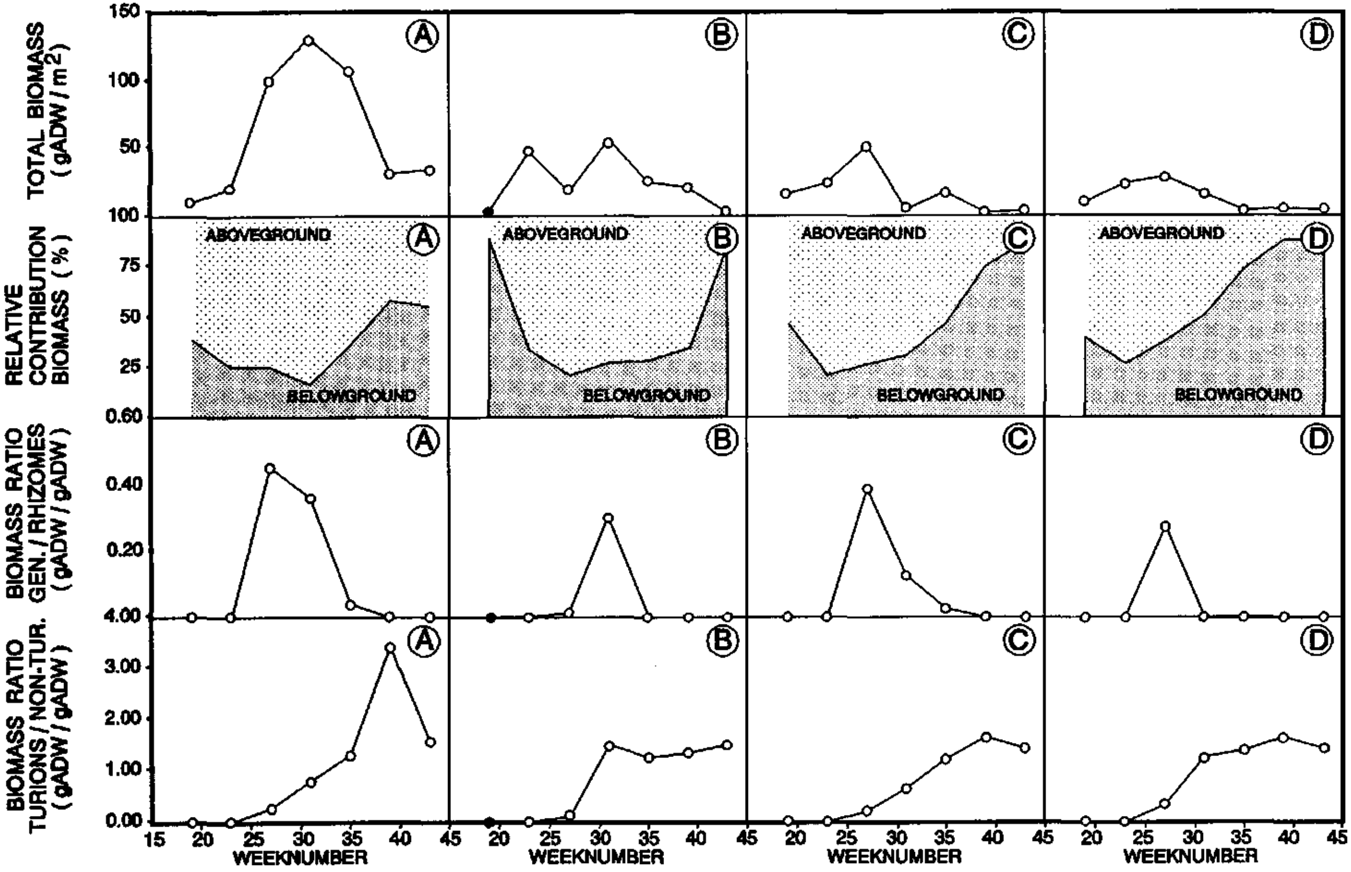

Fig. 5.5 The total biomass (gADW·m^{-2}), the biomass distribution in above ground (shoots) and belowground (rhizomes) parts (%), the biomass ratio between generative shoots and rhizomes (gADW·gADW^{-1}) and the biomass ratio between turions (rhizomes with short internodes formed in 1989) and non-turions (rhizomes with long internodes formed in 1989) (gADW·gADW^{-1}) of *Zostera noltii* under four different light intensities (A = 0%, B = 55%, C = 70%, D = 85%) on the tidal flats of Terschelling from May to October 1989 (○ n = 2, ● n = 1).

Table 5.4 Degrees of freedom (df), sum of squares (SS) and level of significance (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$) of the effects of time, shading and block on total biomass, the biomass ratio of aboveground and belowground parts, the biomass ratio of generative shoots and rhizomes and the biomass ratio of turion and non-turion rhizomes of *Zostera noltii* in the Dutch Wadden Sea from May to October 1989.

	Total biomass ($gADW{\cdot}m^{-2}$)			**Above-/belowground** ($gADW{\cdot}gADW^{-1}$)			**Gen.shs/rhizomes** ($gADW{\cdot}gADW^{-1}$)			**Turs/non-turs** ($gADW{\cdot}gADW^{-1}$)		
	df	SS	p	df	SS	p	df	SS	p	df	SS	p
Time	6	15517	***	6	62.66	***	6	0.671	***	6	32.58	***
Shading	3	20837	***	3	6.92		3	0.061		3	0.48	
Linear	1	20460	***	1	5.88	*	1	0.046		1	0.37	
Quadratic	1	369		1	1.04		1	0.002		1	0.11	
Deviations	1	8		1	0.00		1	0.013		1	0.00	
Block	1	288		1	0.07		1	0.012		1	0.07	
Time x Shading	18	22747	***	18	22.92		18	0.325		18	8.27	
Time x Block	6	209		6	4.93		6	0.030		6	2.82	
Shading x Block	3	447		3	1.19		3	0.033		3	1.44	
Error	17	2934		17	13.96		18	0.189		18	52.31	

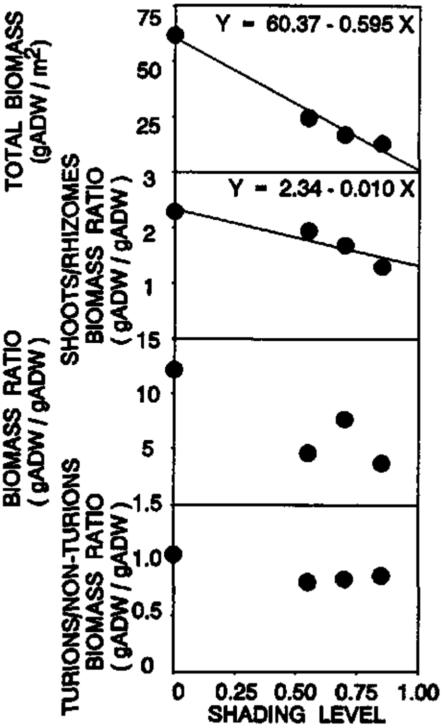

Fig. 5.6 The effect of shading on the mean total biomass ($gADW{\cdot}m^{-2}$), the biomass ratio of the aboveground (shoots) and belowground (rhizomes) parts ($gADW{\cdot}gADW^{-1}$), the biomass ratio between generative roots and rhizomes ($gADW{\cdot}gADW^{-1}$), and the biomass ratio between turions (rhizomes with short internodes formed in 1989) and non-turions (rhizomes with long internodes formed in 1989) ($gADW{\cdot}gADW^{-1}$) of *Zostera noltii* on the tidal flats off Terschelling from May to October 1989 (straight lines shows significant linear relations).

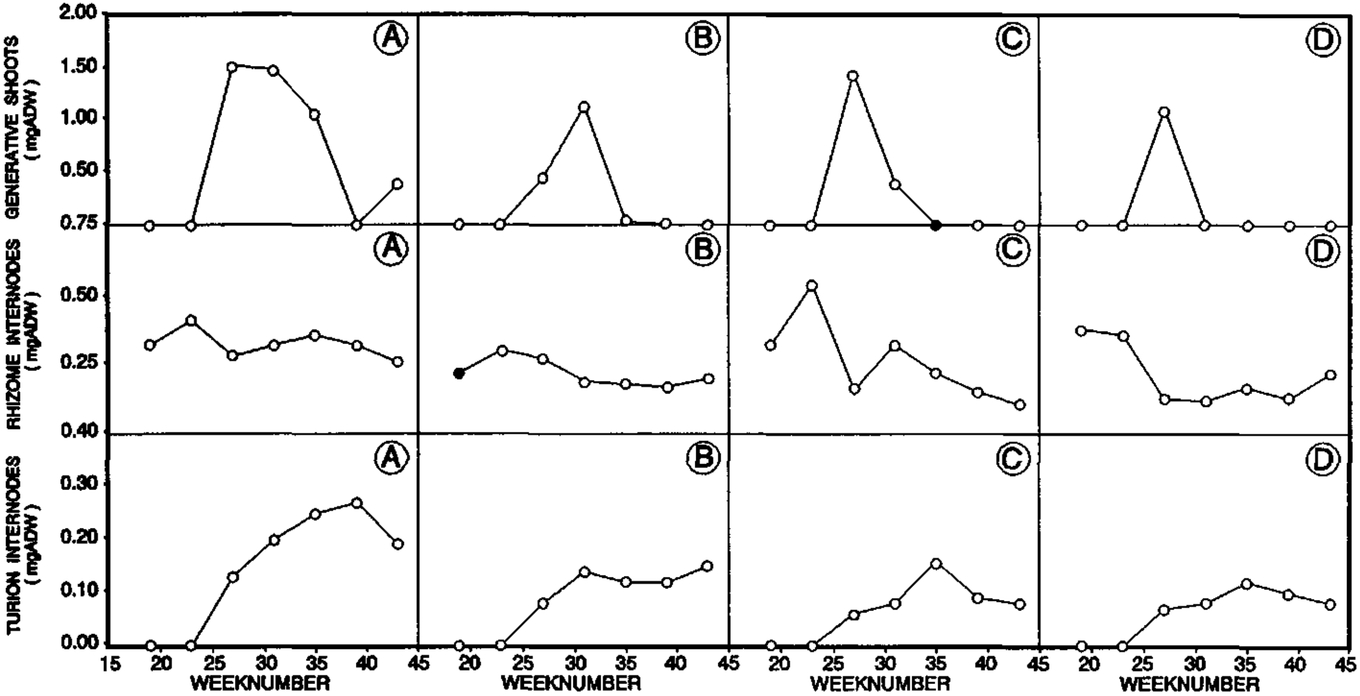

Fig. 5.7 The individual biomass of the generative shoots (mgADW), rhizome internodes formed in 1989 (mgADW) and turion rhizome internodes formed in 1989 (mgADW) of *Zostera noltii* under four different light intensities (A = 0%, B = 55%, C = 70%, D = 85%) on the tidal flats of Terschelling from May to October 1989 (○ n = 2, ● n = 1).

Table 5.5 Degrees of freedom (df), sum of squares (SS) and level of significance (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$) of the effects of time, shading and block on the individual biomass of generative shoots, the individual biomass of rhizome internodes and the individual biomass of turion rhizome internodes of *Zostera noltii* in the Dutch Wadden Sea from May to October 1989.

	Generative shoots (mgADW)			Rhizome internodes (mgADW)			Turion internodes (mgADW)		
	df	SS	p	df	SS	p	df	SS	p
Time	6	9.60	***	6	0.312	**	6	0.212	***
Shading	3	1.96	***	3	0.096	*	3	0.061	***
Linear	1	1.88	***	1	0.083	**	1	0.060	***
Quadratic	1	0.06		1	0.001		1	0.001	
Deviations	1	0.02		1	0.011		1	0.000	
Block	1	0.23	*	1	0.064	*	1	0.006	*
Time x Shading	18	4.33	***	18	0.177		18	0.045	*
Time x Block	6	0.31		6	0.114		6	0.003	
Shading x Block	3	0.06		3	0.009		3	0.003	
Error	17	0.70		17	0.157		18	0.019	

The ratio between the biomass of the generative shoots and rhizomes of *Z. noltii* ($gADW \cdot gADW^{-1}$) was affected by time and shading, no significant interactions were found (Table 5.4, Fig. 5.5). The distribution of biomass over the turion and non-turion rhizome internodes was only affected by time and no significant effect of shading nor significant effects of interactions were found (Table 5.4, Fig. 5.5).

The individual biomass of the generative shoots was affected by time, shading and emersion period and the interaction between time and shading was significant (Table 5.5, Fig. 5.7). The generative shoots originating from the experimental block with a relatively short emersion period weighted on average 50% more than the ones which were sampled in the other block. This biomass ratio was found to be linearly related with shading (Table 5.5, Fig. 5.8).

The individual biomass of the rhizome internodes of *Z. noltii* was affected by time, shading and emersion period and no significant interactions were found (Table 5.5, Fig. 5.7). The biomass of the rhizome internodes originating from the experimental block with a relatively short emersion period was on average 30% higher than the biomass of the rhizome internodes of the other block. The biomass of the rhizome internodes was linearly related with shading (Table 5.5, Fig. 5.8). The individual biomass of the rhizome internodes of the turions of *Z. noltii* was affected by time, shading and block, and the interaction between shading and time was significant (Table 5.5, Fig. 5.7). The biomass of turion rhizome internodes originating from the experimental block with a relative short emersion period was on average 25% higher than that of the turion rhizome internodes of the other

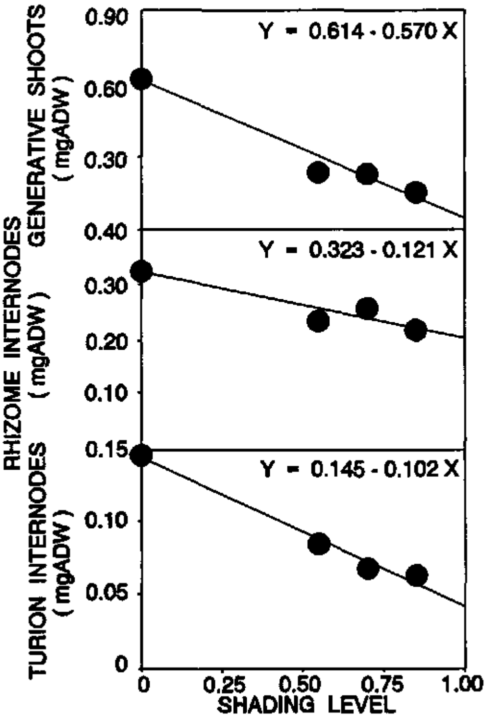

Fig. 5.8 The effect of shading on the mean individual biomass of the generative shoots (mgADW), rhizome internodes formed in 1989 (mgADW) and turion rhizome internodes formed in 1989 (mgADW) of *Zostera noltii* on the tidal flats of Terschelling from May to October 1989 (straight lines show significant linear relations).

block. The biomass of the turion rhizome internodes was linearly related with shading (Table 5.5, Fig. 5.8).

DISCUSSION AND CONCLUSIONS

The longer emersion period seemed more unfavourable for *Zostera noltii* than the shorter period, considering the lower individual biomass of generative shoots and rhizome internodes. The optimum position for seagrass in an intertidal zone is considered to be a compromise between desiccation and light conditions (Keller & Harris 1966). Although light conditions were better in the high experimental block with a long emersion period than in the low experimental block, this positive effect seemed to have been overruled by environmental stress due to desiccation.

The negative effect of shading on the relative growth rate of *Z. noltii* indicated a reduction of photosynthesis by limiting light conditions. The relative leaf growth does not depend on photosynthesis alone, but also on the allocation of photosynthetic material. Storage of photosynthetic material in the rhizomes was measured (Kuo & Cambridge 1978, Pellikaan & Nienhuis 1988, Pirc 1983) or suggested (Bulthuis 1983, Pangallo & Bell 1988, Robertson & Mann 1984) for several seagrass species. Carbohydrate reserves in the rhizomes are generally consumed and diluted during the early and mid growing season to support

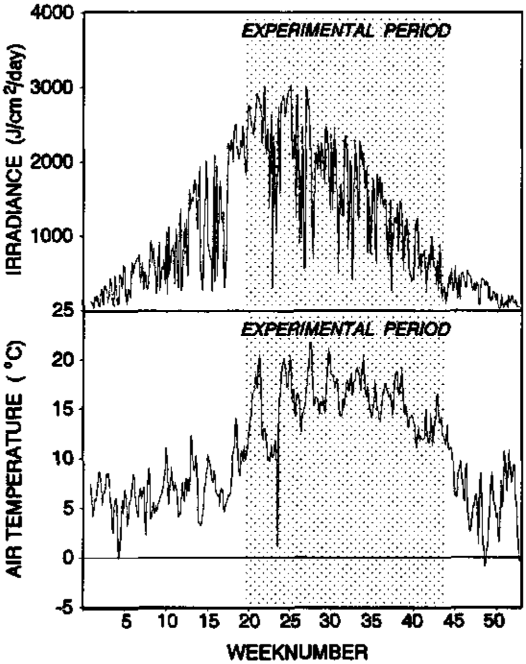

Fig. 5.9 Daily insolation ($J \cdot cm^{-2} \cdot day^{-1}$) and air temperature (°C) at the meteorological station "De Kooy" (Fig. 1) from January to December 1989.

extensive plant growth (Madsen 1991). Reallocation of reserves from the rhizomes of *Z. noltii* may, therefore, have maintained leaf growth during the first period of the experiment (Bulthuis 1983), diminishing the effects of shading.

Shading also affected leaf loss. Susceptibility to sloughing may have been increased by deterioration of leaf material under low light conditions, as is suggested for *Z. noltii* under reduced light conditions in Mauritania (Vermaat *et al.* 1993). Apparently, photosynthesis was not sufficient to maintain the leaf material. This effect will be enforced if the plant increases its allocation of material from the leaves to generative and vegetative propagules. Indeed, the formation of inflorescences and turions was followed by an increase in leaf loss. These findings on the seasonal dynamics of *Z. noltii* are in agreement with Madsen (1991), who stated that vegetative propagule development starts at the end of the active biomass development, at the same time as flower development and seed formation.

The diminished photosynthesis under low light conditions resulted in lower biomass of *Z. noltii*. During the summer period, the maximum biomass of *Z. noltii* under the normal light conditions was almost ten times higher than those under the low light conditions. Although the insolation is maximal during this season (Fig. 5.9), the summer is a critical period for maintenance and growth of vegetative shoots due to other environmental conditions. These shoots have to (1) support increased respiration of aboveground- and belowground material due to higher temperatures (Bulthuis 1983, Fig. 5.9), (2) cope with reduced photosynthesis as the result of self-shading by surviving shoots (Bulthuis 1983), and (3) supply photosynthetic material to the generative and vegetative propagules (Madsen 1991). Due to these three restraining conditions, seagrasses often show dips in leaf growth rates during summer (Short 1980, this paper). The effects of shading may, therefore, be most severe during summer.

Both the total and the individual biomass of propagules decreased under reduced light conditions. Apparently, the photosynthetic material was not able to support propagule growth. The biomass shift from shoots to rhizomes may be a result of enforced deterioration and subsequent sloughing of shoots. It is also possible that *Z. noltii* responded to shading by increasing its allocation of photosynthetic material to the rhizomes, as was found for the brackish water macrophyte *Potamogeton pectinatus* (Van Dijk & Van Vierssen 1991). The survival of *Z. noltii* mainly depends on vegetative propagules, seeds do not seem to play an important role in the year-to-year survival (Jacobs *et al.* 1983, Loques *et al.* 1988, Vermaat *et al.* 1987, Chapter 4). If the seagrass increased its allocation of photosynthetic material to the rhizomes, this survival mechanism was obviously not sufficient to counteract the negative effects of shading on the propagules.

