ORIGINAL ARTICLE

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Material exchange and food web of seagrass beds in the Sylt-Rømø Bight: how significant are community changes at the ecosystem level?

Abstract Material exchange, biodiversity and trophic transfer within the food web were investigated in two different types of intertidal seagrass beds: a sheltered, dense *Zostera marina* bed and a more exposed, sparse *Z. noltii* bed, in the Northern Wadden Sea. Both types of *Zostera* beds show a seasonal development of above-ground biomass, and therefore measurements were carried out during the vegetation period in summer. The exchange of particles and nutrients between seagrass beds and the overlying water was measured directly using an in situ flume. Particle sedimentation [carbon (C), nitrogen (N) and phosphorus (P) constituents] from the water column prevailed in dense seagrass beds. In the sheltered, dense seagrass bed, a net particle uptake was found even on windy days (7–8 Beaufort). Dissolved inorganic N and orthophosphate were mainly taken up by the dense seagrass bed. At times of strong winds, nutrients were released from the benthic community to tidal waters. In a budget calculation of total N and total P, the dense seagrass beds were characterised as a material sink. The seagrass beds with sparse *Z. noltii* were a source of particles even during calm weather. The uptake of dissolved inorganic N in the sparse seagrass bed was low but significant, while the uptake of inorganic phosphate and silicate by seagrasses and their epiphytes was exceeded by release processes from the sediment into the overlying water. Estimates at the ecosystem level showed that material fluxes of seagrass beds in the Sylt-Rømø Bight are dominated by the dense type of *Zostera* beds. Therefore, seagrass beds act as a sink for particles and for dissolved inorganic nutrients. During storms, seagrass beds are distinct sources for inorganic nutrients. The total intertidal area of the Sylt-Rømø Bight could be described as a sink for particles and a source for dissolved nutrients. This balance of the material budget was estimated by either including or excluding seagrass beds.

Including the subtidal part, the function of the ecosystem as a source for particles increased, supposing that all seagrass beds were lost from the area. During the vegetation period, seagrass beds act as a storage compartment for material accumulated in the living biomass of the community. There was great biodiversity among the plant and animal groups found in intertidal seagrass beds of the Sylt-Rømø Bay, representing 50–86% of the total number of species investigated, depending on the particular group. Since most species are not exclusively seagrass residents, the loss of intertidal seagrass beds would be of minor importance for biodiversity at the ecosystem level. Food web structure in seagrass beds is different from other intertidal communities. Primary production and detritus input is high, but secondary production is similar to that of unvegetated areas, although the relative importance of the trophic guilds is different. The loss of seagrass beds leads to profound alterations in the food web of the total ecosystem. Historical as well as recent changes in material fluxes and energy flow due to man-made alterations to the ecosystem are discussed.

Key words Seagrass beds · Particle fluxes · Nutrient fluxes · Species diversity · Trophic transfer

Introduction

Seagrass beds are characterised by a high productivity and biodiversity and are therefore of great ecological (den Hartog 1970; Phillips 1984; Phillips and Meñez 1988; Nienhuis 1992; Nienhuis et al. 1996) and economic value (Halliday 1995). Subtidal seagrasses, in particular, increase the species diversity of the ambient ecosystem (Heck et al. 1995) whereas in temperate areas the promoting effect of intertidal seagrass beds on species diversity is assumed to be low (den Hartog 1983). Present day research on the functioning of seagrass beds focuses on the growth and productivity of seagrass beds (van Lent et al. 1991; Buia et al. 1992; Terrados and Ros 1992; Olesen and Sand-Jensen 1994; Philippart 1995;