Most changes in leaf growth rates, biomass and survival mechanisms of *Z. noltii* were linearly related with shading, suggesting that the present light conditions in the control are suboptimal. If eutrophication of the Wadden Sea resulted in an increased epiphyte biomass and subsequent decline of seagrasses, then nutrient reduction may result in restoration of the seagrass populations. Recuperation of a reduced seagrass stand is, however, only possible if the vegetative propagules are still of sufficient quality to support the extensive vegetative growth at the beginning of the growing season.

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CHAPTER 6

EFFECTS OF VARIOUS LIGHT PERIODS ON GROWTH, BIOMASS AND PRODUCTION OF *ZOSTERA NOLTII*

ABSTRACT In the Dutch Wadden Sea, the area and density of the intertidal seagrass stands of *Zostera noltii* decreased over the last decades. This decline may be attributed to cultural eutrophication, causing an increase in periphyton on the seagrass leaves. Increased shading by periphyton shortens the light periods, i.e. the photosynthetic and the photoperiod. In general, a decrease in photosynthetic period will result in lower growth rates, and subsequently in a lower biomass. Shortening of the photoperiod may affect the photoperiodic responses of the seagrass, e.g. the quantity and quality of the rhizomes. During laboratory experiments, no relation was found between growth and biomass development of this seagrass species and the length of the photosynthetic and photoperiod. The biomass values and development of the seagrass was different for material originating from the Netherlands compared to Mauritania all along the experimental period. However, results have to be interpreted with caution due to the low number of replicates.

INTRODUCTION

Over the last decades, seagrass communities of *Zostera noltii* on the tidal flats in the Dutch Wadden Sea decreased in area and density (Den Hartog & Polderman 1975, Chapter 3). This decline of seagrass stands may be attributed to cultural eutrophication according to the mechanism described for freshwater macrophytes by Phillips *et al.* (1978). The hypothesis rests on the premise that seagrass stands in the intertidal zone occur above a lower limit imposed by penetration of light (Shepherd *et al.* 1989). The light availability for seagrass is determined by tidal height, turbidity of the water and by epiphyte density on the leaves of the seagrasses. Primary production and chlorophyll-*a* of microphytobenthos on tidal flats in the western Wadden Sea doubled over the period 1968-1981 (Cadée 1984). Although no data are available on the long-term changes in biomass of epiphytes on seagrass in the Wadden Sea, it is hypothesized that these algae also increased during this period and subsequently caused an increased light reduction and a shortening of the light periods for the Wadden Sea seagrasses.

Shortening of the light periods may affect the seagrass stands in different ways. The photosynthetic period is defined as the period in which irradiance levels are high enough to sustain positive net photosynthesis, i.e. gross photosynthesis is higher than respiration (Chatterton & Silvius 1979). In general, a shortening of the photosynthetic period will result in reduced growth rates and, as a consequence, in a lower biomass. In addition, light periods can influence photoperiodic responses in aquatic macrophytes (Chambers *et al.* 1985), such as dormancy, flowering and germination (Daubenmire 1974). The photoperiod is defined as the daily period in which photon flux densities exceed the lower sensitivity limit of the phytochrome system (Van Dijk & Van Vierssen 1991), i.e. approximately 10 $\mu E \cdot m^{-2} \cdot s^{-1}$ (Chatterton & Silvius 1979). In the temperate climatical zones, the winters can be too dark and too cold to sustain seagrass photosynthesis. *Z. noltii* survives this unfavourable growth periods mainly by shoot-bearing rhizomes in which reserve material is accumulated (Duarte *et al.* 1993). It is hypothesized that a shortening of the photoperiod may result in a postponed timing of the photoperiodic responses, subsequently affecting the quantity and quality of the seagrass rhizomes.

This chapter presents the results of a laboratory experiment on the relationships between the length of the photosynthetic and photoperiod and the growth, biomass and production of *Z. noltii*. Plant material originated from two different locations, the temperate Netherlands and tropical Mauritania, to additionally examine if possible responses to different light periods are related to the origin of these plants.

MATERIALS AND METHODS

Experimental set-up

Seagrass *Zostera noltii* was sampled as whole shoots including rhizomes in two different countries, i.e. the Netherlands and Mauritania. Seagrass from the Netherlands was sampled at the tidal flat near the island of Terschelling in the Wadden Sea (53° 24′ N, 5° 21′ E) in April 1987 and cultivated in the laboratory for 2 years. The seagrass from Mauritania was sampled at a tidal flat near Iouik at the Banc d'Arguin (19°45 N, 16°16 W) in September 1988 and cultivated in the laboratory for 6 months. All material was cultivated under similar circumstances. At the start of the experiment, the cultivated material was selected for similar plant units, consisting of a newly formed rhizome branch with short internodes and one apical shoot.

Sampled seagrass units were planted in small plastic containers (8 x 4 x 3 cm^3) filled with sand, one plant unit per container. The containers were placed in an artificial ditch (4.5 x 0.5 x 0.5 m^3) in the laboratory, which was divided into three separate light-tight compartments (Fig. 1). Each compartment included 90 containers with seagrass units originating from the Netherlands and 90 containers with material originating from Mauritania. The seagrass plants were kept free of algae by mudsnails, *Hydrobia ulvae*. The ditch was flushed with natural seawater (20 $l \cdot min^{-1}$), which could pass the partitioning walls. Light was provided by means of two Philips SON-T 400 Watt lamps per compartment, situated at 20 cm above the water surface. The inside walls of the compartments were clothed with light-reflecting foil, which was kept free of algae by means of periwinkles, *Littorina littorea*. This set-up resulted in a more or less homogeneous insolation of 400 $\mu E \cdot m^{-2} \cdot s^{-1}$ (PAR) at the bottom of the compartments.

During the first 5 months preceding the experiment (April-August 1989), all seagrass plants were cultivated under similar long-day light conditions of 16 hours and 8 hours darkness (16L/8D). It was assumed that this period was long enough to smooth out any possible phenotypic differences between the individual seagrass units, due to former growth conditions. During the following experimental period of 5 months (Sept 1989-Jan 1990), the light conditions were different for the three different compartments of the artificial ditch. The long-day light conditions (16L/8D) were maintained in one of the compartments (Fig. 6.1). The seagrass in one of the other compartment obtained short-day conditions (8L/16D). The plants in the remaining compartment were treated with so-called "intermediate" light

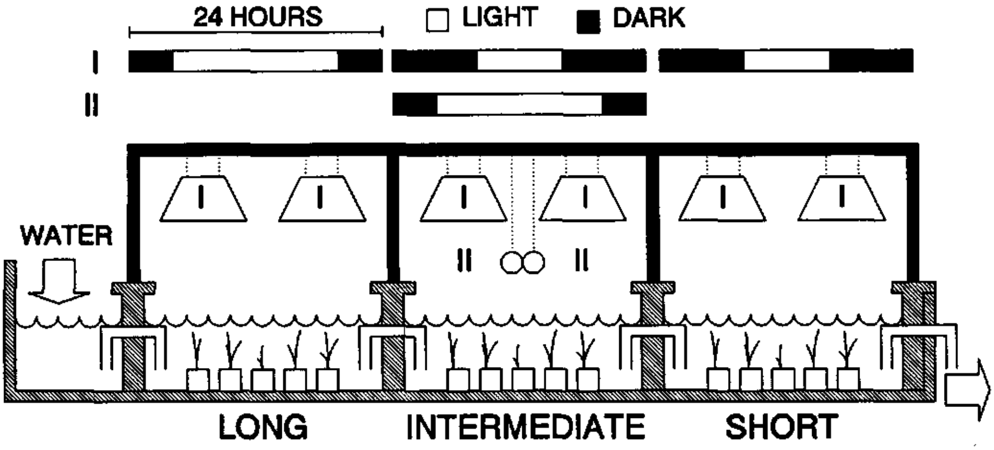

Fig. 6.1 Experimental set-up of different light periods constructed with 400 Watt lamps (I) and 7 Watt lamps (II) in the laboratory.

conditions, a *combination of long-day dim-light conditions* (16L/8D) *and short-day* full-light conditions (8L/16D), simulating a photoperiod of 16 hours and a photosynthetic period of 8 hours, respectively. The dim insolation was provided by means of two Philips 7 Watt lamps and started 4 hours before and continued 4 hours after the full-light insolation.

Leaf growth rates

The relative leaf growth rate (LGR), leaf loss rate (LLR) and leaf net-growth rate (LNR) of vegetative shoots of *Zostera noltii* ($mm^2 \cdot mm^{-2} \cdot day^{-1}$) were measured by means of an adjusted leaf marking technique (Vermaat *et al.* 1987). All individual leaves of a shoot were measured and marked at a fixed distance from the leaf sheath by means of a felt pen. After exposure for 5 days, the length and width (± 1 mm) of the leaves and the distance between the mark and the leaf sheath were measured. The leaf growth rates were calculated for one plant, i.e. all shoots in one container together. For each light condition, 2 replicates were distinguished.

Biomass, numbers and morphology

The biomass, numbers and morphology of shoots and rhizomes of *Zostera noltii* were determined at the beginning and at the end of the experimental period. The plant material was divided into shoots, rhizomes and roots. The roots were excluded from further analysis, because it was impossible to distinguish correctly between dead and living material. The number of shoots and rhizome internodes in each subsample was counted and the surface of the leaves and the total length

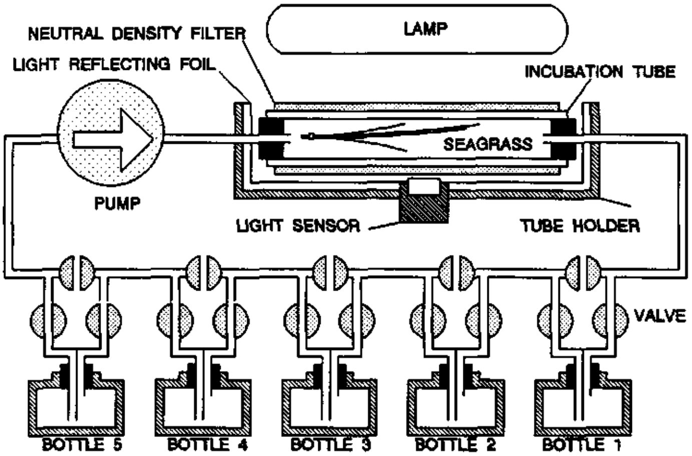

Fig. 6.2 Experimental system for determining the light-response curves of *Zostera noltii.*

of the rhizomes were measured. Ash-free dry weight (ADW) of all subsamples was determined as the difference between the dry weight (24 hours at 105 °C) and ash weight (2 hours at 550°C).

Light-response curves

The light-response curves of *Zostera noltii* material were determined at the end of the experimental period in a closed water system (Fig. 6.2). The system consisted of a perspex tube, 3 to 5 glass bottles of 250 ml each, an Eheim circulation pump and PVC tubing. The total volume of this system was 1.026 l, bottles excluded. The equipment was placed in a flow-through water bath, which kept the temperature in the system between 18 and 20 °C. Light was provided by a Philips SON-T 400 Watt lamp. Different light levels were created using neutral density filters, which were wrapped around the perspex tube. In this way, it was possible to vary the light levels between 0 and 900 $\mu E \cdot m^{-2} \cdot s^{-1}$. The tube was placed in a semi-cylindrical container of which the inner sides were clothed with light reflecting foil. The light intensity (PAR) was measured by means of a LI-COR LI-192SB underwater sensor.

Seagrass material was collected from randomly chosen containers. Earlier experiments showed that at least 200 mg fresh weight leaf material, i.e. 6 to 10 containers, was required to allow accurate measurements. The underground parts of the seagrass samples were removed and the leaves were cleaned from periphyton by pulling them gently through folded GF/C glassfibre filters. The cleaned leaves were bundled and fixed with a string in the centre of the perspex tube (Fig. 6.2). After the measurements, the leaves were separated from the leaf sheaths and their ash-free dry weight (ADW) was determined.

Each series of measurements was preceded by a control, without any seagrass material. The series of measurements started from the lowest light level upwards to the highest level, to prevent irreversible or prolonged effects of photoinhibition on the production of the seagrass at the lower light levels. One series of measurements was performed for each treatment, i.e. three light periods and two lands of origin.

At each light level, seawater in the system was bubbled through with nitrogen gas before the measurements to remove most of the oxygen to prevent oxygen saturation during the incubation period. The water was pumped through the entire system with all bottles connected and open for 20 minutes before each measurement to obtain an equal oxygen concentration throughout the system. After this mixing period, all connections between the system and the bottles were closed except for the second bottle which remained flushed by water from the system. The first bottle was disconnected and its oxygen fixated. After 5 minutes, the third bottle was opened and the second bottle closed, disconnected and its oxygen fixated. This procedure was repeated with the remaining bottles until all bottles were disconnected. This procedure was conducted for all light levels.

Oxygen in the bottles was fixated by adding 2 ml MnCl (600 g $MnCl_2.4H_2O\cdot l^{-1}$) and 4 ml NaOH-KJ (250 g NaOH & 350 g $KJ\cdot l^{-1}$). Subsequently, oxygen content was determined by Winkler titration with a 0.025 N $Na_2S_2O_3$ solution. The oxygen production was calculated as the slope of the linear course of the amount of oxygen in the entire system, including connected and disconnected bottles, and subsequently corrected by control values.

The light-response curves were fitted according to two models, viz. a rectangular hyperbola (eq. 1), also known as the Michaelis-Menten model, and the hyperbolic tangent (eq. 2), introduced by Jassby & Platt (1976):

$$P_I = P_{\max} \cdot \frac{I}{(I_k + I)} - R \qquad (1)$$

$$P_I = P_{\max} \,.\, \tanh\left(\frac{I}{I_k}\right) - R \qquad (2)$$

$$\alpha = \frac{P_{\max}}{I_k}$$

where:	P_I	gross productivity at light level I	$(mgO_2\cdot min^{-1})$
	I	light level at which productivity is measured	$(\mu E\cdot m^{-2}\cdot s^{-1})$
	P_{max}	maximum rate of gross productivity	$(mgO_2\cdot min^{-1})$
	I_k	light level at which the line is described as $P_I = \alpha\cdot I$ is equal to P_{max} (Talling 1957)	$(\mu E\cdot m^{-2}\cdot s^{-1})$
	R	respiration	$(mgO_2\cdot min^{-1})$
	α	initial slope of the curve	$(mgO_2\cdot min^{-1})\cdot(\mu E\cdot m^{-2}\cdot s^{-1})^{-1}$

The models were fitted by iterative estimation of the parameters using the computer programme STEM (ReMeDy 1990). The minimal required variance during the iteration procedure was set on 1E-8.

Statistical analysis

The data at the end of the experiment were analyzed for effects of light periods and land of origin using Generalized Linear Model (GLM-) ANOVAs (Dobson 1983, McCullagh & Nelder 1989). Two different forms of GLM-ANOVAs were employed, viz. a logarithmic and a logit link function. The logarithmic link function was used if the observations were scaled from 0 to infinity. If so, then an overdispersed or underdispersed Poisson distribution was assumed, and expectations were supposed to be additive on a logarithmic scale, i.e. multiplicative on the original scale. The logit link function was used if the observations were scaled from 0 to a (positive) total. Subsequently, an overdispersed or underdispersed binomial distribution was assumed, and expectations were supposed to be additive on a logistic scale, i.e. log(part/(total-part)). Estimation of the main effects and their standard errors included all interactions possible in the model. The data of the beginning of the experiment were analyzed for effects of origin by means of Students t-tests.

RESULTS

Leaf growth rates

At the end of the experiment, the mean leaf growth rates (LGR), leaf loss rate (LLR) and leaf net-growth rate (LNR) did not significantly differ for the various light periods (Table 6.1). The leaf loss rate (LLR) was more or less similar to the LGR, resulting in very low and even negative leaf net-growth rates (Fig. 6.3). None of these leaf growth rates were significantly influenced by the differences in land of origin (Table 6.1).

Biomass, numbers and morphology

At the beginning of the experiment, the biomass of the shoots originating from Mauritania was more than twice as high as that of the shoots from the Netherlands (Fig. 6.4). This was not caused by a higher number of shoots, but by a significant higher total leaf area (Fig. 6.4, Table 6.2). Although the total rhizome biomass did not significantly differ for the two countries (Table 6.2), the biomass per mm of the rhizomes originating from Mauritania was twice as high as that from the Netherlands (Fig. 6.4). The total biomass did not significantly differ for the land of origin, the relative contribution of aboveground material to the total biomass was significantly higher for the Mauritanian than for the Netherlands material (Table 6.2).

Table 6.1 Degrees of freedom (df), deviance and level of significance (* p < 0.05, ** p < 0.01, *** p < 0.001) of the effects of land of origin and light period on the leaf growth rate (LGR), leaf loss rate (LLR) and leaf net-growth rate (LNR) of *Zostera noltii* at the end of the experimental period.

	df	LGR[a]	LLR[b]	LNR[c]
Light period	2	0.0167	0.0001	0.0003
Land of origin	1	0.0028	0.0341	0.0004
Light*land	2	0.0060	0.0130	0.0001
Error	6	0.0182	0.0391	0.0016

[a] *GLM-analysis with logarithmic link function*

[b] GLM-analysis with logit link function

[c] ANOVA analysis

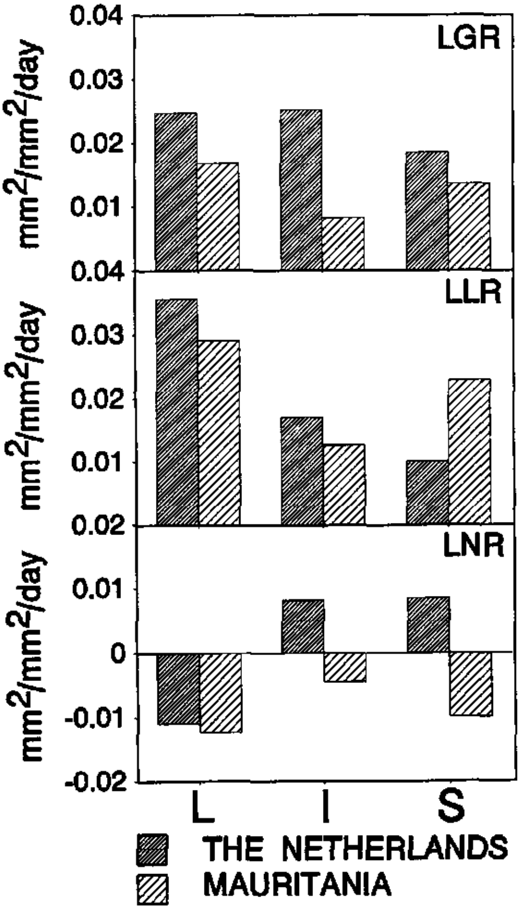

Fig. 6.3 Mean relative leaf growth rate (LGR), leaf loss rate (LLR) and leaf net-growth rate (LGR) of *Zostera noltii* originating from the Netherlands and Mauritania and cultivated under long-day light conditions (L), intermediate light conditions (I) and short-day light conditions (S) *in the laboratory* for 5 months. Number of replicates is 2.

Table 6.2 Significance of the effects of land of origin on the biomass, numbers and morphology of shoots and rhizomes of *Zostera noltii* at the beginning of the experimental period. All data were log-transformed. Number of replicates is 5 or 6.

		p
Biomass	Total	0.120
	Shoots	*0.029*
	Rhizomes	0.389
	Shoots/total	*0.000*
	Internodes	*0.002*
Number	Shoots	0.556
	Internodes	0.637
Morphology	Shoot	0.198
	Rhizomes	0.315

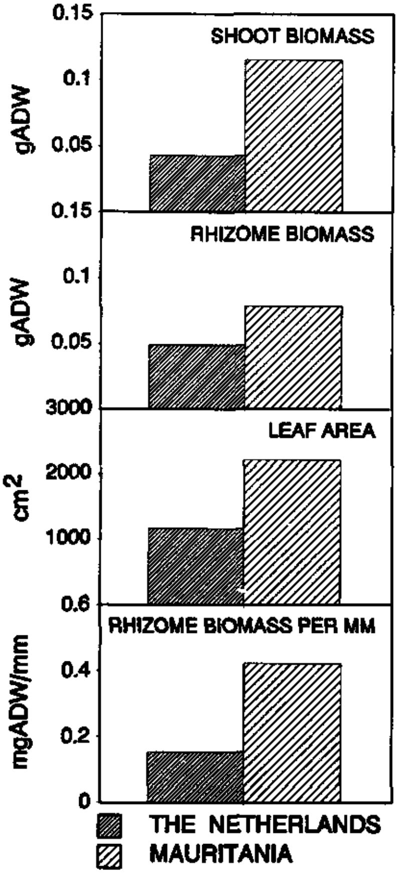

Fig. 6.4 Mean biomass, numbers and morphology of shoots and rhizomes of *Zostera noltii* originating from the Netherlands and Mauritania and cultivated under long-day light conditions in the laboratory for 5 months (April-August 1989). Number of replicates is 5 or 6.

Table 6.3 Degrees of freedom (df), deviance and level of significance (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$) of the effects of light period and land of origin on the biomass, numbers and morphology of shoots and rhizomes of *Zostera noltii* at the end of the experimental period.

	df:	Light period 2	Land 1	Light*land 2	Error 6
Biomass	Total[a]	0.0719	1.9182^{**}	0.0604	0.1619
	Shoots[a]	0.0418	1.0236^{**}	0.0154	0.1742
	Rhizomes[a]	0.0339	0.9216^{***}	0.0490	0.0737
	Shoots/total[b]	0.0067	0.0298	0.0011	0.0861
	Internodes[a]	0.0348	1.2518^{***}	0.0821	0.0685
Number	Shoots[a]	6.930	0.224	2.745	16.112
	Internodes[a]	59.91	0.40	2.21	106.00
Morphology	Shoots[a]	1385	19266^{**}	291	3363
	Rhizomes[a]	26.27	50.21	5.46	349.31

[a] GLM-analysis with logarithmic link function
[b] GLM-analysis with logit link function

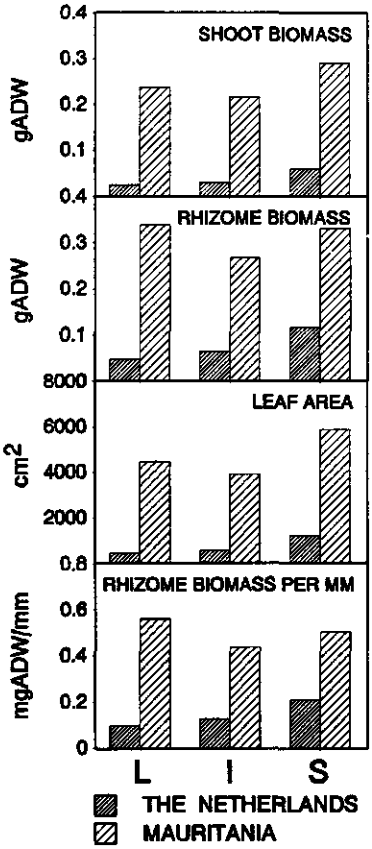

Fig. 6.5 Mean biomass, numbers and morphology of shoots and rhizomes of *Zostera noltii* originating from the Netherlands and Mauritania and cultivated under long-day light conditions (L), intermediate light conditions (I) and short-day light conditions (S) in the laboratory for 5 months (Sept 1989-Jan 1990). Number of replicates is 2.

Table 6.4 Degrees of freedom (df), sum of squares and level of significance (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$) of the effects of light period and land of origin on the parameter estimates of the light-response curves of *Zostera noltii* at the end of the experimental period.

		Michaelis-Menten model			**Jassby & Platt model**		
	df	Ik[a]	Pmax[a]	R[a]	Ik[a]	Pmax[a]	R[a]
Light period	2	1063	0.0057	0.0067	607	0.0028	0.0056
Land of origin	1	4108	0.0025	0.0039	4707	0.0007	0.0041
Error	5	8006	0.0160	0.0050	4107	0.0064	0.0045

[a] ANOVA analysis

At the end of the experimental period, biomass and numbers of shoots and rhizomes, leaf area and total rhizome length of *Zostera noltii* were not significantly different for the various photosynthetic and photoperiods (Table 6.3). The differences between material originating from two different countries became, however, more pronounced during the experiment (Table 6.3). Mauritanian shoot biomass was more than six times higher than Netherlands shoot biomass, the rhizome biomass approximately four times and the total biomass almost five times (Fig. 6.5). Total leaf area of the Mauritanian seagrass was more than six times higher and the rhizome biomass per mm was more than three times higher than that of the Netherlands seagrass (Fig. 6.5). Number of shoots and rhizome internodes, however, did not significantly differ between the two countries (Table 6.3).

Light-response curves

The parameter estimates of the light-response curves of *Zostera noltii* were not significantly influenced by differences in preceding light conditions or by land of origin (Table 6.4). These estimates were, therefore, averaged to describe a mean light-response curve for *Z. noltii* by the Michaelis-Menten model as well as the Jassby & Platt model (Fig. 6.6). Although the parameter estimates were considerably different for the two models (Table 6.5), both light-response curves still show a more or less similar pattern (Fig. 6.6).

DISCUSSION

The length of the photosynthetic period did not influence growth, biomass and production of *Zostera noltii*. Growth rates in the laboratory were more or less similar to natural growth rates (Vermaat *et al.* 1987, Van Lent et al 1991, Vermaat *et al.* 1993). Apparently, leaf growth$\cdot$day^{-1} and biomass were not favoured by doubling the light availability from 8 to 16 hours.

Table 6.5 Means of estimates of main parameters (Ik, Pmax and R) and derivates (α and LCP) of the light-response curve of *Zostera noltii* as fitted by the Michaelis-Menten and Jassby & Platt model.

Parameter		Michaelis-Menten	Jassby & Platt
Ik	$\mu E \cdot m^{-2} \cdot s^{-1}$	172	239
Pmax	$mgO_2 \cdot gADW^{-1} \cdot min^{-1}$	0.3622	0.2819
R	$mgO_2 \cdot gADW^{-1} \cdot min^{-1}$	0.0925	0.0839
α	$(mgO_2 \cdot gADW^{-1} \cdot min^{-1}) \cdot (\mu E \cdot m^{-2} \cdot s^{-1})^{-1}$	$22.17 \cdot 10^{-4}$	$11.98 \cdot 10^{-4}$
LCP	$\mu E \cdot m^{-2} \cdot s^{-1}$	59	73

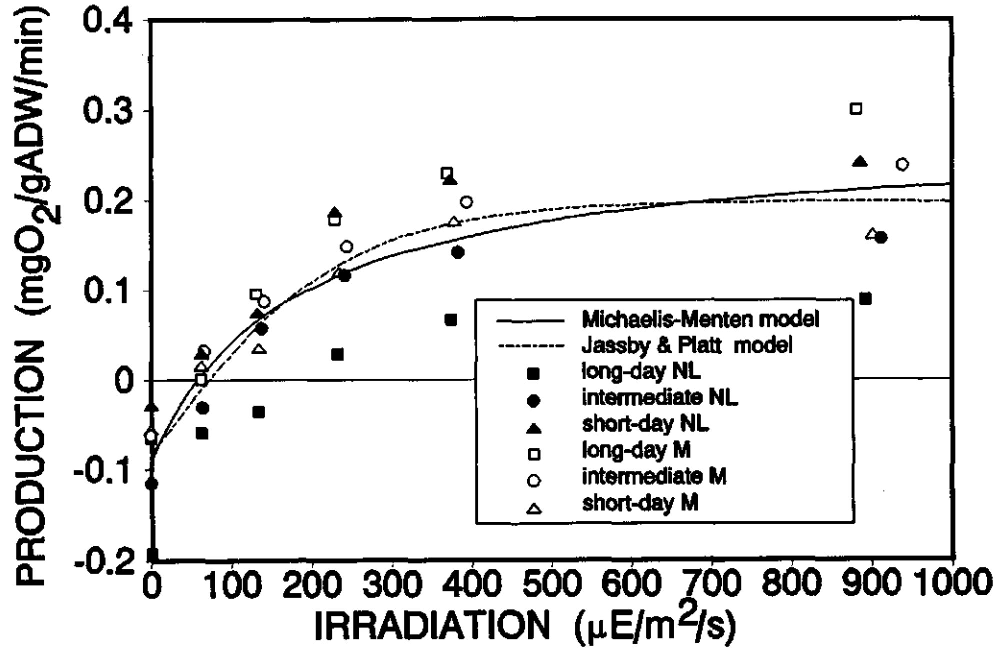

Fig. 6.6 Light-response curves of shoots of *Zostera noltii* originating from the Netherlands (NL) and Mauritania (M) and cultivated under long-day light conditions, intermediate light conditions and short-day light conditions in the laboratory for 5 months, and mean light-response curves as estimated by the Michaelis-Menten and the Jassby & Platt model.

The present results suggest that seasonality of *Z. noltii* is not determined by length of the photoperiod, because no effects of photoperiod on seagrass biomass, growth and production were found. The light-response curves were not significantly different for material cultivated under different light conditions and originating from different countries. The mean curve of the material originating from the Netherlands and Mauritania showed a light compensation point of 59 to 35 $\mu E\cdot m_{-2}\cdot s^{-1}$ and the light saturation level was approximately 600 to 1000 $\mu E\cdot m_{-2}\cdot s^{-1}$, depending on the model applied. This light-response curve resembles more or less the curve as published for *Z. noltii* originating from Spain, with estimates for respiration of approximately -0.02 $mgO_2\cdot min^{-1}$ and maximum net production of 0.16 $mgO_2\cdot min^{-1}$ (Jiménez *et al.* 1987). However, the light compensation point (30-35 $\mu E\cdot m_{-2}\cdot s^{-1}$) is lower and the light saturation level (3600 $\mu E\cdot m_{-2}\cdot s^{-1}$) is higher for the Spanish seagrass compared to the Netherlands and Mauritanian seagrass. These differences are more probably due to differences in methods and seagrass material (the Spanish curve was based on young leaves) than to actual phenotypic or genotypic variation within this seagrass species.

In conclusion, no effects of photosynthetic and photoperiod on growth, biomass and production of *Z. noltii* were found. However, results must be interpreted with much caution due to the low number of replicates, which was a result of the time-consuming measurements.

Although leaf growth rates and light-response relationships were not significantly different for the seagrass originating from the Netherlands and Mauritania, biomass values and development differed all along the experimental period. Whilst the biomass of the Netherlands seagrass remained more or less the same during the experimental period, the biomass of the Mauritanian plants almost doubled. This result can be ascribed to the fact that the preceding cultivation period of almost one year in the laboratory under similar conditions was not long enough to smooth out phenotypic differences between the two seagrass communities. The difference in biomass development during the experimental period, however, suggest that the seagrass may have also been genotypically adjusted to the different environments of temperate and tropic climate zones.

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CHAPTER 7

EFFECTS OF GRAZING BY *HYDROBIA ULVAE* ON THE GROWTH OF *ZOSTERA NOLTII* IN THE DUTCH WADDEN SEA

ABSTRACT The decrease of the intertidal seagrass *Zostera noltii* in the Dutch Wadden Sea may have been the result of enhanced periphyton load due to eutrophication. The decrease of this seagrass species coincided with an increase in the mudsnail *Hydrobia ulvae*. The feeding of this mudsnail on periphyton may have partly counteracted an increase of periphyton biomass. Exclosure experiments on seagrass stands in the Dutch Wadden Sea showed that the density of periphyton on the leaves of *Z. noltii* was related to the grazing rate of mudsnails. Grazing indirectly controlled the density and biomass of the seagrass, in particular of the underground parts. Since this seagrass species survives winter in temperate climate zones mainly by rhizomes, grazing may also influence the seagrass dynamics in the long term. The grazing rate is probably determined by food supply, predation and intraspecific interactions. The results of the experiment were in agreement with field observations on coinciding low densities of mudsnails and high densities of fouling of seagrass stands on the tidal flats of western Wadden Sea in the late 1970s.

INTRODUCTION

The mudsnail *Hydrobia ulvae* is one of the most abundant epibenthic faunal species living on the tidal flats of the Wadden Sea. The mean density in the Dutch area was 866 animals·m^{-2} (Beukema 1976) and maximum densities of over 200.000 animals·m^{-2} were found near Knechtsand, Germany (Hauser & Michaelis 1975). Mudsnails play a more modest role concerning biomass. Although their contribution to the total macrofaunal biomass can rise to over 80% in the German Wadden Sea (Asmus & Asmus 1985), the mean contribution of *H. ulvae* to the macrofaunal biomass of the Dutch Wadden Sea is less than 1% (Beukema 1976). The mudsnail is generally considered to be a grazer, feeding on microphytobenthos, bacteria and detritus (Newell 1965, Fenchel 1975, Jensen & Siegismund 1980), but possesses is also able to behave as a deposit- and a filter-feeder (McLusky & Elliot 1981).

Hydrobiidae are often found in temperate *Zostera* beds (Borum 1987, Hellwig-Armonies 1988). The mean annual biomass of mudsnails in seagrass stands can be over 25 gADW·m^{-2} (Asmus & Asmus 1985). They feed not only on benthic material but also on the periphyton present on the seagrass leaves (McLusky & Elliot 1981, Asmus *et al.* 1980). Periphyton may have negative effects on seagrass photosynthesis and growth as the result of shading and competition for carbon and nutrients (Sand-Jensen 1977, Silberstein *et al.* 1986, Shepherd *et al.* 1989). Periphyton biomass may also be suppressed by grazing epifauna (Dennison & Alberte 1986, Borum 1987, Orth & Moore 1988). In this way, the feeding activity of the periphyton grazers can significantly promote macrophyte growth and development, as is found for freshwater macrophytes (Brönmark 1985) and seagrasses (Hootsmans & Vermaat 1985, Howard & Short 1986). Field experiments and observations indicate that *H. ulvae* can keep the biomass of microphytobenthos on tidal flats of the Wadden Sea at a low level (Asmus 1982, Cadée 1980).

During the last thirty years, the Wadden Sea seagrass *Zostera noltii* (Hornem.) decreased in the Dutch Wadden Sea (Den Hartog & Polderman 1975, Chapter 3). The decline of the seagrass coincided with eutrophication of this area, with

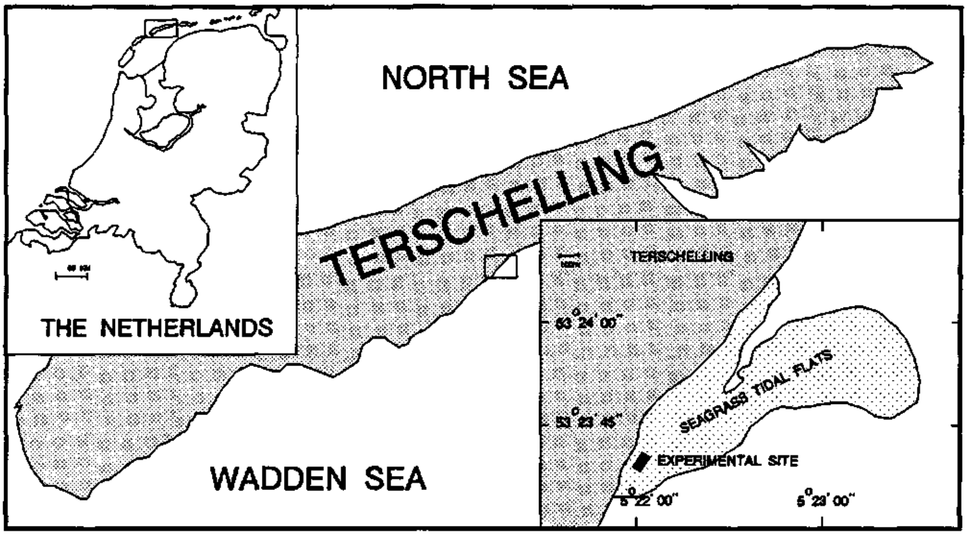

Fig. 7.1 Location of the experimental site on the tidal flats off Terschelling.

nutrient levels increasing simultaneously with primary and secondary biomass (Cadée & Hegeman 1986, Beukema 1989, Van der Veer *et al.* 1989). Since the primary production and chlorophyll a of the microphytobenthos doubled over the period 1968-1981 (Cadée 1984), it may be expected that production of epiphytes on the seagrass leaves also increased during this period. The periphyton biomass, however, may have been partly controlled by an increase of the mudsnails. In general, eutrophication of the Wadden Sea coincided with a doubling of the macrofauna biomass and turnover rate (Reise & Schubert 1987, Beukema 1989). Though erratically fluctuating, the mean density of *H. ulvae* increased during the 1970s and the 1980s in the western half of the Dutch Wadden Sea to reach several thousands per m^2 in 1987 (Beukema 1989). If the mudsnails were able to consume the total or a part of the increased biomass of periphyton, they may have reduced the negative effects of eutrophication on *Z. noltii* in the Dutch Wadden Sea.

This paper discusses the results of an exclosure experiment on seagrass stands in the Dutch Wadden Sea, which was carried out to examine the influence of *H. ulvae* on the growth and biomass development of *Z. noltii*.

MATERIAL AND METHODS

The experiment was launched in the week from 11 to 15 June 1987, and ran from 16 June to 8 September 1987. The experimental plot was located on the tidal flat near Terschelling in an area with a dense and homogeneous seagrass stand (Fig. 7.1). The experimental plot contained six exclosures, consisting of a PVC frame covered with gauze, with a mesh-width of 1 mm on the bottom and 0.85 mm on the walls. The ground diameter of the exclosures was 1 m, the diameter at the top was 1.4 m. The exclosures were secured by means of poles, pins and ropes (Fig. 7.2).

At the start of the experiment, the upper layer of sediment (5 cm) was removed with a shovel in all exclosure sections. The removed sediment was partly dried and subsequently frozen in the laboratory at -30°C in order to remove most of the inhabiting macrofauna. The defrosted sediment was redistributed over the bottom of the exclosures. The seagrass plants and mudsnails were sampled in six round areas with a diameter of 1 m in close proximity of the experimental area. The seagrass plants were cleared of mudsnails and randomly divided into six equal portions, based on number of shoots (± 1200) and fresh-weight (± 200 g) of the material. The seagrass was transplanted by hand in all six exclosures. The mudsnails were sampled by means of a 1 mm sieve in six round areas with a diameter of 1 m in close proximity of the experimental area. The mudsnails were cleared of sediment, mixed and divided into four equal portions, based on fresh-weight and volume. The mudsnails were transplanted into three of the six exclosures, randomly chosen. The remaining fourth portion of mudsnails was analyzed in the laboratory for biomass and size distribution.

The relative leaf growth rates (LGR), leaf loss rates (LLR) and leaf net-growth rates (LNR) of the seagrass were measured regularly during the experimental period according to an adjusted leaf-marking method (Vermaat *et al.* 1987). Biomass and chlorophyll-*a* and chlorophyll-*b* contents of the periphyton were determined five times during the second half of the experiment. During each sampling period, eight shoots per exclosure were sampled and put in plastic bottles filled with Whatman GF/C filtered seawater, four shoots in one bottle for determination of biomass and four shoots in the other bottle for the determination of chlorophyll. Per bottle, the periphyton was carefully removed from the leaves to the filtered seawater by means of a scalpel. The seawater was transferred to Whatman GF/C filters. These filters were precombusted and preweighted for the determination of the biomass. The filters for the determination of chlorophyll were frozen at a temperature of -20 °C until further handling. The chlorophyll content of the periphyton was determined according the method of Wellburn and Lichtenthaler (1984) with 80% acetone. The biomass (ADW) of periphyton, seagrass and mudsnails was determined as the difference in dry-weight (24 hours; 105 °C) and ash-weight (2 hours; 450 °C).