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Reyes et al. 1995; Duarte et al. 1996; Ibarra-Obando et al. 1997; Livingston et al. 1998). The importance of seagrass beds for epifauna (Schneider and Mann 1991; Webb and Parsons 1991; Gambi et al. 1992; Isaksson and Pihl 1992; Murphey and Fonseca 1995; Jernakoff and Nielsen 1998) and endofauna should not be underestimated (Kalejta and Hockey 1991; Somaschini et al. 1994; Valentine et al. 1994; Hughes et al. 2000). Recent research has revealed that seagrass beds are important habitats for fish (Sogard and Able 1991; Bell et al. 1992; Worthington et al. 1992; Ferrell et al. 1993; Connolly 1994a, b; Edgar and Shaw 1995a, b; Borg and Pihl 1997; Francour 1997). The nutrient demand of different seagrass species and their reactions to nutrient enrichment and eutrophication up to toxic levels of ammonium and nitrate have been investigated (Brix and Lyngby 1985; Burkholder et al. 1992; Fourqurean et al. 1992; Pedersen and Borum 1992, 1993; Hemminga et al. 1994; Lapointe et al. 1994; Pérez-Lloréns and Niell 1995; Short et al. 1995; van Lent et al. 1995; Agawin et al. 1996; Stapel et al. 1996; Alcoverro et al. 1997; Kraemer et al. 1997; Pedersen et al. 1997; Udy and Dennison 1997; van Katwijk et al. 1997; Rimmelin et al. 1998). The role of whole seagrass bed communities for the material exchange between bottom and overlying water at the ecosystem level is less well investigated (Caffrey and Kemp 1990, 1992; Williams 1990; Hemminga et al. 1991; Asmus et al. 1994; Erftemeijer and Middelburg 1995; Johnson and Johnstone 1995; Taylor et al. 1995a, b; Viaroli et al. 1996). However, there is strong evidence that seagrass beds are important for sediment stability (Fonseca 1989) and for the retention of particles (Bulthuis et al. 1984; Dauby et al. 1995), since the canopy of leaves diminishes wave energy and currents (Fonseca and Fisher 1986; Gambi et al. 1990; Fonseca and Calahan 1992). Losses of seagrass beds have been observed all over the world (den Hartog and Polderman 1975; Orth and Moore 1983; Giesen et al. 1990; Tomasko and Lapointe 1991; de Jonge and de Jong 1992; Nienhuis 1992; Walker and McComb 1992; Durako 1994), and these losses led to profound changes in the material budget of coastal ecosystems (Asmus R and Asmus H 1998), because of the key role of seagrass beds. If seagrass beds are lost, the food web of the ambient ecosystem is altered, and primary and secondary production, as well as the energy flow, decrease (Heck et al. 1995). On both sides of the North Atlantic, losses of seagrasses were found early in the 1930s due to the wasting phenomenon (den Hartog 1987). The subtidal stocks survived in closed embayments and fjords where salinity was reduced, as in the Baltic Sea (Giesen et al. 1990). In the Wadden Sea, only the intertidal seagrass beds have recovered and reestablished their former ecological function to some extent. Due to the extinction of seagrass beds, major ecosystem changes have probably occurred in the twentieth century. The decrease in seagrass beds also still continues in the intertidal region of the Wadden Sea. It is the aim of this study to evaluate the functional role of the still existing intertidal seagrass beds in the

Sylt-Rømø Bight at an ecosystem level. We therefore examine the material exchange, the diversity and the energy flow of a dense *Z. marina* bed, which is representative of dense *Z. noltii* and dense mixed stands of *Z. noltii* and *Z. marina*, and we also examine a sparse *Z. noltii* bed.

Materials and methods

Site

The investigation area, the Sylt-Rømø Bight, is part of the Wadden Sea bordering the coastline of the south-eastern North Sea from the Netherlands up to Denmark. The bight is a closed basin situated between the mainland and the two islands, Sylt and Rømø, which are connected to the mainland by causeways (Fig. 1). There is only one connection to the North Sea through a deep tidal gully between the two islands. The whole area is 406 km^2 in extent, including 135 km^2 of tidal flats. The main intertidal area is occupied by sandflats. Dense *Zostera* beds cover 8% and sparse *Zostera* beds only 4% of the intertidal area. The coverage of the communities was measured by remote sensing (Murphy and Doerffer, personal communication) as well as by mapping (Reise and Lackschewitz 1998) directly on the tidal flats (Asmus H and Asmus R 1998).