At the end of the experimental period, the exclosures were sampled by means of a sediment core with a diameter of 14.5 cm, three samples per exclosure. The material was washed through a 1 mm sieve. The seagrass was divided into aboveground (shoots) and underground (rhizomes and roots) material. The number of shoots was counted. The mudsnails were dried and subsequently divided into five groups of different size by means of 1, 1.4, 1.8, 2.24 and 2.5 mm sieves. The number of mudsnails which was supposed to be alive during sampling, recognisable by the green-brownish colour instead of whitish, was counted in each size group. In addition, the most common macrofauna in the exclosures were

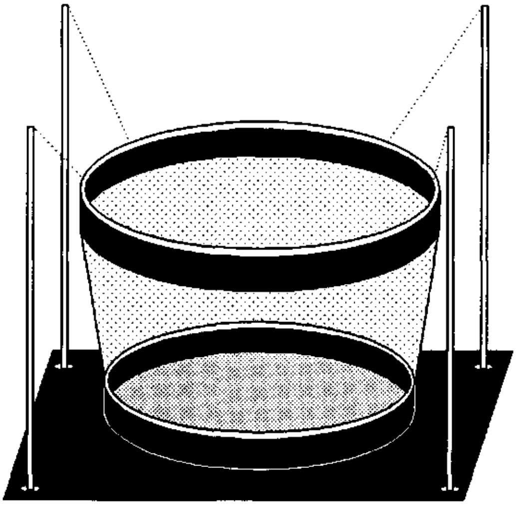

Fig. 7.2 An exclosure as used for the grazing experiment in the seagrass stands on the tidal flats off Terschelling.

counted. Mudsnails, periphyton, seagrass and common macrofauna species were also sampled in two sites in close proximity of the exclosures to check whether the experimental conditions were more or less similar to the natural conditions. The biomass (ADW) of mudsnails and seagrass was determined as mentioned before.

Statistical analysis of most data was performed by means of Generalized Linear Model (GLM-) ANOVAs (Dobson 1983, McCullagh & Nelder 1989). Two different forms of GLM-ANOVA were employed for this research, viz. a logarithmic and a logit link function. The logarithmic link function was used when the observations were scaled from 0 to infinity. If so, then an overdispersed or underdispersed Poisson distribution was assumed, and expectations were supposed to be additive on a logarithmic scale, i.e. multiplicative on the original scale. The logit link function was used if the observations were scaled from 0 to a (positive) total. Subsequently, an overdispersed or underdispersed binomial distribution was assumed, and expectations were supposed to be additive on a logistic scale, i.e. log(part/(total-part)). As many interactions as possible were included in the model while estimating the main effects and their standard errors. In some models, however, the highest order interactions were assumed not to exist because it was not possible to test these interactions statistically. Several models had main effects nested within other effects or within interactions, e.g. the effect of exclosure was nested within the effect of treatment. If so, then the nested effects were assumed to be of a higher order than the ones in which they were nested. The leaf net-growth rate (LNR) was statistically analyzed by means of an ANOVA.

Table 7.1 Degrees of freedom (df), deviance (D) and level of significance (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$) of GLM-ANOVAs for effects of grazing capacity (treatment), size distribution of the mudsnails (fraction) and nested effects of exclosures on the density and biomass of *Hydrobia ulvae*.

	Density[a] ($\cdot m^{-2}$)			**Biomass**[a] ($gADW \cdot m^{-2}$)		
	df	D	p	df	D	p
Treatment	1	22611	***	1	20.30	***
Fraction	4	714800	***	4	350.78	***
Trt x fraction	4	28645	**	4	27.09	***
Trt x exclosure[b]	4	40596	***	4	18.35	***
Trt x fraction x exclosure[c]	16	27101		16	8.97	
Error	60	78210		56	24.26	

[a] GLM analysis with logarithmic link function

[b] effect of exclosure nested in treatment

[c] effect of exclosure nested within interaction between treatment and exclosure

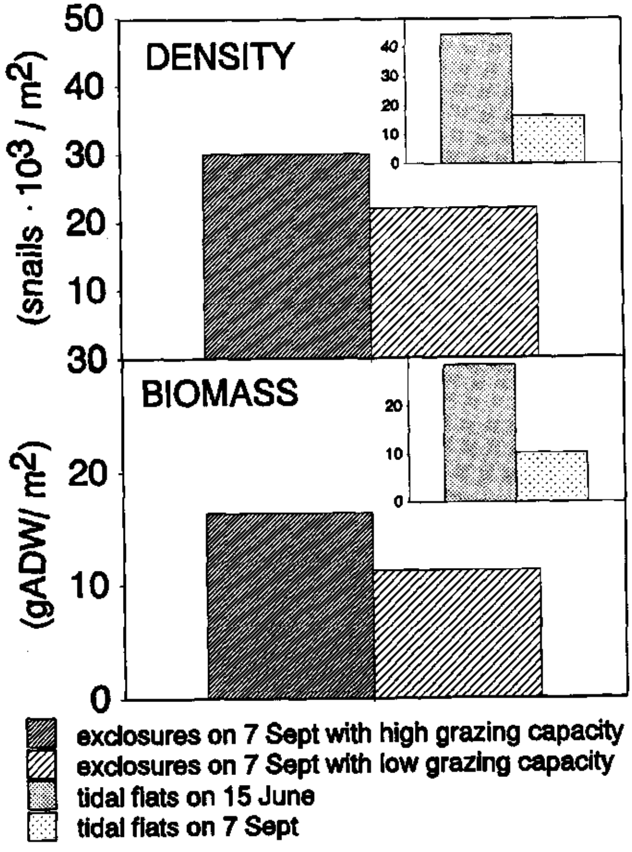

Fig. 7.3 Mean density and biomass of *Hydrobia ulvae* in the exclosures with high and low grazing capacity in the seagrass stands of Terschelling at the end of the experimental period (7 September 1987), and in the seagrass stands of Terschelling at the beginning (15 June 1987) and at the end of the experimental period.

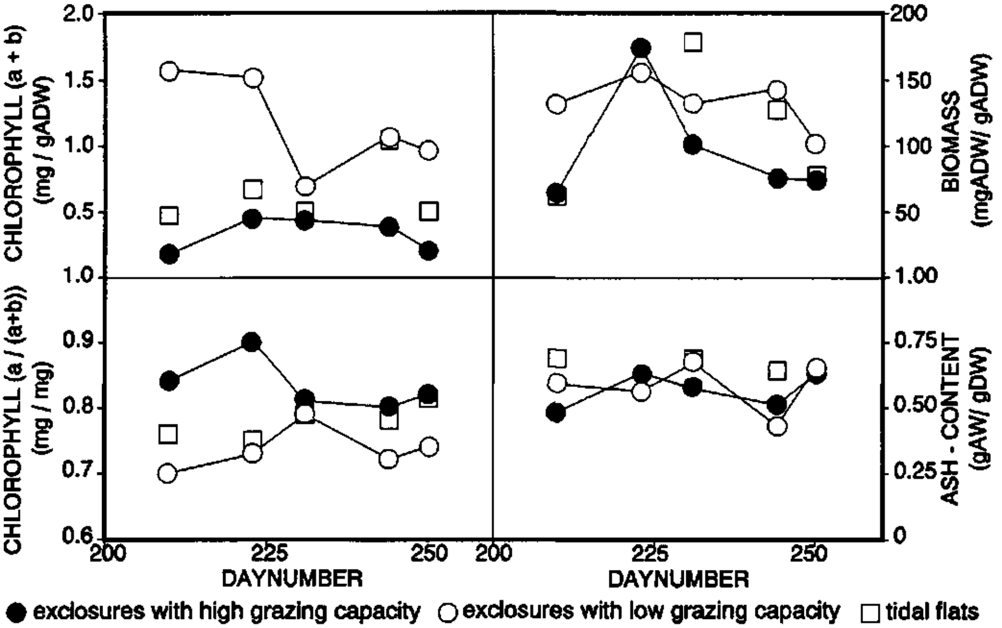

Fig. 7.4 Mean chlorophyll contents, chlorophyll ratio, biomass and ash-content of periphyton on the leaves of *Zostera noltii* in the exclosures with high and low grazing capacity in the seagrass stands of Terschelling from 29 July to the end of the experimental period (7 September 1987), and in the seagrass stands of Terschelling from 29 July to 7 September 1987.

RESULTS

Unfortunately, the mudsnails managed to recolonize the exclosures from which they were excluded (Fig. 7.3). The significance of the interactions between treatment and exclosure indicates that there were also differences in mudsnail density and biomass between the exclosures (Table 7.1). The mean density and biomass of the mudsnails were, however, still significantly higher in the grazed exclosures than in the initially ungrazed exclosures (Table 7.1, Fig. 7.3). To account for the changes in grazing capacity during the experiment, the grazed and initially ungrazed exclosures will henceforth be referred to as exclosures with high and low grazing capacity, respectively.

The grazing capacity in the exclosures significantly influenced the density of the periphyton on the seagrass leaves (Table 7.2). The total chlorophyll contents were almost twice as high in the exclosures with low grazing capacity as in the ones with high grazing capacity (Fig. 7.4). The periphyton biomass was generally higher in the extensively grazed exclosured than in the intensively grazed ones,

Table 7.2 Degrees of freedom (df), deviance (D) and level of significance (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$) of GLM-ANOVAs for effects of time and grazing capacity (treatment) on chlorophyll contents, chlorophyll ratio, biomass and ash-content of the periphyton on leaves of *Zostera noltii.*

		CHLa[a] (g·gADW^{-1})		**CHLb**[a] (g·gADW^{-1})		**CHLa+b**[a] (g·gADW^{-1})		**CHLa/a+b**[b] (g·g^{-1})		***Biomass***[a] (g·gADW^{-1})		**Ash%**[2,3] (g·g^{-1}·100%)	
	df	D	p	D	p	D	p	D	p	D	p	D	p
Time	4	1100		87		1057		118		0.198		44.29	*
Treatment	1	7056	***	516	***	7310	***	251	***	0.091	*	0.91	
Time x trt	4	922		196	*	1039		92		0.090		21.67	
Error	20	4090		319		4164		244		0.351		58.78	

[a] GLM analysis with logarithmic link function

[b] GLM analysis with logit link function

[c] effect on ash% ((gAW/gDW)*100%) was analyzed as (ash%/(100-ash%))

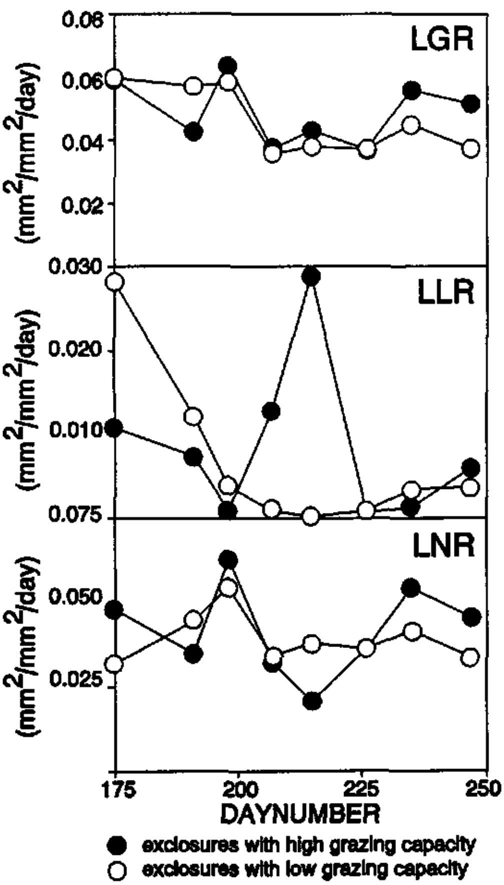

Fig. 7.5 Mean relative leaf growth rate (LGR), leaf loss rate (LLR) and leaf net-growth rate (LNR) of *Zostera noltii* in the exclosures with high and low grazing capacity in the seagrass stands of Terschelling from 24 June to 7 September 1987.

Table 7.3 Degrees of freedom (df), deviance (D) and level of significance (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$) of ANOVAs and GLM-ANOVAs for the effects of time, grazing capacity (treatment) and exclosures on the leaf growth rate (LGR), leaf loss rate (LLR) and leaf net-growth rate (LNR) of *Zostera noltii.*

	LGR[a] ($mm^2 \cdot mm^{-2} \cdot day^{-1}$)			LLR[b] ($mm^2 \cdot mm^{-2} \cdot day^{-1}$)			LNR[d] ($mm^2 \cdot mm^{-2} \cdot day^{-1}$)		
	df	D	p	df	D	p	df	D	p
Time	7	0.0734	*	7	0.2456	**	7	0.0036	*
Treatment	1	0.0019		1	0.0039		1	0.0001	
Time x trt	7	0.0164		7	0.1849	*	7	0.0015	
Trt x exclosure[c]	4	0.0075		4	0.0734		4	0.0081	
Error	26	0.0852		26	0.2226		28	0.0057	

[a] GLM analysis with logarithmic link function

[b] GLM analysis with logit link function, and LLR as part of 1

[c] effect of exclosure nested in treatment

[d] ANOVA analysis

with the exception of the second sampling period (Table 7.2, Fig. 7.4). In addition, grazing capacity influenced the composition of chlorophyll Table 7.2), resulting in relatively more chlorophyll-*a* under intensively grazed conditions (Fig. 7.4). No significant effect of grazing on the ash-content of the periphyton was found (Table 7.2).

The relative leaf growth rate (LGR), leaf loss rate (LLR) and leaf net-growth rate (LNR) of *Z. noltii* were not influenced by the grazing capacity (Table 7.3). The leaf loss rate was generally lower than the leaf growth rate, resulting in a positive leaf net-growth rate (Fig. 7.5). The leaf loss rate showed a significant effect of the interaction between grazing and time (Table 7.3). The leaf loss rate in the exclosures with a high grazing rate was first low, increased during the experiment and then levelled off again. The leaf loss rate of *Z. noltii* in the extensively grazed exclosures was high at the start of the experimental period and subsequently decreased to a relative low level (Fig. 7.5). No significant differences in leaf growth rates between exclosures were observed (Table 7.3).

The grazing capacity significantly influenced the development of the *Z. noltii* stands in the exclosures (Table 7.4). The shoot density was more than 35% higher and the total biomass more than 50% higher in the intensively grazed exclosures than in the more extensively grazed ones (Fig. 7.6). In addition, the seagrass in the exclosures with a low grazing capacity developed not only absolutely but also relatively less underground material, i.e. rhizomes and roots (Table 7.4). The interaction between grazing capacity and exclosure was significant for shoot density, underground biomass, total biomass and the relative contribution of the aboveground to the total biomass (Table 7.4).

Table 7.4 Degrees of freedom (df), deviance (D) and level of significance (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$) of GLM-ANOVAs for effects of grazing capacity (treatment) and exclosures on shoot density, biomass and biomass ratio of seagrass *Zostera noltii*.

		Density	Biomass			
		Shoots[a] ($\cdot m^{-2}$)	Aboveground[a] ($gADW \cdot m^{-2}$)	Underground[a] ($gADW \cdot m^{-2}$)	Total[a] ($gADW \cdot m^{-2}$)	Above/total[b] ($g \cdot gADW^{-1}$)
	df	D p	D p	D p	D p	D p
Treatment	1	3839 *	24.43 **	63.89 ***	73.35 ***	14.95 *
Trt x exclosure[c]	4	6192 *	31.05	69.20 **	49.55 **	50.69 **
Error	12	5515	26.55	25.88	26.11	26.33

[a] GLM analysis with logarithmic link function

[b] GLM analysis with logit link function

[c] effect of exclosure nested in treatment

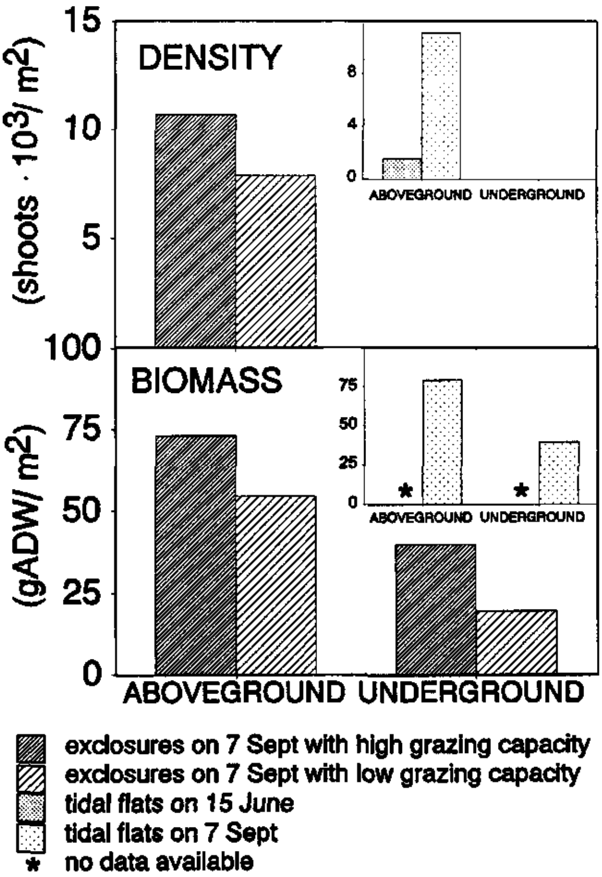

Fig. 7.6 Mean shoot density, biomass and biomass ratio of seagrass in the exclosures with high and low grazing capacity in the *Zostera noltii* stands of Terschelling at the end of the experimental period (7 September 1987), and in the seagrass stands of Terschelling at the beginning (15 June 1987) and at the end of the experimental period.

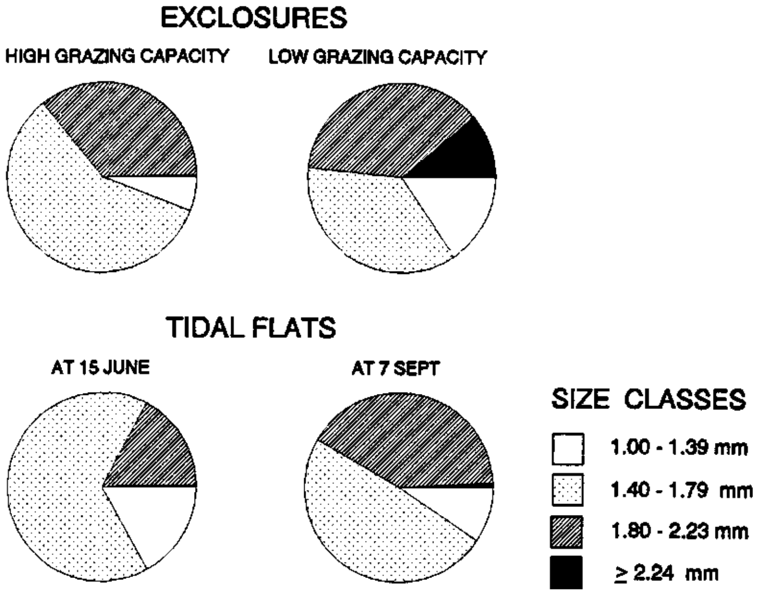

Fig. 7.7 Distribution of biomass (gADW·m^{-2}) over the different size classes of *Hydrobia ulvae* in the exclosures with high and low grazing capacity in the seagrass stands of Terschelling at the end of the experimental period (7 September 1987), and in the seagrass stands of Terschelling at the beginning (15 June 1987) and at the end of the experimental period.

Finally, the grazing capacity also influenced the mudsnails themselves. Their size distribution was significantly different for the exclosures with a high and a low grazing capacity, both in density and in biomass (Table 7.1). Especially the large snails, i.e. ≥ 2.24 mm, were relatively more abundant in the extensively grazed exclosures than in the intensively grazed ones (Fig. 7.7). Not only mudsnails, but also many other macrofaunal species managed to recolonize the exclosures within the experimental period (Table 7.5).