Types of seagrass beds

Two seagrass species, *Zostera marina* L. and *Zostera noltii* Hornem., are found in intertidal parts of the Sylt-Rømø Bight. The
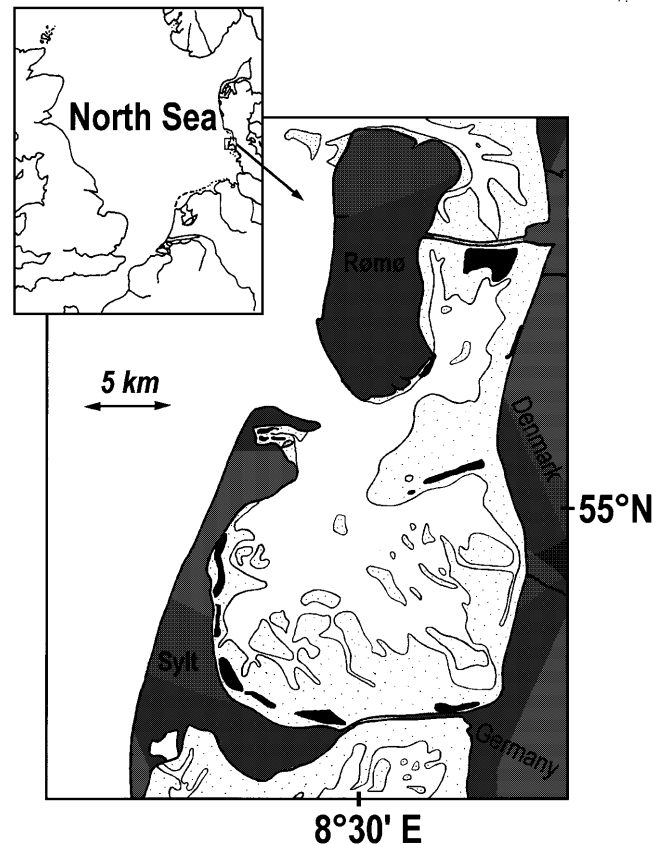

Fig. 1 Map of the Sylt-Rømø Bight, with distribution of seagrass beds

subtidal form of *Z. marina* occurred until 1933 when the wasting disease reached the area (Wohlenberg 1935). This subtidal *Z. marina* was described as a perennial (Wohlenberg 1935). The intertidal form of *Z. marina* generally shows an annual life cycle at the investigation sites, but there is a great variability in the percentage of plants that develop every year from seedlings, growing to maximal biomass in August and September (Asmus R et al. 1998). In contrast with *Z. marina*, *Z. noltii* plants are perennial. They also lose their leaves in autumn, but they resist winter conditions by means of rhizomes remaining in the substrate.

A typical *Z. marina* meadow grows mainly in sheltered muddy substrates of the intertidal parts of the Sylt-Rømø Bight (or of the Wadden Sea) (Fig. 1). The bottom level in these areas is often slightly depressed, so that a thin water layer remains even during low water. In October seagrass plants are grazed to a large extent by brent geese (*Branta bernicla*) and wigeons (*Anas penelope*), but ungrazed plants lose their leaves until the end of October. In autumn and winter the sites of seagrass beds are bare mudflats with only a few scattered seagrasses.

Z. noltii beds also grow well in sheltered places. Pure *Z. noltii* stocks are rarely developed. In most years, *Z. noltii* and *Z. marina* form mixed stands. In sandy places only *Z. noltii* occurs. This type of a *Zostera* bed is more exposed to wind and waves than the dense type of seagrass bed.

Sylt Flume

The material exchange between seagrass beds and the overlying water was measured in a large flume (Fig. 2) in *Z. marina* beds in 1987 and 1991, and in a sparse *Z. noltii* bed in 1990. The flume technique has already been described (Asmus et al. 1994). One lane enclosed the natural seagrass bed, while in the other lane seagrasses were plucked off, so that the bare sediment was left. This lane served as a control. Every 30 min, water samples were collected 15 cm above the bottom by electric pumps at the inflow of the flume, and a corresponding set of samples was taken when the water had passed the flume. The parameters measured were particulate organic C, particulate organic N, ammonium, nitrate, nitrite, total N, total P, dissolved inorganic P, and dissolved silicate. The differences in concentration between inflow and outflow were used to estimate the material flux, considering the water volume passing in this time period. Current velocity was measured by drifting buoys as well as by induction current meters.

Species diversity

Species diversity was estimated in seagrass beds of the Sylt–Rømø Bay during the period from 1980 to 1998 by analysing the lists of species of 12 published reports and publications and two unpublished summaries. The authors, references, seagrass types, faunal and floral groups investigated and the methods for obtaining species diversity data are summarised in Table 1.

Trophic transfer: biomass, productivity and consumption

Biomass values from Reise and Lackschewitz (1998) were used. Productivity was estimated from these biomass data using P:B ratios for the different species (Asmus H 1984; 1987). Consumption was estimated by adding respiration and production in g C for the dominant species. Respiration was calculated using R:B-values (Asmus H 1984, 1994) for the particular species.

Table 1 References (including reports and doctoral theses) regarded for estimating faunal species diversity in intertidal seagrass beds of the Sylt-Rømø Bay

Group investigated	Community type	Observed year	Reference
Macrofauna (>500 µ)	*Z. noltii*	1980	Asmus and Asmus 1985
Parasites	of dominant macrofauna	1980–1998	Lauckner (personal communication)
Turbellaria	*Zostera* beds	1981	Riebensahm 1981
Mobile epifauna	*Z. marina*	1988	Hellwig-Armonies 1988
Macrofauna (>1 mm)	*Z. noltii*	1990	Reise et al. 1994
Macrofauna	*Z. marina*	1991	Blankenhorn 1992
Macrofauna (>1 mm)	*Z. noltii* and *Z. marina* Beds	1992–1994	Lackschewitz 1998
Mobile epifauna	*Z. noltii* and *Z. marina*	1993	Gerbersdorf 1994
Mobile epifauna	*Z. noltii*	1995	Schomburg 1997
Endofauna (>250 µ)	*Z. noltii*	1995	Suhr 1996
Macrofauna	*Z. noltii*	1997	Nacken 1998
Macrofauna	*Z. noltii* and *Z. marina*	1997–1999	Schanz (personal communication)

Fig. 2 Sylt Flume in *Zostera* beds (Photo: H. Asmus)
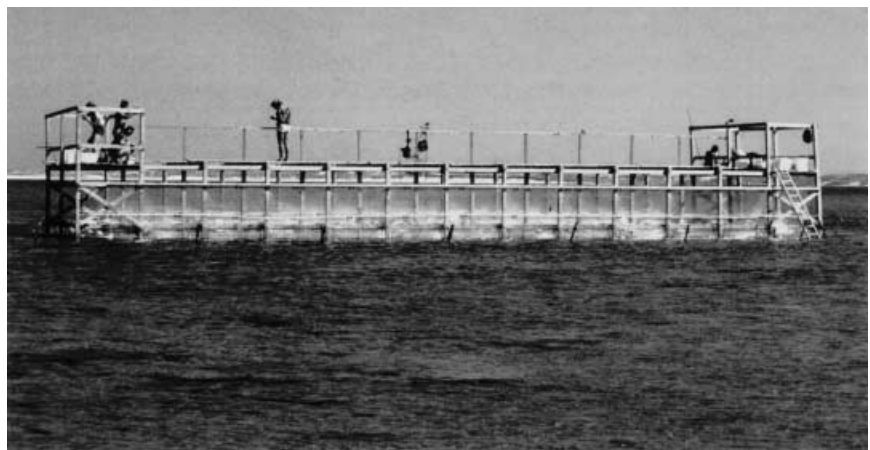
Results