At the end of the experiment, mudsnail density and biomass in the seagrass stands were more or less similar to those in the exclosures with low grazing capacity (Fig. 7.3). The characteristics and development of periphyton were more or less similar in the exclosures and in the seagrass stands (Fig. 7.4). Seagrasses increased during the experimental period to values comparable to those for the exclosures with the high grazing capacity (Fig. 7.6). The mudsnails in the seagrass stand generally increased in size during the experimental period (Fig. 7.7). At the end of the experimental period, the natural size distribution resembled the distribution as found in the exclosures with a high grazing capacity (Fig. 7.7). The densities of other macrofaunal species in the exclosures were more or less similar to those found in the seagrass stands, but differed among species (Table 7.5).

Table 7.5 Means and standard errors of the densities of the most common macrofaunal grazers (g), suspension-feeders (s), deposit-feeders (d) and predators (p) in the exclosures with low and high grazing capacity and in the seagrass stands of Terschelling at the end of the experimental period. Number of replicates is 3 for the exclosures and 2 for the seagrass stand.

Species		**Exclosures** (ind·m^{-2})				**Seagrass stands** (ind·m^{-2})	
		low		**high**			
		mean	e	mean	se	mean	se
Carcinus maenas	p	135	76	108	31	303	0
Cerastoderma edule	s	67	62	54	23	141	29
Corophium volutator	d	121	88	47	31	0	0
Littorina littorea	g	1023	748	693	596	676	614
Macoma balthica	d	13	23	128	76	414	14
Mytilus edulis	s	3456	1243	1823	309	3270	742
Polychaetes	d/p	20	20	236	152	353	243

DISCUSSION

The conditions in the exclosures were more or less similar to the natural conditions in the seagrass stand. Since the mudsnail densities were higher in the grazed exclosures than in the seagrass stands, the situation in these exclosures can be considered as an increase of the natural grazing capacity. In the exclosures with low grazing capacity, however, the mudsnail density and biomass was zero at the beginning of the experiment and comparable with the field situation at the end. Assuming that the recolonization of mudsnails occurred more or less gradual during the experimental period, the situation in the exclosures with a low grazing capacity represented a decrease of the natural grazing capacity.

The grazing capacity significantly influenced the periphyton load and subsequently the development of *Zostera noltii.* A decrease of the grazing capacity resulted in an increase of the chlorophyll contents and biomass of the periphyton. Although no significant relationships between mudsnail abundance and leaf growth and loss rates were found, the density and biomass of the seagrass were obviously affected by a decrease in grazing capacity. The increased grazing capacity not only promoted the development of the total seagrass biomass, but also enlarged the relative contribution of the underground biomass. Since the survival of *Z. noltii* in the seagrass stands off Terschelling mainly depends on rhizomes (Jacobs *et al.* 1983, Philippart unpublished), grazing by *H. ulvae* will also affect the biomass dynamics of this seagrass species in the long term. If eutrophication resulted in an increase of periphyton growth, the coinciding increase of mudsnails must have (partly) counteracted a subsequent increase in periphyton biomass.

The mudsnail abundance was higher in the exclosures with a high grazing capacity than in the seagrass stands. This difference may be the result of protection against predation by shorebirds and crabs in the exclosures. Caging experiments showed that the predatory crab *Carcinus maenas* can significantly reduce the standing-stock of *H. ulvae* (Reise 1985, Frid & James 1988). No crabs were present in the exclosures at the beginning of the experiment, and densities were still lower inside the exclosures than in the seagrass stands at the end of the experimental period. At the end of the experiment, the mudsnails were generally larger in the exclosures with low grazing capacity than in the exclosures which were more intensively grazed. These findings indicate that food is limiting in dense mudsnail communities. Intraspecific competition for food between *Hydrobia* sp. in natural densities is found in the laboratory as well as in the field (Fenchel 1976, Levinton 1979, López-Figueroa & Xavier Niell 1987). The grazing capacity of mudsnails is, therefore, controlled by biotic factors, such as food supply, predation and intraspecific interactions.

Since the grazing capacity is related to the density of the mudsnails, a decrease in snail density will result in a decrease of seagrass density and biomass. Although this process may be slowed down by the buffering effect of the intraspecific interactions between the mudsnails, a strong decline of grazing mudsnails most probably severely affects seagrass stands. Several Dutch marine biologists observed a considerable decrease of mudsnails at the beginning of the 1970s on the tidal flats of the Wadden Sea (J.J. Beukema pers comm. 1994, C. Den Hartog pers. comm. 1994, C. Swennen pers. comm. 1993). This decline may be attributed to natural fluctuations, possibly caused by an increased mortality due to an outbreak of parasites in the mudsnail population (Lauckner 1990). Low mudsnail densities may, however, also be the result of human impact. The relatively low densities of mudsnails on the Dutch tidal flats coincided with maximum concentrations of pollutants in the river Rhine (Essink & Wolff 1978). In agreement with the results of the experiment, C. Den Hartog (pers. comm. 1994) noticed an abnormally high density of fouling on the leaves of the seagrass stands on the tidal flats of the Balgzand and off Terschelling during this period of low mudsnail densities. The decrease of *Z. noltii* in the Wadden Sea may, therefore, have been started when the periphyton-grazing mudsnails suddenly declined at the beginning of the 1970s.

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CHAPTER 8

INTERACTIONS BETWEEN *ARENICOLA MARINA* AND *ZOSTERA NOLTII* ON A TIDAL FLAT IN THE WADDEN SEA

ABSTRACT On the tidal flats off Terschelling in the Dutch Wadden Sea, the seagrass *Zostera noltii* Hornem. and adult lugworms *Arenicola marina* L. show strictly separate distributions with an abrupt border between the two communities. Since seagrass and lugworms do not show different limitations regarding sediment type and the emersion period, the border must be the result of other environmental factors or of plant-animal interactions. Transplantation experiments on the tidal flats showed that the seagrass was quite capable of growing on the lugworm tidal flat when worms were absent. However, the seagrass density and biomass were severely influenced in the presence of lugworms, most probably due to the worms' sediment-reworking activities. Lugworms quickly disappeared from the experimental sites on the seagrass tidal flat, irrespective of the actual presence of seagrass. A local survey of the seagrass area showed that funnel formation by lugworms to sufficient depth was restricted by a dense clay layer under the sediment surface, a remnant of a former salt marsh. These results indicate that an increase of lugworm densities in the Dutch Wadden Sea may have contributed to the decrease of the area covered by *Z. noltii* on the tidal flats off Terschelling over the last 20 years.

INTRODUCTION

The seagrass *Zostera noltii* Hornem. has become rare in the Dutch Wadden Sea (Den Hartog & Polderman 1975, Chapter 3). Throughout the Wadden Sea, this seagrass species can be found to coexist with adult lugworms *Arenicola marina* L. (Asmus & Asmus 1985, Michaelis 1987, Reise *et al.* 1989). However, the characteristic faecal castings of the lugworms are absent in the *Z. noltii* community on the tidal flat south of the Dutch island of Terschelling. This seagrass stand extends several hundred meters from a dike to an area with a high density of lugworms (ca 60 ind. m^{-2}), which is completely devoid of seagrass (Chapter 3). The change from the seagrass community to that of the lugworms is not gradual but abrupt. This sharp border can be the result of different environmental preferences or limitations of seagrass and lugworms, or be due to interactions between the species.

The distribution of intertidal benthic organisms is often related to sediment composition and emersion period (Dankers & Beukema 1983, Dijkema 1991). The seagrass *Z. noltii* occurs on all sediment types of the Wadden Sea, but shows a preference for sediments with a silt content over 5% (Philippart *et al.* 1992). It occurs over the entire tidal range in tidal flats of the Wadden Sea, but the optimal emersion period differs for different locations. The optimal emersion period ranges from less than 50% in the area east of the island of Fanø, the most northerly part of the Wadden Sea, to more than 67% south of the Eiderstedt peninsula in the German Bight. Near the island of Terschelling, the optimal emersion period for *Z. noltii* is around 50% of the tidel period (Philippart *et al.* 1992). The lugworm *A. marina* also occurs within a broad range of sediment types, with highest densities at silt contents of 2% to 12% (Beukema & de Vlas 1979). In the Dutch Wadden Sea, adult lugworms occur in the littoral zone between 1.9 m below and 0.4 m above the Mean Tidal Level (MTL). Highest densities were found between -0.7 m and +0.1 m MTL (Beukema & De Vlas 1979, Dankers & Beukema 1983), which roughly corresponds to an emersion period between 25% and 50%. At the study site on the tidal flats of Terschelling, the top layer of the sediment consists of sand with a silt content of less than 5% (Dijkema *et al.* 1989) and the emersion period varies between 25% and 75% (Chapter 3). The abrupt border between seagrass and lugworms can therefore not be explained by different preferences for sediment type or emersion period, because these factors lie well within the suitable ranges of both seagrass and lugworm habitats. It must be the result of other environmental factors or of a plant-animal interaction.

Dense seagrass stands can possibly hamper bioturbation of lugworms when established rhizome mats restrict funnel formation. In addition, dense seagrass stands shade the sediment surface and decrease the growth of microalgae on tidal flats, and thus can reduce the available food supply (Reise 1992) for lugworms which feed on microphytobenthos (Rijken 1979). However, the seagrass on the tidal flats of Terschelling does not have a dense rhizome mat and it covers the sediment completely only for a short period of the year (Chapter 4). Therefore, it is unlikely that lugworms are restricted by the actual presence of seagrass on the seagrass tidal flat.

Lugworms are known to affect the density and settlement of species inhabiting the tidal flats of the Wadden Sea, e.g. the tube-building polychaete *Pygospio elegans* (Reise 1985), the amphipod *Corophium volutator* (Flach 1992a) and juveniles of various worm and bivalve species (Flach 1992b). Reise (1985) found that *Z. noltii* can invade and settle in a lugworm tidal flat from which the lugworms have been removed. This indicates that lugworms can restrict expansion of seagrass stands. The restriction is most probably caused by the effect of sediment-reworking during feeding of the lugworms. Adult lugworms with a density of 85 ind. m^{-2} rework an amount of sediment that corresponds with a layer of 33 cm $year^{-1}$ (Cadée 1976). This rate of turnover is likely to affect seagrass growth and survival due to burial of plants.

Although the area of the seagrass stand under consideration decreased by almost 30% within the last 20 years (Chapter 3), the border seems more or less stable during the last five years (pers. obs.). If the interaction between lugworms and seagrass is the main structuring force for the observed distribution patterns, there has to be at least one additional environmental variable which restricts the expansion of lugworms towards the seagrass tidal flats. Earlier investigations on the tidal flats off Terschelling revealed the presence of a layer of dense clay below the sandy surface layer, a remnant of a former salt marsh. This layer may restrict the bioturbation by the adult lugworms, and in this way protect the seagrass community (Chapter 3).

The present study analyses the results of transplantation experiments and a survey. The transplantation experiments were carried out to examine if the strictly separate distribution of seagrass and lugworms on the tidal flats off Terschelling was caused by (1) a mutual interference of seagrass and lugworms, or (2) a restriction by other environmental factors. An additional survey was carried out to examine if the local distributions of seagrass and lugworms were related to the depth of the dense clay layer.

METHODS

Transplantation experiments

The transplantation experiments commenced in the last week of April 1990, at the start of the seagrass growing season. Two experimental plots, 50 m apart, were chosen on the tidal flats off Terschelling. One plot was located on the seagrass tidal flat and the other on the lugworm tidal flat (Fig. 8.1). Each plot contained nine experimental transplantation sites, circles with a diameter of 60 cm. At the start of the experiment, the upper layer of sediment (5 cm) was removed from all sites with a shovel and cleared of seagrass. Rhizomes of *Zostera noltii* generally do not occur deeper than 5 cm in the sediment on the tidal flats off Terschelling (pers. obs.).

On the seagrass tidal flat (S), three treatments were randomly distributed over 9 sites, i.e. three replicates per treatment. In the S_l sites, the cleared sediment was shovelled back and adult lugworms were added. Lugworms were collected on the lugworm tidal flat and transplanted with their heads down into small man-made holes in the experimental sites. Based on a mean density of 56 faecal castings m^{-2} in the experimental plot on the lugworm tidal flat, 16 adult lugworms were added into each site of 0.28 m^2. In three other sites on the seagrass tidal flat, the S_s sites, gauze with a mesh-width of 1 mm was placed at the bottom before refilling with sediment. Seagrass shoots were collected in close proximity to the experimental plot on the seagrass tidal flat and transplanted in these sites in the same density. This density was more or less equal to that of the removed seagrass community, i.e. ca 1000 shoots m^{-2}. Adult lugworms and seagrass were also transplanted in natural densities into the remaining three sites on the seagrass tidal flat, the S_{sl} sites, after the sediment was shovelled back into the holes. As in the other sites, plants were collected from the seagrass tidal flat and lugworms from the lugworm tidal flat.

On the lugworm tidal flat (L), the same three treatments as on the seagrass tidal flat were randomly distributed over nine sites. Sediment was shovelled back in three L_l sites. The L_s sites on the lugworm tidal flat were treated in the same way as the S_s sites on the seagrass tidal flat. The small-meshed gauze was meant to protect the seagrass transplants against undermining lugworm bioturbation. Since the gauze was not expected to have additional effects on seagrass, no wide-meshed gauze was used for the controls. Seagrass was transplanted into natural densities in the remaining three sites on the lugworm tidal flat, the L_{sl} sites, after the sediment was shovelled back into the holes. The seagrass originated from the seagrass tidal flats. No extra lugworms were added to the L_l and L_{sl} sites, because they already contained a natural density of lugworms beneath the upper 5 cm layer of the sediment.

The experimental sites were cleared after 6 weeks (on 6 June). The lugworms and seagrass plants were collected by stratified sieving. The upper 5 cm layer of sediment was washed through a 1 mm sieve, and all seagrass material was collected. Dead seagrass material and loose roots were removed and the number

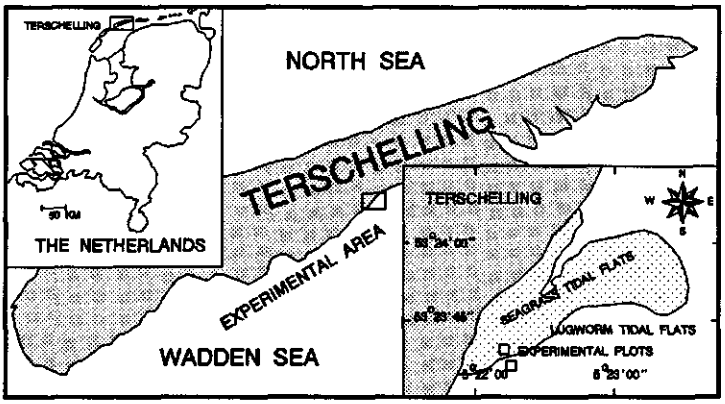

Fig. 8.1 Location of the experimental plots on the tidal flats off Terschelling, the Netherlands.

of live shoots was determined. The biomass (ADW) of the seagrass was determined as the difference between dry weight (24 hours at 105 °C) and ash weight (2 hours at 550 °C). The rest of the sediment was removed down to a depth of 0.3 to 0.5 m, which is sufficiently deep to sample all lugworms present (Beukema & de Vlas 1979). This material was washed through a 2 mm sieve. The lugworms were stored in 5% formalin. The seagrass was frozen at -20 °C until further handling. The number of lugworms in each sample was counted. The biomass (ADW) of the lugworms was determined as the difference between dry weight (2 to 3 days at 60 °C) and the ash weight (2 hours at 600 °C).

Hypothesis A states that lugworms are restricted on seagrass tidal flats by other environmental factors than the actual presence of seagrass. This was examined by comparing the abundance of lugworms in the sites without seagrass on the seagrass tidal flat (S_l sites) to that in the control sites without seagrass on the lugworm tidal flat (L_l sites). If the lugworms were affected by other environmental factors than by the seagrass itself, their abundance would be lower in the S_l sites than the L_l sites at the end of the experiment.

Hypothesis B states that seagrass is restricted on lugworm tidal flats by other environmental factors than the actual presence of lugworms. This was examined by comparing the development of the seagrass transplants in the sites without lugworms on the lugworm tidal flat (L_s sites) to that in the control sites without lugworms on the seagrass tidal flat (S_s sites). If the seagrass on the lugworm tidal flat was affected by other environmental factors than the lugworms, its abundance would be lower in the L_s sites than in the S_s sites at the end of the experiment.

Hypothesis C states that lugworms are restricted on seagrass tidal flats by the actual presence of seagrass. This was examined by comparing the abundance of the lugworms in the sites on the seagrass tidal flats with seagrass (S_{sl} sites) and the control sites without seagrass (S_l sites). If the seagrass restricted the presence

Table 8.1 Sum of squares and significance of effects of habitat and treatment and their interaction on the numbers and biomass of the seagrass *Zostera noltii* and the lugworm *Arenicola marina*, and of the hypotheses A, B, C and D (see text) (* $p<0.0125$).

		Zostera noltii		*Arenicola marina*	
	df	Number	Biomass	Number	Biomass
Habitat	1	227.769*	0.393*	17.405*	2.420*
Treatment	2	707.029*	1.703*	20.961*	5.290*
Habitat x Treatment	2	175.180*	0.498*	1.193	0.276
A	1	16.968	0.089	6.678*	1.033*
B	1	6.448	0.010	2.445	0.232
C	1	315.230*	0.589*	0.273	0.006
D	1	295.261*	0.897*	11.648*	3.139*
Error	12	128.237	0.266	5.712	0.558

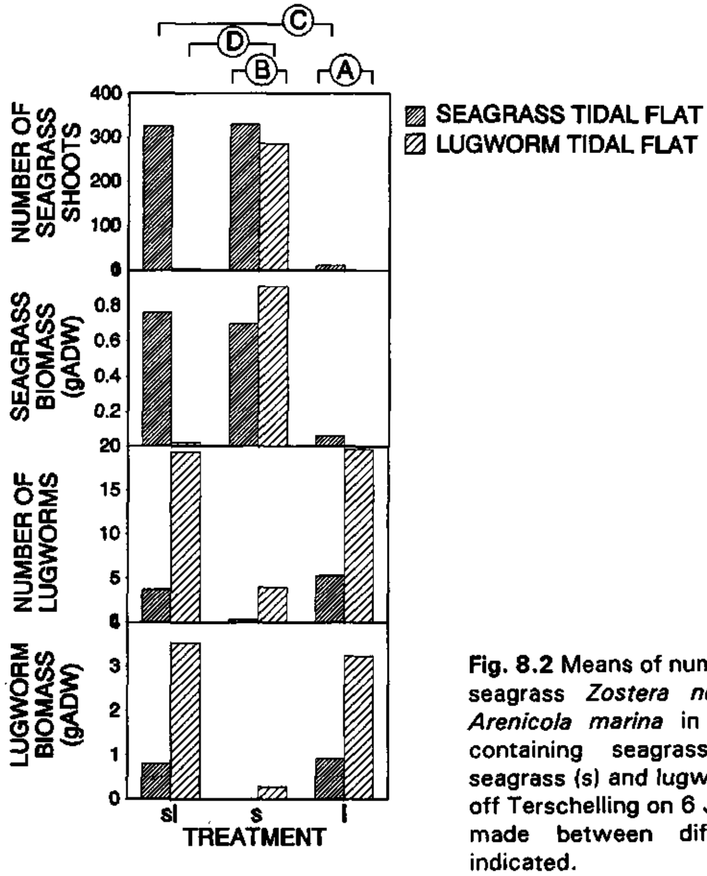

Fig. 8.2 Means of numbers and biomass of the seagrass *Zostera noltii* and the lugworm *Arenicola marina* in the experimental sites containing seagrass and lugworms (sl), seagrass (s) and lugworms (l) on the tidal flats off Terschelling on 6 June 1990. Comparisons made between different treatments are indicated.

of lugworms, the abundance of lugworms would be lower in the S_{sl} than in the S_l sites at the end of the experiment.

Hypothesis D states that seagrass is restricted on lugworm tidal flats by the actual presence of lugworms. This hypothesis was examined by comparing the development of the seagrass in the sites on the lugworm tidal flats with lugworms (L_{sl} sites) and the control sites without lugworms (L_s sites). If the lugworms restricted the presence of seagrass, the abundance of seagrass would be lower in the L_{sl} than in the L_s sites at the end of the experiment.

Prior to statistical analysis, the data were square-root transformed to approach normality and homogeneity of variance. Analysis of variance was used to examine the significance of the effects of habitat, treatment and their interaction on the numbers and biomass of seagrass and lugworms. *A priori* (non-orthogonal) multiple comparisons were made to examine the hypotheses A, B, C and D (Sokal & Rohlf 1981). The significance level was corrected by the Bonferroni approach, i.e. $p \leq 0.0125$ (= 0.05/4).

Survey

The survey was done on 28 June 1990. Four parallel transects, 10 m apart and located perpendicular to the borderline between the seagrass and the lugworm tidal flat, were sampled every 10 m with square frames (25 x 25 cm^2). The coverage of seagrass shoots, expressed as a percentage, was estimated within each frame. Firstly, the character of the sediment was assessed by coring up to a depth of 50 cm in the centre of the frame by means of a perspex core with a diameter of 5 cm. If dense clay was present in the core, the thickness of the sand layer on top of the clay layer was measured. Secondly, the sediment above the clay within the entire frame was sieved up to a maximum depth of 50 cm in a sieve with a mesh width of 1 mm. The clay layer itself was carefully broken up and checked for the presence of lugworms. All lugworms up to a depth of 50 cm were collected and stored in 5% formalin until further handling. The lugworms were divided into two length groups, < 5 cm and ≥ 5 cm. The number of lugworms in each group was counted. Relationships between seagrass coverage, lugworm density and the depth of the clay layer were tested by means of chi-square tests (Elliot 1983).

RESULTS

Transplantation experiments

The number and biomass of seagrass and lugworms showed a significant effect of habitat and treatment (Table 8.1). In addition, the seagrass number and biomass showed a significant interaction between habitat and treatment as the result of different response to the same treatment on the seagrass and on the lugworm tidal flat (Fig. 8.2). Although lugworm densities and biomass were generally lower in the seagrass than in the lugworm tidal flats, the response to the different treatments showed a more or less similar pattern (Fig. 8.2).

Table 8.2 Significance of relationships between coverage (%) of the seagrass *Zostera noltii*, density (n·m^{-2}) of the lugworm *Arenicola marina* with a length of at least 5 cm and shorter than 5 cm, and depth (m) of the clay layer on the tidal flats off Terschelling on 28 June 1990 (n=43; * p<0.05; ** p<0.01; *** p<0.001). Seagrass coverage was divided into 4 classes (0%, 1-24%, 25-49% and ≥50%), density of the large lugworms into 3 classes (0, 1-4 and ≥5 m^{-2}), density of the small lugworms into 3 classes (0, 1-9 and ≥10 m^{-2}) and depth of the clay layer into 3 classes (0-9, 10-24 and ≥25 cm).

			Correlation	X^2	df	p
Seagrass (%)	vs.	Lugworms ≥ 5 cm	-	22.46	6	**
	vs.	Lugworms < 5 cm	+	14.00	6	*
	vs.	Depth of clay layer	-	20.54	6	**
Lugworms ≥ 5 cm	vs.	Lugworms < 5 cm	None	3.37	4	ns
	vs.	Depth of clay layer	+	11.47	4	**
Lugworms < 5 cm	vs.	Depth of clay layer	None	8.19	4	ns

The lugworms in the seagrass tidal flat seemed to have been affected by other environmental factors than by the actual presence of seagrass (Table 8.1, hypothesis A). The density and biomass of the lugworms at the end of the experiment were significantly lower in the experimental sites without seagrass on the seagrass tidal flat (S_l sites) than in the control sites without seagrass on the lugworm tidal flat (L_l sites) (Fig. 8.2). However, these results must be interpreted with caution because the lugworms in the experimental sites on the seagrass tidal flat more intensively handled than the lugworms in the control sites on the lugworm tidal flat. Some seagrass invaded the sites on the seagrass tidal flat and none the sites on the lugworm tidal flat (Fig. 8.2), but this difference was not significant (Table 8.1).

The seagrass in the lugworm tidal flat was not significantly affected at all by other environmental factors than by the actual presence of lugworms (Table 8.1, hypothesis B). The density and biomass of the seagrass at the end of the experiment did not significantly differ in the experimental sites without lugworms on the lugworms tidal flat (L_s sites) from those in the control sites without lugworms on the seagrass tidal flat (S_s sites) (Fig. 8.2). Several lugworms invaded the experimental sites without lugworms. However, lugworm densities and biomass were not significantly different in the L_s and the S_s sites (Table 8.1).

Apparently, the lugworms on the seagrass tidal flat were not restricted by the actual presence of seagrass (Table 8.1, hypothesis C). The density and the biomass of the lugworms were not significantly different in the experimental sites on the seagrass tidal flat with seagrass transplants (S_{sl} sites) compared to the control sites without seagrass (S_l sites) (Fig. 8.2). As noticed before, some seagrass recolonized the bare sites on the seagrass tidal flat. However, the seagrass density and biomass were still significantly higher in the S_{sl} sites than in the S_l sites (Table 8.1).

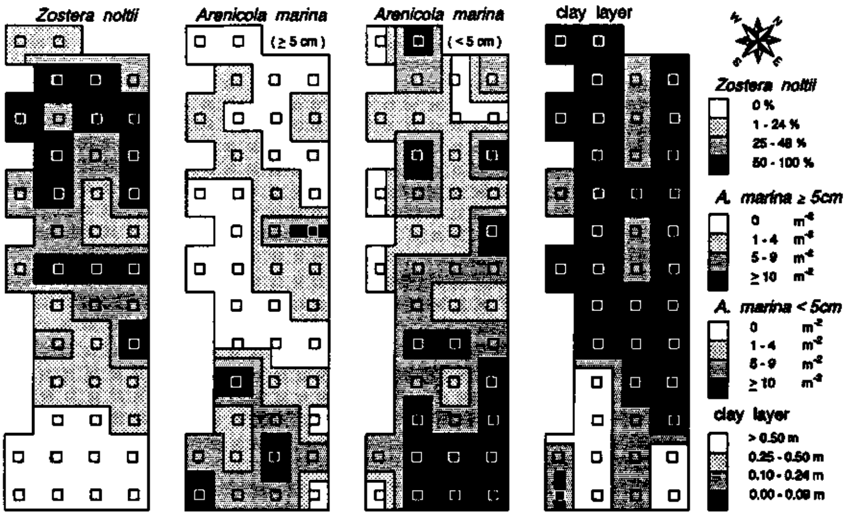

Fig. 8.3 Coverage (%) of the seagrass *Zostera noltii*, density (ind$\cdot$m^{-2}) of the lugworm *Arenicola marina* ≥ 5 cm and < 5 cm, and depth (m) of the clay layer on the surveyed part of the tidal flats off Terschelling on 28 June 1990.

The seagrass on the lugworm tidal flat was obviously affected by the actual presence of the lugworms (Table 8.1, hypothesis D). The density and the biomass of seagrass transplants on the lugworm tidal flat were significantly lower in the experimental sites without protection against bioturbation by lugworms (L_{sl} sites) than in the control sites with protection (L_s sites) (Fig. 8.2). As was expected, the gauze restricted the presence of lugworms. The density and biomass of the lugworms were significantly higher in the unprotected L_{sl} sites than in the protected L_s sites (Table 8.1).

Survey

The seagrass density varied between 0% in the southeastern part of the study area to more than 50% in the northwestern part, the small (< 5 cm) and large (≥ 5 cm) lugworms occurred mainly in the southeastern part of the study area, and the clay layer was mainly present at less than 24 cm depth in the north-western part of the study area (Fig. 8.3). Lugworms were present only in the sandy sediment, none were found in the dense clay layer. The coverage of seagrass was positively correlated with the density of the small lugworms, and negatively correlated with the density of the large lugworms and the depth of the clay layer under the sediment surface (Table 8.2). The density of the large lugworms was positively correlated with the depth of the clay layer under the sediment surface, the density of the small lugworms was not (Table 8.1). No significant relationship was found between the density of the large lugworms and that of the small ones (Table 8.2).

DISCUSSION

Effects of lugworms on seagrass

On the tidal flats off Terschelling, the seagrass *Zostera noltii* appears to be restricted at its border with the lugworm tidal flat by no other condition than the actual presence of adult lugworms. The immediate effects of bioturbation are coverage of seagrass shoots by faecal castings and burrowing material by funnels. The mean density of the lugworms in the experimental control sites was 68 worms m^{-2}, which are able to rework sediment equivalent to a layer of 26 cm $year^{-1}$ (Cadée 1976). The sediment-reworking activities of the lugworms probably constituted the most direct and important effect on biomass and density of *Z. noltii* on lugworm tidal flats near Terschelling, because the transplanted seagrass shoots disappeared within six weeks in the unprotected sites on the lugworm tidal flat and were obviously buried.

In addition, bioturbation by lugworms may prevent the survival of seagrass during unfavourable growth periods by burial of vegetative propagules (rhizomes), or seeds and seedlings as is likewise found for the plant-animal interaction between *Salicornia europaea* and *Corophium volutator* (Gerdol & Hughes 1993). Furthermore, bioturbation could change nutrient budgets of seagrass communities by increasing the sulphate reduction and nitrate reduction in the sediment (Andersen & Kristensen 1991). Nutrients may then become either more available to the seagrass or be lost from the seagrass communities as the result of dilution by water transport.

In conclusion, bioturbation can influence seagrass stands in several ways, depending on the density and the activity of the lugworms present. High densities of adult lugworms are expected to have mostly negative effects on seagrass stands as the result of burial of seagrass material; low densities of juvenile lugworms may be beneficial as the result of increased nutrient fluxes.

Restrictions for lugworms

Seagrass could restrict bioturbation by lugworms if the plants established a dense rhizome mat as observed for other seagrasses. However, on the seagrass tidal flat near Terschelling, closed seagrass stands with dense rhizomes mats are only found in small parts of the seagrass bed during August/September (Chapters 3 & 4). The transplantation experiments confirm the hypothesis that the absence of *Arenicola marina* in this seagrass stand does not depend on the actual presence of seagrass. Therefore, the adult lugworms must here be restricted by one or more other environmental factors.

Most of the seagrass stand, and in particular the area where a high coverage of *Zostera noltii* occurred, is located over a layer of clay at a depth of not more than 10 cm. The compactness of this clay layer inhibits funnel formation by lugworms, which need a burrowing depth of at least 10 to 20 cm (Rijken 1979). Shortened head shafts can make feeding for the lugworm suboptimal if not impossible. In addition, shallow burrows may make lugworms more susceptible to predation by birds, flatfish and crabs. Expansion of the lugworm area into the seagrass area seems, therefore, restricted by the presence of the clay under the sediment surface, which inhibits funnel formation at sufficient depth.

These findings are in agreement with the lugworm distribution on the tidal flats east of Hallig Hooge in the German Wadden Sea. Like the tidal flats of Terschelling, part of Hallig Hooge used to be a salt marsh located on silty sediment. At that time, the area was drained by man-made ditches. After the total area was covered with sand, adult lugworms only settled in those areas where the sand layer was thicker than 10 to 12 cm, i.e. in the former ditches (Plath 1943).

Historical changes

Reise (1985) found that an experimentally induced increase of lugworm density was followed by gradual sidewards emigration of the lugworms. It was concluded that a strong year class of juveniles probably does not increase the adult density, but would more likely result in the colonization of marginal habitats. From 1970 to 1990, the biomass of *Arenicola marina* significantly increased on the Balgzand tidal flats in the western part of the Dutch Wadden Sea (Beukema 1992). A simultaneous increase in density of the lugworms on the tidal flats off Terschelling may have resulted in an extension of the area of this lugworm tidal flat in the direction of the seagrass stand. The transplantation experiments show that seagrass is unlikely to survive when invaded by adult lugworms. Decrease of seagrass species in coastal waters of the industrial countries during the last 30 to 50 years is generally contributed to eutrophication, which causes an increase of periphyton and subsequent decline of the plants (Phillips *et al.* 1978, Cambridge *et al.* 1986). In the Dutch Wadden Sea, however, the undermining effect of the lugworms on seagrass may also have played an important role in the observed decrease of *Zostera noltii* over the last 20 years. Subsequently, this devastating process may now have been stopped on the tidal flats off Terschelling owing to the presence of remnants of a former salt marsh.

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CHAPTER 9

DISCUSSION AND CONCLUSIONS

CHAPTER 9

DISCUSSION

Recent developments

In general, the observed decline of several intertidal seagrass stands of *Zostera noltii* in the Dutch Wadden Sea during the 1960s continued until the 1990s (Chapter 3). The seagrass stand on the Balgzand tidal flats almost completely disappeared and the area of the main stand off Terschelling decreased by more than 25% to 0.84 km^2. Still, the total area of all stands increased from 1.4 km^2 in the early 1970s to 2.60 km^2 at the end of the 1980s because of a rapid re-establishment of this seagrass species in the salt-marsh works off Groningen after a change in management.

These observations on the seagrass decline in the Dutch Wadden Sea are in agreement with developments of intertidal seagrass stands reported for other areas in the Wadden Sea during the last 20 years. In the seventies, intertidal seagrasses were found to be decreasing in Niedersachsen (Lüning & Asmus 1990), and in 1989 a decrease of seagrass stands compared to the situation in 1983 was reported for the area of Schleswig-Holstein (Brunckhorst & Reise 1989). In Denmark there has been a slow decrease in intertidal seagrass stands in the past 17 years (De Jong *et al.* 1993).

This chapter summarizes and discusses possible mechanisms for the wax and wane of *Z. noltii* stands in the Dutch Wadden Sea as examined or touched upon in the previous chapters.

Mussel and Cockle fisheries

In the Wadden Sea, seagrass abundance varies greatly between different regions (Dijkema *et al.* 1989, Dijkema 1991, Chapter 2). These differences in distribution were satisfactorily explained by differences in emersion period, sediment composition, sediment stability and an unknown environmental factor which was found to be related with geographical region (Chapter 2). This factor may comprise large-scale differences in intertidal habitats and human impact (Table 9.1). The abrupt difference in *Zostera noltii* abundance as observed at the state border between the Netherlands and Germany at least suggests an effect of human activities and their management (Dijkema 1994).

One of the main differences in management between these Wadden Sea regions is the intensity of cockle and mussel fisheries (Fig. 9.2). The majority of cockels is caught in the Dutch part of the Wadden Sea by means of specialised dredges (Dankers 1993). Cockle fishery was always very limited in Schleswig-Holstein and Niedersachsen, and stopped there in 1989 and 1992, respectively. Danish cockle fishery is restricted to small parts of the tidal flats (De Jong *et al.* 1993). In the Dutch Wadden Sea, approximately 4% of the tidal flats are fished for cockles every year (Dankers & De Vlas 1992).

Since 1949, mussel culture has developed in the Wadden Sea. At present, fishing on the natural beds is mainly restricted to very small and medium size

Table 9.1 Regional subdivision of the Wadden Sea based on mean tidal range (m), presence of a barrier system, relative abundance of emerging flats and sandy sediment (Dijkema 1991), and organisation responsible for management (nl: Dutch government; g-ns: National park Niedersachsen, Germany; g-sh: National park Schleswig-Holstein, Germany; dk: Danish government).

area	tidal range	barrier system	emerging flats	exposition	sandy sediments	salt marshes	management
I	1.4-1.8	***	*	***	***	*	nl
II	1.8-2.6	***	***	**	**	**	nl
III	2.3-3.0	***	***	**	**	**	g-ns
IV	3.0-3.8	-	***	*	*	**	g-ns
V	3.0-3.5	*	***	***	**	**	g-ns
VI	3.0-3.5	*	***	***	***	**	g-sh
VII	3.5-2.0	**	***	**	**	**	g-sh
VIII	1.8-1.4	***	***	**	**	***	dk

*	less than average
**	average
***	more than average
-	not occurring

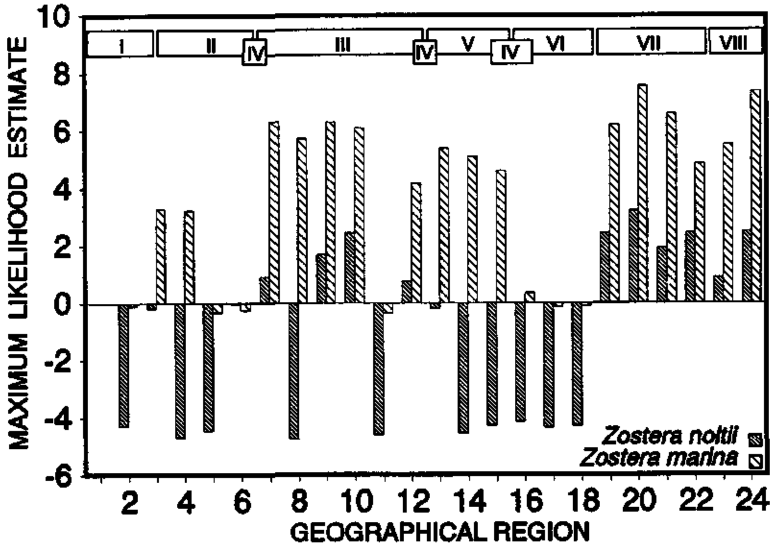

Fig. 9.1 Maximum likelihood estimates for geographical regions in the Wadden Sea for the seagrass species *Zostera noltii* and *Z. marina*, and regional subdivision of the Wadden Sea into eight areas (Roman numbers) based on large-scale variations in intertidal habitats and differences in management.

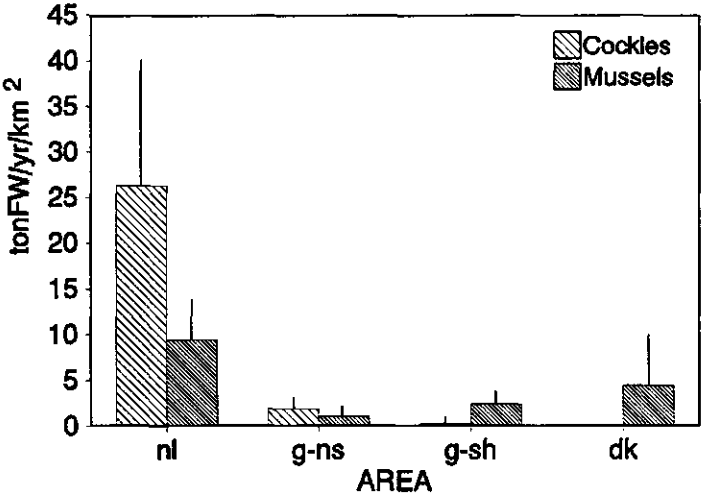

Fig. 9.2 Mean shellfish fisheries effort on the tidal flats in different regions of the Wadden Sea, calculated as the total landings (ton fresh-weight·yr^{-1}) of Cockles and Mussels between 1979 and 1988 per region divided by the regional area of tidal flats. Although the mussel landings consists mainly of mussels fished from the culture plots, it is assumed that the efficiency of mussel culture (= seeded/produced amount) equals one and that 20% of the seed mussels is collected from the tidal flats (data from Dankers 1993, De Jong *et al.* 1993).

mussels, which are subsequently dispersed on the culture plots. Only a minor part (5%) of marketable mussels are still fished from natural beds. Mussel culture ceased completely in the Danish Wadden Sea, but increased considerable in Germany since 1980 (Dankers 1993). In the Dutch Wadden Sea, most of the seed mussels are fished in the subtidal area, only a small part (ca. 20%) originates from intertidal mussel beds (Dankers & De Vlas 1992).