Flume measurements

Particulate organic C

Particulate organic C (POC) was mainly imported into a dense intertidal *Z. marina* bed ($P<0.05$) (Fig. 3). The muddy unvegetated control lane showed variable rates with an insignificant mean release of POC**.** The difference in POC flux between the vegetated and unvegetated flume lane was significant over whole tidal cycles (Mann Whitney U-test, $P<0.05$; $n=23$). This difference became more distinct during an ebbing tide (same test, $P<0.005$, $n=11$) in that particles were held back in the seagrass bed while they were exported from the muddy sediment with increasing currents. The particle uptake was only evident in dense seagrass beds, whereas in sparse *Z. noltii* communities POC was released ($P<0.05$) (Fig. 3). In sparse *Z. noltii* beds, the benthic–pelagic POC-exchange was not significantly different between vegetated and unvegetated flume lanes. The particle exchange between seagrass beds and the overlying water is strongly influenced by hydrodynamics (Fig. 4). The uptake of particles on calm days is only half the value of that on stormy days. Dense seagrass beds are situated in sheltered places of the Sylt-Rømø Bight, and these seagrass beds further diminish the currents and waves. Because the particle load of tidal waters increases during storms, the sedimentation rate between the seagrass leaves may also increase. In this way calm and stormy days may determine the direction and height of POC-fluxes. The stormy situation represents a wind of 6–8 Beaufort. This is the maximum wind speed at which experiments on the flume are possible.
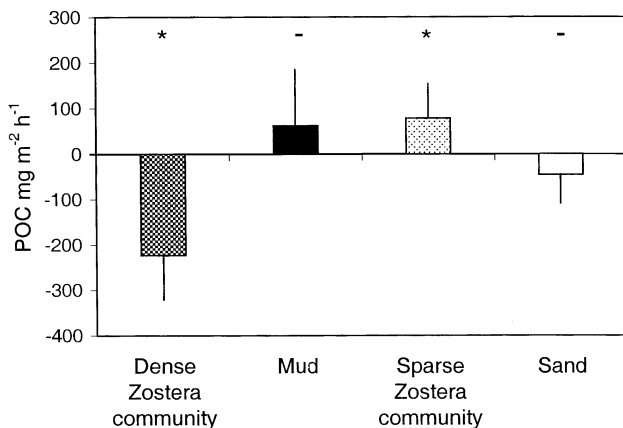
N measurements

In dense seagrass beds dissolved inorganic N (DIN) is significantly taken up ($P<0.05$, $n=36$). There is a tendency for the uptake of particulate N (PN) and for a release of total N (TN), although this is not significant over the whole growing season (Fig. 5). Sparse seagrass beds release TN (significant, $P<0.05$) and PN (not significant) and take up only small amounts of DIN ($P<0.05$). In both types of seagrass beds, only DIN is significantly different between vegetated and unvegetated areas (Mann-Whitney U-test, $P<0.05$, *Z. noltii* $n=50$, *Z. marina* $n=38$).
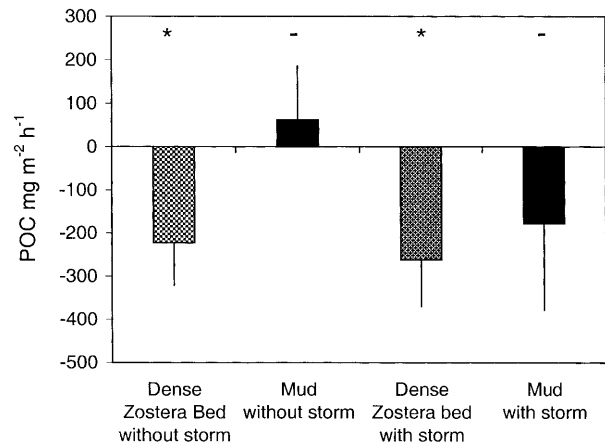