Seagrass is hardly found in areas where cockles are normally fished in the Dutch Wadden Sea (Dankers & De Vlas 1992). Shellfish fisheries have devastating effects on seagrass stands (De Jonge & De Jong 1992, Van Katwijk 1993, own observations). Recovery of seagrass stands which are damaged by mussel and cockle fisheries is severely restricted, especially when no rhizomes and roots of plants are left in the sediment.

Therefore, shellfish fisheries may have contributed to the decline of seagrass stands. In addition, development of new *Z. noltii* stands is most probably restricted as long as shellfish fisheries are maintained in potential seagrass habitats (Dankers & De Vlas 1992, De Jonge & De Jong 1992, Philippart *et al.* 1992, Dijkema 1994). However, shellfish fisheries alone cannot explain the decline of the seagrass stands in the Dutch Wadden Sea because of the relatively low area of the tidal flats which is affected.

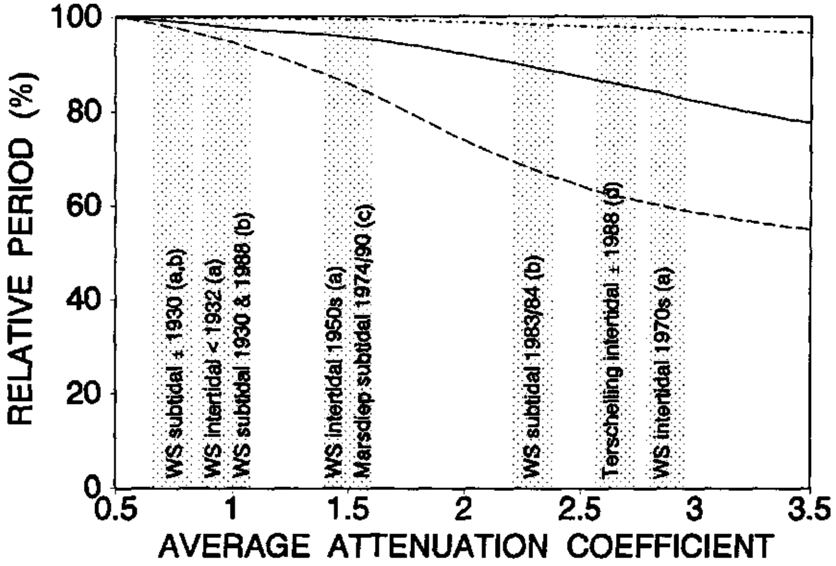

Fig. 9.3 Relationship between the average attenuation coefficient (m^{-1}) and the relative total photosynthetic period (%) of *Zostera noltii* on the tidal flats off Terschelling at Mean Sea Level (-), 0.5 m above MSL (-.-) and 0.5 m under MSL (- -). The shaded areas refer to average attenuation coefficients in the western Wadden Sea (WS), Marsdiep and tidal flats off Terschelling as supplied for different years by different authors ([a] Giesen *et al.* 1990, [b] De Jonge & De Jong 1992, [c] Cadée & Hegeman 1991, [d] Chapter 3).

Turbidity

Possible changes in turbidity of Dutch Wadden Sea waters since the 1930s are still a matter of discussion. Although suspended-matter concentrations significantly increased from the end of the 1970s to the beginning of the 1980s followed by a decrease for all Wadden Sea sampling stations (De Jonge & De Jong 1992), part of these trends can be satisfactorily explained by systematic changes in sampling procedures (Maiwald & Verhagen 1991). Secchi-disk readings which were consistently taken at high tide in the Marsdiep tidal inlet, however, did not indicate obvious changes in turbidity between 1974 and 1990 (Cadée & Hegeman 1991).

Based on former occurrence of eelgrass, Giesen *et al.* (1990) state that turbidity, expressed as the average attenuation coefficient, in the Wadden Sea increased from 0.9 m^{-1} in the 1930s to 2.8 m^{-1} in the 1970s. The effects of changing light conditions resulting from suggested changes in turbidity on an intertidal *Zostera noltii* stand can be estimated by means of the light model as described in chapter 3. The photosynthetic period has been calculated for three different positions in the intertidal zone (Fig. 9.3). The results show that if light conditions did severely deteriorate during the last 60 years, the photosynthetic period of this seagrass species would hardly have been affected at higher tidal flats, i.e. 0.5 m above mean sea level. Only for seagrass growing at lower tidal flats, an increase in turbidity from 0.9 to 2.8 m^{-1} would have resulted in a decrease in photosynthetic period of approximately 35%.

The interaction effect between emersion period and geographical region contributed significantly to the outcome of models on the presence of seagrasses, which implies the existence of regional differences in light conditions in the Wadden Sea (Chapter 2). Turbidity most probably plays a role in the distribution of *Z. noltii* in the Wadden Sea and may again be related to human impact (Chapter 2).

Unfortunately as long as variations in suspended-matter concentrations in former, present and potential seagrass habitats are not accurately known, it is not possible to determine the role of turbidity in the observed variations in time and space of *Z. noltii* in the Dutch Wadden Sea. It is unlikely, however, that this seagrass species was severly affected in stands above Mean Sea Level.

Macroalgae

Although no significant relationship between abundance of macroalgae and *Zostera noltii* was found in the seagrass stands of the Dutch Wadden Sea (Chapter 3), macroalgae cannot be neglected as a possible factor controlling the abundance and distribution of Wadden Sea seagrasses. Cultivated *Z. noltii* plants in outdoor concrete basins at the Institute for Forestry and Nature Management at Texel were suffocated by a massive and uncontrollable development of macroalgae, *i.e.* *Enteromorpha* sp. and *Ulva* sp. (own observations). In June 1988, the most sheltered parts of the *Z. marina* stand in the harbour of Terschelling were covered by thick layers (2-10 cm) of macroalgae (own observations).

These findings are in agreement with observations in other temperate *Zostera* stands. Brunckhorst & Reise (1989) observed a decline of seagrasses in Schleswig-Holstein. Since 1979 a mass development of macroalgae (*Enteromorpha*, *Cladophora*, *Chaetomorpha* and *Ulva*) was reported in this area, which is supposed to be due to a long-term increase of nutrients (Reise *et al.* 1989, Reise 1989). Recently, Den Hartog (1994) observed a sudden disappearance of a mixed intertidal stand of *Z. noltii* and *Z. marina* from Langstone Harbour (Hampshire, UK), most probably as the result of suffocation by *Enteromorpha radiata*.

Macroalgae such as *Enteromorpha* and *Ulva* prosper under eutrophicated conditions (Sfriso *et al.* 1987), in particular during light and warm periods without much wind (Den Hartog 1994). The macroalgae distribution is very patchy and its biomass varies considerably from year-to-year in the Wadden Sea (Peletier 1992, Reise & Siebert 1994). In the German Wadden Sea, macroalgae mainly occurred on sheltered, sandy flats in the outer part of the region (Reise & Siebert 1994). In 1989, thick layers (2-15 cm) of macroalgae were observed at a tidal flat east off Texel (Peletier 1992), which was once a habitat of *Z. marina* (Chapter 1, Fig. 1.1). On Balgzand, accumulation of macroalgae frequently occurs in summer in the high intertidal where *Z. marina* once flourished (J.J. Beukema pers. comm. 1994).

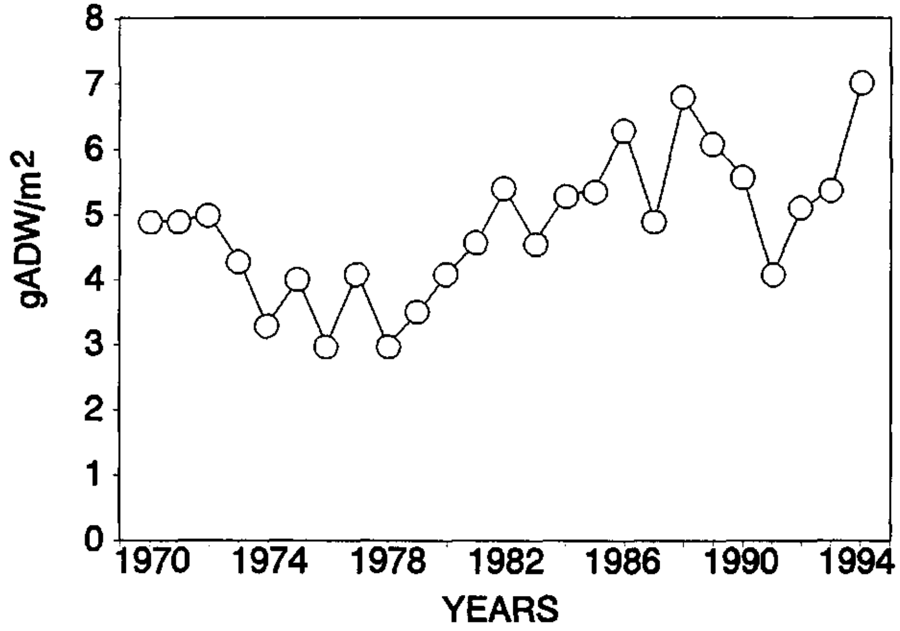

Fig. 9.4 Spring biomass values (gADW·m^{-2}) of the lugworm *Arenicola marina* on the tidal flats of Balgzand between 1970 and 1994 (updated figure 3B of Beukema 1992).

Occasional macroalgal blooms which are triggered by an additional nutrient supply or particular meteorological conditions may, therefore, cause disappearance and restrict re-establishment of seagrass stands, especcially at sheltered places in the upper part of the intertidal zone, in the Dutch Wadden Sea.

Lugworms

Bioturbation by adult lugworms (*Arenicola marina)* determines the lower border of a *Zostera noltii* stand on the tidal flats of Terschelling (Chapter 8). Therefore, possible increase in numbers of lugworms may be related to the observed decline of *Z. noltii* if the lugworm areas extended into the seagrass stands. Although lugworm biomass has varied considerably in time (Fig. 9.4), Beukema (1992) found a significant increase in biomass of lugworms on the Balgzand tidal flats in the westernmost part of the Wadden Sea. Such an increase, possibly due to eutrophication, may have coincided with an expansion of the lugworm's habitat as observed during experimental work by Reise (1985). Unfortunately, no historical data are available on the distribution of lugworms on the tidal flats off Terschelling. It is concluded that lugworm increase may have played a part in the decrease of the seagras stands, in particular at the lower tidal flats, but this role cannot be quantified.

Eutrophication model

Hypothesis

The hypothetical model for the decline of the *Zostera noltii* stands used at the start of this study is that nutrient enrichment favoured growth of epiphytic algae (Phillips *et al.* 1978). These algae have negative effects on seagrass photosynthesis and growth due to shading and competition for carbon and nutrient resources (Sand-Jensen 1977, Silberstein *et al.* 1986, Shepherd *et al.* 1989). In surviving seagrass stands, the increase in epiphyte biomass should have been partly but not completely suppressed by grazing epifauna (Orth & Van Montfrans 1984, Hootsmans & Vermaat 1985), in particulary the mudsnail *Hydrobia ulvae*.

Eutrophication

At present, nutrient concentrations and primary and secondary production in the western Wadden Sea are still relatively high compared to the situation at the beginning of the 1970s (Klein & Van Buuren 1992). Phytoplankton concentrations rapidly increased from 1976 to a peak value in 1981, followed by a more or less stable period of relatively high levels up to 1992 (Cadée & Hegeman 1993). Primary production by phytoplankton increased from 1975 to 1985 and stayed, although strongly fluctuating, relatively high up to 1992 (Cadée & Hegeman 1993). The average biomass of the macrofauna on the tidal flats of the western part of the Dutch Wadden Sea doubled in the period from 1971 to 1989 (Beukema 1991). The increase of primary and secondary production in the western Wadden Sea is often attributed to an increase in nutrients originating from the river Rhine e.g. De Jonge & Van Raaphorst (1994).

Epiphytes

At present, epiphyte coverage on the leaves of *Zostera noltii* is indeed considerable (Chapter 4). The biomass of periphyton contributes 20% to 50% to the total aboveground vegetative biomass of seagrass shoots and periphyton. The shading caused by periphyton varied between 10% and 90%, depending on the time of the year, distribution of periphyton over the leaves and relationship between periphyton and light reduction which was applied. The average periphyton biomass on the seagrass off Terschelling was relatively high compared to that on an intertidal *Z. noltii* stand near Köningshafen in the German Wadden Sea (Asmus & Asmus 1985).

Artificial shading of the seagrass stand off Terschelling showed that the lowering of light levels caused a significant decrease in leaf growth rates and biomass of *Z. noltii* (Chapter 6). It was concluded that subsequent improvement of light conditions would result in restoration of the deteriorated seagrass vegetation, but only as long as the propagules were still of sufficient quality to support the extensive spring growth.

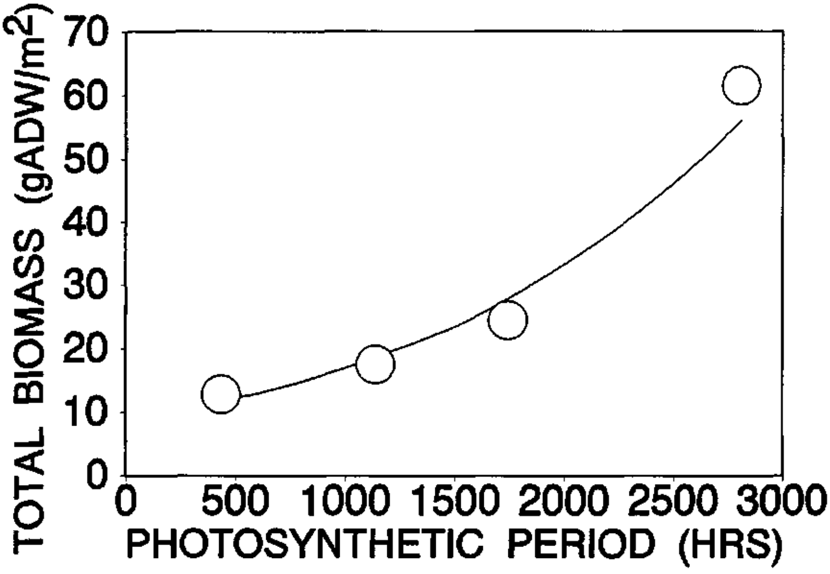

Fig. 9.5 Relationship between the estimated total photosynthetic period (hours·year^{-1}) in 1988 as estimated by the light model and the total biomass (gADW·m^{-2}) of *Zostera noltii* as measured during the artificial shading experiment in 1989 on the tidal flats off Terschelling.

The light conditions for these shaded seagrass vegetations can be estimated by means of the light model as described in chapter 3. The photosynthetic period has been calculated for four levels of artificial shading, assuming that the artificial shading has to be added to an average shading by periphyton of 50%, resulting in total shading of 50%, 77.5%, 85% and 92.5%, respectively. Under these light conditions, the average total biomass during the growing season was found to be exponentially related with the estimated photosynthetic period (Fig. 9.5).

It is concluded that epiphytes have a negative effect on the *Z. noltii* stand off Terschelling. It is not certain, however, whether the periphyton density indeed increased during the period in which the intertidal seagrass stands declined. Because the primary production and chlorophyll-*a* of microphytobenthos on a tidal flat in the western Wadden Sea doubled over the period 1968-1981 (Cadée 1984), it may be assumed that epiphytes did also increase during this period.

Mudsnails

At present, densities of the mudsnail *Hydrobia ulvae* in the *Zostera noltii* stand at the tidal flats off Terschelling vary between 50,000 and 100,000 snails·m^{-2} (Chapter 4). Although total biomass and density of mudsnails did not significantly vary during the season, significant variations in different size classes were observed which were probably the combined result of spat fall, growth, mortality and migration (Dekker 1979). Densities of mudsnails in the Terschelling seagrass stand were two orders of magnitude higher than the average density in the Wadden Sea, i.e. approximately 866 animals·m^{-2} (Beukema 1976).

Exclosure experiments on the tidal flats revealed that a decrease in mudsnails leads to an increase in periphyton load and a subsequent decline in density and biomass of *Z. noltii* (Chapter 7). At the end of the experimental period, individual mudsnails in exclosures with a low snail density were larger than the mudsnails incubated at higher densities. These results indicate that intraspecific competition for food limits the grazing of a mudsnail community.

The theoretical grazing capacity of the mudsnail community on the tidal flat off Terschelling generally exceeded the standing stock and estimated production of periphyton on the leaves of *Z. noltii* (Chapter 4). Nevertheless, a considerable amount of periphyton was present during the growing season indicating that the mudsnails were not able to keep periphyton levels to a minimum. Since the grazing capacity is related to density of mudsnails, a decrease in snail density will result in a decrease of seagrass density and biomass. Although this process may be slowed down by the buffering effect of the intraspecific interactions between the mudsnails, a strong decline of grazing mudsnails most probably severely affects seagrass stands.

Although erratically fluctuating, the mean density of mudsnails increased during the 1970s and the 1980s in the western half of the Dutch Wadden Sea (Beukema 1989). At Balgzand, mudsnail densities at the higher tidal flats, i.e. above Mean Sea Level, were generally more stable than those at lower flats (J.J. Beukema pers. comm. 1994). Several Dutch marine biologists observed a considerable decrease of mudsnails at the beginning of the 1970s on tidal flats of the Wadden Sea (J.J. Beukema pers. comm. 1994, C. Den Hartog pers. comm. 1994, C. Swennen pers. comm. 1993). In agreement with the results of the exclosure experiment, C. Den Hartog (pers. comm. 1994) noticed an abnormally high density of fouling on leaves of seagrass stands on tidal flats of the Balgzand and off Terschelling during this period of low mudsnail densities. At the one frequently sampled station in this area with an intertidal stand of *Z. marina*, the occurrence of low densities of mudsnails of approximately 600 m^{-2} in 1969 was followed by a rapid decline in the seagrass stand (J.J. Beukema pers. comm. 1994). Although still present in low densities in 1973, this seagrass stand did not recover when mudsnail densities increased during the following years to 18,000 m^{-2} in 1975 (Fig. 9.6).

It is concluded that the hypothetical model used at the start of the study may indeed explain the decline of *Zostera noltii* in the Dutch Wadden Sea. Growth, biomass and survival of this seagrass species was found to be restricted by a decrease in light conditions and the epiphyte biomass is controlled, but not completely suppressed, by mudsnails. In addition, the observed increase in primary and secondary production in the western Wadden Sea suggests a simultanuous increase in epiphytes and mudsnails because of eutrophication in former and present seagrass stands.

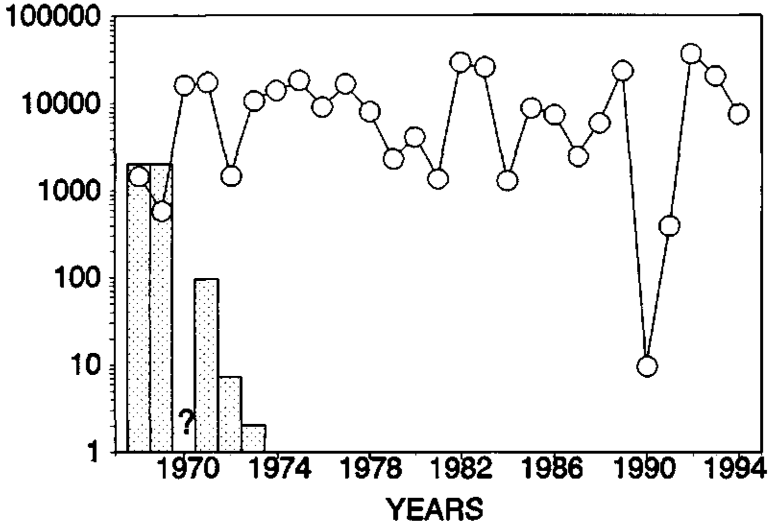

Fig. 9.6 Density (ind·m^{-2} logscale) of the mudsnail *Hydrobia ulvae* (○) and occurrence (shaded areas) of the seagrass *Zostera marina* (clumps·1000 m^{-2} logscale) at **one** sampling station located close to mean sea level on Balgzand in summer between 1968 and 1977 (Beukema unpublished).