Fig. 4 Influence of storms on particle exchange (POC) in a *Zostera marina* bed. Uptake of particles is significant (*), while flux rates in the muddy control lane are not significant (–) (significance test Dixon and Mood, Mann Whitney U-test, $P<0.05$, Sachs 1983)
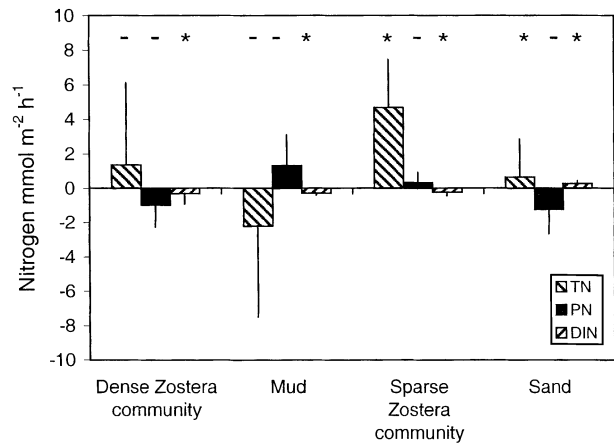

Fig. 3 Uptake (negative values) and release (positive rates) of particulate organic carbon (POC) in two dense seagrass beds, mainly *Zostera marina* (measured in 1987 and 1991), a muddy control lane (in 1991), and a sparse *Zostera noltii* bed with a sandy control lane (in 1990): * indicates that mean flux rates are significant over whole study periods (significance test Dixon and Mood, Mann Whitney U-test, $P<0.05$, Sachs 1983), whereas – indicates that fluxes are not significant over the whole study period

Fig. 5 Nitrogen dynamics in dense and sparse *Zostera* beds. Uptake of DIN (mainly ammonium) by seagrass meadows, in the muddy control lane and the ammonium release in the sandy lane are significant (*). Release of particulate nitrogen from a sparse seagrass beds is also significant while other fluxes of PN and total nitrogen (TN) over whole study periods are not significant (–) (significance test Dixon and Mood, Mann Whitney U-test, $P<0.05$, Sachs 1983)

P measurements

The P compounds show a more regular pattern (Fig. 6). Dense *Zostera* beds were sinks for dissolved inorganic phosphate (DIP) and total P (TP). There was a significant difference between the TP uptake in the dense seagrass lane of the flume and the release of TP in the unvegetated muddy lane (Mann Whitney U-test, $P<0.01$, $n=23$). The TP flux rates treated separately in the seagrass lane are not significant, while the TP rates in the muddy control are significant ($P<0.05$). DIP was taken up ($P<0.05$), but there was a significant difference between vegetated and unvegetated lanes only during ebbing tides (Mann Whitney U-test, $P<0.005$, $n=19$). Sparse *Zostera* stocks release TP ($P<0.05$) which could be explained by a release of DIP ($P<0.05$). Neither the P flux rates in the sandy control lane nor the difference in TP and DIP exchange between vegetated and unvegetated lanes in the sparse *Z. noltii* bed were significant.

Silicate

Silicate was released in significant amounts by the muddy and sandy unvegetated flume lanes probably due to bioturbating infauna ($P<0.05$) (Fig. 7). Also, in the sparse *Z. noltii* stand silicate was released, but this was not significant. There was a tendency for silicate uptake in the dense seagrass bed, although this was not significant over the whole growing season.