CONCLUSIONS

From this research, it is concluded that the variations in light conditions, periphyton load and mudsnail densities appropriately explain variations in the biomass of *Zostera noltii* as described in the eutrophication model used at the start of this study. In addition, it was found that the abundance of this seagrass species in the Wadden Sea is certainly related with lugworm density and possibly with turbidity, the abundance of macroalgae and the intensity of shellfish fisheries.

It seems reasonable to assume that changes in most of these environmental factors, with the exeption of macroalgae, will have had the greater effect on seagrass growing low in the intertidal zone. Seagrass located at the higher tidal flats is less sensitive to such changes, as it is less affected by an increase in periphyton load, experiences less variation in mudsnail densities and is more remote from the lugworm tidal flats. Therefore, the observed decline most probably took place from the lower border of the seagrass stands upwards.

Although the seagrass-decline model indicates that the decline of *Z. noltii* was due to changes in environmental factors under the influence of variations in nutrient concentrations, there are insufficient long-term field data on the density of seagrass, periphyton, mudsnails and lugworms to demonstrate whether eutrophication caused the observed changes in seagrass abundance and distribution. Finally, it must be questioned whether the observed changes in marine *organisms in the western Wadden Sea were indeed directly related to human-*induced eutrophication because they often occurred more or less simultaneously with similar changes on a larger scale, e.g. the North Sea, the Atlantic Ocean and even the Pacific Ocean (Josefson *et al.* 1993, Lindeboom *et al.* 1994, Miller *et al.* 1994).

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ACHTERUITGANG VAN KLEIN ZEEGRAS

Het Klein Zeegras (*Zostera noltii*) is de meest voorkomende zeegrassoort van de Nederlandse Waddenzee. Het oppervlak van het zeegrasareaal bedroeg ongeveer 2.6 km^2 in 1988/89. Ruim 15 jaar daarvoor, in 1970/72, was het oppervlak dat in de Nederlandse Waddenzee door Klein Zeegras bedekt werd ca. 1.4 km^2. De toename in zeegras tussen het begin van de zeventiger en het eind van de tachtiger jaren is nagenoeg geheel te danken aan het ontstaan van twee nieuwe velden in de landaanwinningswerken van Groningen. Het Klein Zeegras kwam hier voor de aanleg van de landaanwinningswerken ook al voor. De toename is meest waarschijnlijk veroorzaakt door het stopzetten van het graven van greppels in deze gebieden, waardoor de omstandigheden voor het zeegras verbeterden.

In de meeste velden waar het zeegras al geruime tijd voorkwam, verliepen de ontwikkelingen minder voorspoedig. Van het zeegrasveld op de wadplaten van het Balgzand met een oorspronkelijk oppervlak van 0.12 km^2 in 1970/72 was aan het eind van de tachtiger jaren niet meer over dan enkele sprietjes. Het grootste zeegrasveld van de Nederlandse Waddenzee ten zuiden van het eiland Terschelling bij Hoorn kromp in minder dan twintig jaar van 1.15 km^2 naar 0.84 km^2. Over de oorzaak van deze afname in de oudere zeegrasvelden, die al aan het eind van de zestiger jaren inzette, was niets met zekerheid te zeggen.

EUTROFIËRING ALS MOGELIJKE OORZAAK VAN ACHTERUITGANG

Het vermoeden bestond dat de achteruitgang van het Klein Zeegras in de oudere velden te maken had met de toename van voedingsstoffen in de Waddenzee. Bij zoetwaterplanten was immers geconstateerd dat eutrofiëring kon leiden tot een toename van microscopisch kleine algen (epifyten). Epifyten kunnen samen met bacteriën, anorganische (slib en klei) en organische deeltjes (dode algen, plantedelen, diertjes) een laag (perifyton) op de bladeren van de waterplanten vormen. Dit perifyton vangt niet alleen een deel van het licht voor de waterplanten weg, maar bemoeilijkt tevens de uitwisseling van opgeloste stoffen tussen planten en water. Hierdoor kan de plant minder snel groeien en zelfs afsterven.

Het was bekend dat in de Waddenzee zowel de voedingsstoffen als de hoeveelheid algen in het water en op de bodem waren toegenomen in de periode dat het oppervlak van de oudere velden Klein Zeegras was verminderd. Hierdoor leek het aannemelijk dat de eutrofiëring ten grondslag lag aan de achteruitgang van het Klein Zeegras door een toename van perifyton. Om deze hypothese te testen zijn effecten van licht op de groei van Klein Zeegras onderzocht.

Licht in de getijzone

De optimale positie van zeegras in de getijzone wordt beschouwd als een compromis tussen uitdroging en lichtomstandigheden. Naarmate zeegras hoger in de getijzone groeit, zal het langer droogvallen tijdens laagwater en daardoor een grotere kans lopen om uit te drogen. Staat zeegras daarentegen relatief laag in de getijzone, dan staat er vaker en meer water boven de planten waardoor deze minder licht krijgen gedurende een getijcyclus.

Aan de hand van een kaart van de Nederlandse, Duitse en Deense Waddenzee is onderzocht op welke hoogte in de getijzone het zeegras het meest voorkomt. Hierbij bleek de optimale positie voor Klein zeegras af te hangen van de locatie van het deelgebied, variërend tussen delen die meer dan 67% of minder dan 50% van de tijd droogvallen. Dit wordt mogelijk veroorzaakt door verschillen in lichtomstandigheden als gevolg van een variaties in troebelheid van het zeewater of begroeiing van het zeegras met perifyton.

Relatie tussen licht en produktie van Klein Zeegras

In het laboratorium is gekeken naar het effect van licht op de produktie van zuurstof van Klein Zeegras. De relatie tussen primaire produktie en licht kan bepaald worden door de hoeveelheid zuurstof te meten die de plant bij een aantal verschillende hoeveelheden licht afgeeft dan wel opneemt. Voor Klein Zeegras was de hoeveelheid licht waarbij de plant evenveel zuurstof produceert als consumeert (het z.g. compensatiepunt) 59 $\mu E \cdot m^{-2} \cdot s^{-1}$ bij toepassing van het Michaelis-Menten model voor de beschrijving van deze relatie.

Met dit getal en gegevens over de getijverschillen en troebelheid van het water in de Waddenzee kon vervolgens berekend worden hoeveel uren per jaar het zeegras voldoende licht ontvangt om te kunnen groeien. Bij afwezigheid van perifyton ontvangt het Klein Zeegras in de zomer meer dan 16 uur licht per dag dat hoger is dan het compensatiepunt. Op een hoogte van 50 cm boven NAP ontvangt het zeegras ongeveer 4000 uur licht van meer 59 $\mu E \cdot m^{-2} \cdot s^{-1}$ per jaar, op een hoogte van 50 cm onder NAP is deze tijdsduur met bijna 25% gereduceerd. Bij beschaduwing door perifyton neemt de periode waarin het zeegras voldoende licht ontvangt voor positieve produktie snel af. Als perifyton 50% van het invallende licht wegneemt, wordt de fotosynthetische periode 10% tot 25% korter voor planten op respectievelijk 50 cm boven en 50 cm onder NAP.

Seizoensdynamiek van Klein Zeegras

De groei en ontwikkeling van Klein Zeegras varieert met de hoeveelheid licht die de planten gedurende het jaar bereikt. De bladeren van Klein Zeegras groeien het hardst tussen mei en augustus met een gemiddelde snelheid van ongeveer 0.04 $mm^2 \cdot mm^{-2} \cdot dag^{-1}$. Omdat de zeegrasplanten in het voorjaar nauwelijks bladeren verliezen, neemt de bovengrondse biomassa gedurende deze periode snel toe. In augustus bedraagt de totale biomassa (wortels uitgezonderd) meer dan 110 $gADW \cdot m^{-2}$, waarvan ongeveer een kwart uit wortelstokken en de rest uit bovengrondse zeegrasbundels bestaat. Het bladverlies neemt vanaf de zomer toe, bereikt een maximumwaarde van 0.06 $mm^2 \cdot mm^{-2} \cdot dag^{-1}$ in september, en overtreft vanaf eind augustus de bladgroei. Hierdoor neemt de bovengrondse biomassa dan ook snel af in het najaar. In de winter weegt het resterende zeegrasmateriaal minder dan 10 $gADW \cdot m^{-2}$ en bestaat voor bijna driekwart uit wortelstokken.

Ondanks het feit dat Klein Zeegras wel bloeit in Nederland, lijkt het zaad een geringe rol te spelen bij de jaar-op-jaar overleving van deze soort. Zowel op de wadplaten onder Terschelling als op andere standplaatsen in Europa en Afrika worden zelden zaailingen gevonden. In het voorjaar lopen bestaande wortelstokken opnieuw uit. Deze wortelstokken zullen dus gedurende het groeiseizoen voldoende materiaal moeten opslaan om de zeegrasplanten de winter te doen overleven en de snelle voorjaarsgroei te kunnen ondersteunen.

Beschaduwing van Klein Zeegras door perifyton

Gedurende het groeiseizoen van Klein Zeegras, varieert de bedekking van zeegrasbladeren door perifyton uitgedrukt in biomassa tussen ca. 1,5 mgADW$\cdot$cm^{-2} in het voorjaar en ca. 0,5 mgADW$\cdot$cm^{-2} in het najaar. Uitgedrukt in chlorofylgehalten, varieert de perifytonbedekking tussen ca. 0.2 mgCHL(a + b)$\cdot$cm^{-2} in het voorjaar en ca. 1.5 mgCHL(a + b)$\cdot$cm^{-2} in de zomer. Blijkbaar neemt het chlorofylgehalte van het perifyton sterk toe gedurende het groeiseizoen van Klein Zeegras. Afhankelijk van de omrekening die toegepast wordt om deze bedekking om te rekenen naar beschaduwing, varieert de hoeveelheid licht welke wordt weggevangen door het perifyton tussen 10% en 90% van de hoeveelheid licht die op de zeegrasplanten valt.

Het effect van verschillende hoeveelheden perifyton op de groei van Klein Zeegras werd onderzocht door netten met verschillende maaswijdten boven de planten te spannen. Hierdoor vielen er verschillende hoeveelheden licht op de bladeren van het zeegras. Tijdens dit experiment bleek dat een extra beschaduwing leidt tot een verminderde groei van Klein Zeegras. Niet alleen nam door deze kunstmatige beschaduwing het aantal en gewicht van de zeegrasplanten af, maar er bleef ook minder energie over voor de voortplanting. In de meeste gevallen, heeft Klein Zeegras wortelstokken van voldoende kwaliteit nodig om de winter te overleven en in het voorjaar weer te groeien. De extra beschaduwing resulteerde in lagere individuele gewichten van de wortelstokken, waardoor zeer waarschijnlijk de kans op overleving van de winter gereduceerd werd.

Begrazing van perifyton door wadslakjes

De zeegrasvelden bevatten niet alleen zeegras, maar ook veel andere plante- en diersoorten. Eén van de meest voorkomende dieren in het zeegrasveld onder Terschelling is het wadslakje (*Hydrobia ulvae*). Dit slakje wordt slechts enkele millimeters groot en hun aantallen in het zeegrasveld onder Terschelling variëren tussen 50.000 en 100.000 dieren per m^2. Wadslakjes grazen o.a. op organisch bodemmateriaal en op zeegrasepifyten.

Het effect van wadslakjes op Klein Zeegras werd onderzocht door op het wad zeegras te laten opgroeien bij twee verschillende dichtheden wadslakjes. Uit dit experiment bleek dat door de aanwezigheid van hoge dichtheden wadslakjes de levensomstandigheden voor het zeegras verbeterden. De dichtheid van het perifyton was hoger bij het Klein Zeegras dat met een lage dichtheid wadslakjes was opgegroeid. Tevens leidde de aanwezigheid van weinig slakjes gedurende het groeiseizoen tot lagere aantallen en gewichten van de zeegrasplanten. Wadslakjes leveren dus een aanzienlijke bijdrage aan de groei en overleving van Klein Zeegras bij de huidige dichtheden van perifyton.

In de zeventiger en tachtiger jaren zijn wadslakjes in aantal toegenomen in de westelijke Waddenzee. Hierdoor is het mogelijk dat bij een toename van epifyten produktie als gevolg van eutrofiëring een toename in de hoeveelheid perifyton enigszins is afgeremd door een gelijktijdige toename van de begrazing door wadslakjes.

ANDERE MOGELIJKE OORZAKEN VAN ACHTERUITGANG

Interacties tussen zeegras en wadpieren

Tijdens het onderzoek op het wad viel het op dat het zeegrasveld begrensd werd door onbegroeide vlakten met zandhoopjes van de Wadpier (*Arenicola marina*). De overgang van de gebieden met en zonder zeegras was niet geleidelijk maar scherp. Hierdoor ontstond het vermoeden dat er sprake kon zijn van een wisselwerking tussen Klein Zeegras en wadpieren.

De wisselwerking tussen het zeegras en de wadpieren is onderzocht door middel van transplantatie experimenten, waarbij respectievelijk zeegrasplanten tussen de wadpieren, en wadpieren tussen het zeegras gezet werden. De wadpieren waren na transplantatie in het zeegrasveld weer snel verdwenen, onafhankelijk of er nu zeegras op die plek stond of niet. Blijkbaar waren de natuurlijke omstandigheden van het zeegrasveld niet ideaal voor deze dieren. Het zeegras bleek het daarentegen goed te doen in het pierenveld, mits het beschermd werd tegen de ondergravende werking van de wadpieren met behulp van een stuk gaas. Bij afwezigheid van dat gaas werd het zeegras in korte tijd door de wadpieren ingegraven. Geconcludeerd werd dat het gebied waarin de wadpieren voorkomen op zich wel geschikt is voor het Klein Zeegras. Het is echter de aanwezigheid van de pieren met hun destructieve eetgewoonten die zorgt dat het zeegras hier niet kan overleven.

De rand van het zeegrasveld wordt dus bepaald door de aanwezigheid van hoge dichtheden wadpieren. Een vergroting van het areaal van de wadpier in de Waddenzee kan tot een verkleining van het oppervlak van het zeegrasveld geleid hebben. Het is echter niet waarschijnlijk dat de wadpieren verder zullen oprukken richting zeegrasveld omdat zich een ondoordringbare laag klei op ongeveer 10 cm onder het bodemoppervlak van de wadplaat bevindt waardoor de wadpieren hier niet kunnen leven.

Schelpdiervisserij

Klein Zeegras komt niet overal evenveel voor in de Waddenzee. Deze verschillen zijn slechts ten dele te verklaren uit verschillen in hoogteligging, bodemgesteldheid en -stabiliteit. Voor de verspreiding van zeegras speelt tevens een lokale factor een belangrijke rol. Deze lokale factor bevat grootschalige verschillen tussen de onderzochte deelgebieden, zoals getijverschillen. Het abrupte verschil tussen het voorkomen in zeegras in de Nederlandse en Duitse Waddenzee doet op zijn minst vermoeden dat er ook sprake is van menselijke invloeden.

Eén van de belangrijkste verschillen in beheer tussen de deelgebieden van de Waddenzee is de intensiteit van de schelpdiervisserij welke in het Nederlandse deel hoog is vergeleken met het Duitse en Deense deel. Op die wadplaten in de Nederlandse Waddenzee waar op kokkels en kleine mossels wordt gevist, staat nagenoeg geen zeegras. Dit is niet verwonderlijk, want schelpdiervisserij heeft een desastreuze werking op het zeegras dat geraakt wordt tijdens het vissen. Hierdoor is de schelpdiervisserij niet alleen bedreigend voor de bestaande zeegrasvelden, maar ook voor de potentiële groeiplaatsen van deze plant.

CONCLUSIES

Op basis van de uitkomsten van het onderzoek lijkt het zeer wel mogelijk dat eutrofiëring in de Waddenzee resulteerde in een toename van de dichtheid van perifyton en hiermee tot de achteruitgang van Klein Zeegras leidde. Daarnaast kunnen veranderingen in de aantallen wadslakjes hierin ook een rol gespeeld hebben. Op de wadplaat onder Terschelling hebben wadslakjes een bepalende invloed op perifyton. Een toename in wadslakjes kan hiermee een toename in perifyton afgevlakt hebben.

De toename in voedingsstoffen en aantallen algen en bodemdieren in de westelijke Waddenzee suggereert dat er een gelijktijdige toename van epifyten en wadslakjes op de wadplaten van Terschelling heeft plaatsgevonden. Helaas zijn er onvoldoende gegevens over de lange-termijn veranderingen in dichtheden van deze organismen ter plekke om te kunnen zeggen of de achteruitgang inderdaad volgens bovenstaand mechanisme verlopen is.

Daarnaast is tijdens het werk op het wad gebleken dat ook andere factoren een bijdrage kunnen leveren aan de achteruitgang van het zeegras in de Waddenzee. Wadpieren bepalen de grenzen van het zeegrasveld ten zuiden van Terschelling bij Hoorn. Een vergroting van het wadpieren areaal kan hebben bijgedragen aan een verkleining van het oppervlak van dit zeegrasveld. Een in de bodem voorkomende kleilaag onder het zeegrasveld verhindert dat de wadpieren zich hier vestigen. Ook lijkt de intensieve schelpdiervisserij op de wadplaten van de Nederlandse Waddenzee het actuele en potentiële voorkomen van Klein Zeegras te beperken.

Katja (Catharina Johanna Maria) Philippart werd op 7 mei 1960 geboren te Tilburg. In juni 1978 werd het Atheneum-B diploma behaald aan het Pauluslyceum te Tilburg. Van 1978 tot 1986 studeerde zij biologie aan de Landbouwhogeschool (vanaf 1986 Landbouwuniversiteit) te Wageningen. Tijdens de doctoraalfase werd onderzoek verricht bij de vakgroepen Waterkwaliteit & Aquatische Oecologie (destijds vakgroep Natuurbeheer) en Landmeetkunde & Teledetectie. Het ingenieursdiploma werd behaald in november 1986.

Van 1986 tot 1990 heeft zij als assistent in opleiding gewerkt aan de mogelijke effecten van eutrofiëring op de achteruitgang van Klein Zeegras in de Nederlandse Waddenzee. Dit onderzoek werd bij de vakgroep Waterkwaliteit en Aquatische Ecologie (destijds vakgroep Natuurbeheer) van de Landbouwuniversiteit Wageningen en de afdeling Aquatische Ecologie van het Instituut voor Bos- en Natuuronderzoek (destijds Rijksinstituut voor Natuurbeheer) te Texel uitgevoerd. De resultaten van dit onderzoek worden gepresenteerd in dit proefschrift.

Van 1991 tot 1993 was zij in dienst als onderzoeker bij het Instituut voor Bos- en Natuuronderzoek te Texel. Hier heeft zij twee jaar meegewerkt aan het EG-project "Benthic Eutrophication Studies", waarbij aan de hand van veldstudies in de lagune van Venetië en labstudies in kunstmatige mariene ecosystemen de effecten van eutrofiëring op estuariene ecosystemen werden onderzocht. Daarnaast is in het kader van een opdracht van het Beleidsgericht Ecologisch Onderzoek Noordzee en Waddenzee een literatuurstudie naar de effecten van verschuivingen in nutriëntenconcentraties op Nederlandse kustecosystemen verricht.

Sinds 1994 is zij als wetenschappelijk onderzoeker aangesteld bij de afdeling Beleidsgericht Wetenschappelijk Onderzoek van het Nederlands Instituut voor Onderzoek der Zee te Texel. Hier doet zij onderzoek naar de oorzaken van variatie in mariene ecosystemen aan de hand van analyse van lange termijn series, o.a. ten behoeve van de EG-projecten "Northwest European Shelf Programme" en "IMPACT-II".