Species diversity

The species diversity of the investigated animal groups is comparatively rich (Fig. 8). Plant diversity in the intertidal seagrass beds of Königshafen is dominated by mi-
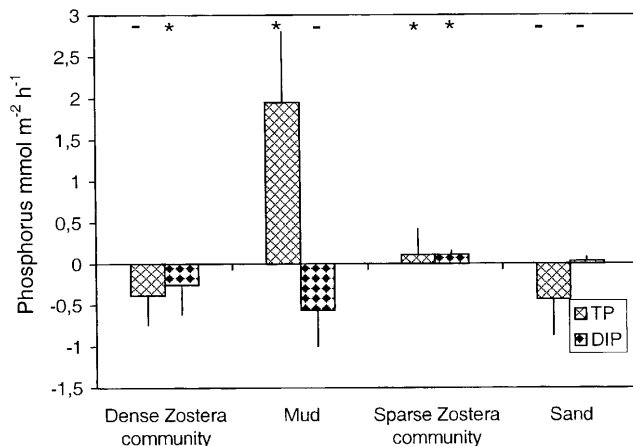
crophytobenthos, with 70 species of diatoms and one species of blue-green algae, and in the total area 108 species of microalgae and one species of blue-green algae were reported (Asmus and Bauerfeind 1994). The diversity of macroalgae growing, for example, as epiphytes on seagrasses has not yet been quantitatively investigated in the seagrass beds of the Sylt-Rømø Bight.

Biodiversity of the animal groups investigated in the intertidal seagrass beds of Sylt-Rømø Bay is high, representing 2–86% of the total number of species, depending on the particular group (Fig. 8). Among classes of animals, free living turbellarians dominate, with 435 species being found in Sylt-Rømø Bay (Reise 1988). However, only 12% of these meiobenthic species were reported from seagrass beds. Regarding macrofauna, polychaetes are reported to show the highest number of species (26 in seagrass beds, 38 in the total ecosystem). Among the *Crustacea*, only *Malacostraca* were included. The species number in this class would have been even higher if ostracodes and copepods had also been registered. Fish are also underestimated in this figure, because only those species which had been caught in ebb pools are shown. In addition, a number of fish species visit intertidal seagrass beds during the inundation period. The number of fish species in the total area is about 50 (Herrmann et al. 1998).

Trophic transfer and energy flow

In Fig. 9 a rough energy flow of the intertidal seagrass beds in the Sylt-Rømø Bight is presented. Only those values which could be measured by different research groups in the ecosystem research project (SWAP) working synchronously between 1990 and 1995 (Gätje and Reise 1998) are shown in this diagram. Primary production is represented by phytoplankton, microphytobenthos and *Zostera* plants. Phytoplankton primary production is
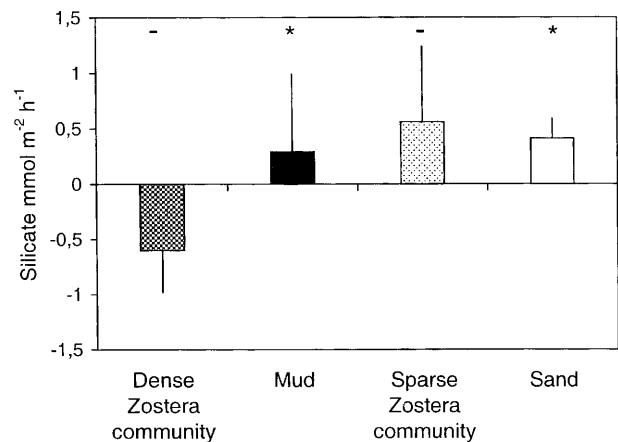

Fig. 6 Dissolved inorganic phosphate (DIP) was significantly (*) taken up by a dense seagrass bed, while it was released by a sparse seagrass bed (significance test Dixon and Mood, Mann Whitney U-test, $P<0.05$, Sachs 1983)
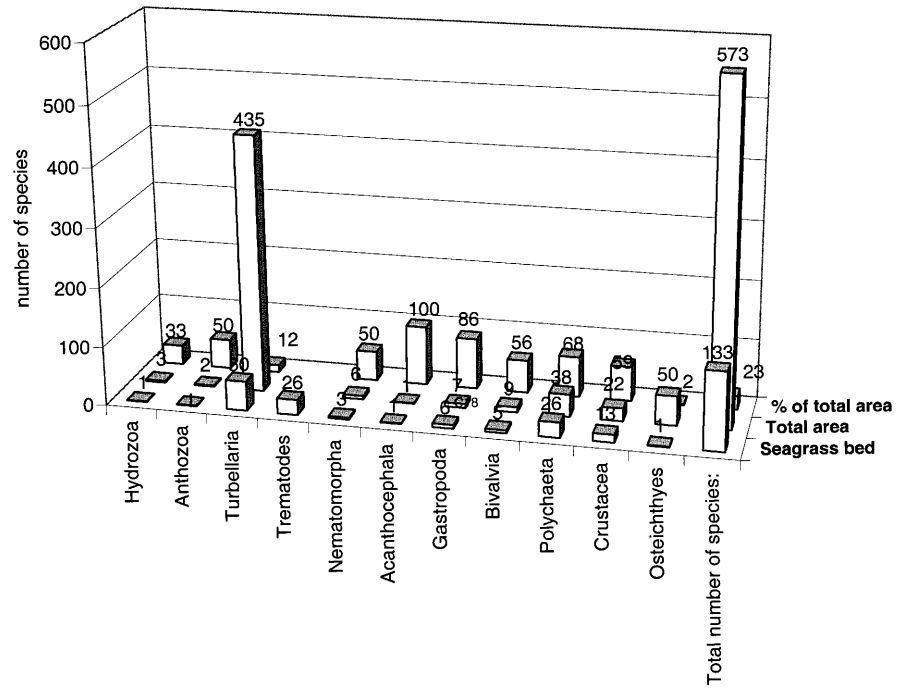

Fig. 7 Mud and sand released silicate in significant amounts (*), while flux rates in the seagrass beds were not significant over whole study periods (–) (significance test Dixon and Mood, Mann Whitney U-test, $P<0.05$, Sachs 1983)

Fig. 8 Species numbers in sea-grass beds of the Sylt-Rømø Bay from different investigations from 1980 to 1998 (for references see Table 1)

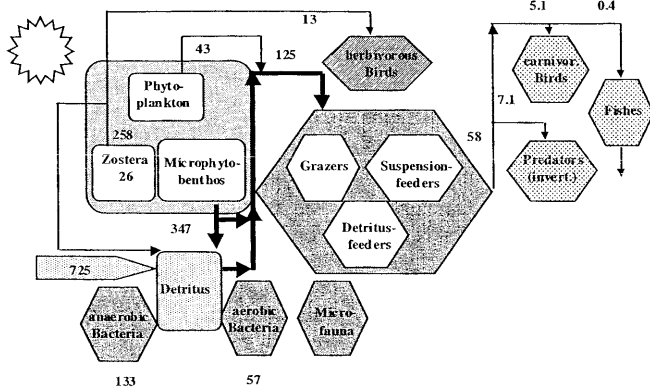**Fig. 9** Energy flow diagram (in g C m^{-2} a^{-1}) of a seagrass community in the Sylt-Rømø Bight

43 g C m^{-2} a^{-1}, microphytobenthos produces up to 347 g C m^{-2} a^{-1}, while *Zostera* produces 258 g C m^{-2} a^{-1}. Additionally, a detritus input of 725 g C m^{-2} is available as a potential primary energy source for the food web. About half (13 g C m^{-2}) of the total *Z.* biomass of 26 g C m^{-2} is used directly by herbivorous birds such as brent geese and wigeons. The phytoplankton, microphytobenthos and detritus are consumed by macrofauna with 125 g C m^{-2} a^{-1} coming from this source. 58 g C m^{-2} a^{-1} is transported along the food web to higher trophic levels, especially invertebrate predators which consume 7.1 g C m^{-2} a^{-1}. Carnivorous birds consume 5.1 g C m^{-2} a^{-1}, while fish consume 0.4 g C m^{-2} a^{-1}. Seals are at the end of this food chain.

Discussion

Material fluxes at a community level

Dense *Zostera* communities of the Sylt-Rømø Bay are effective sinks for particulate material, whereas sparse stocks react only slightly differently from bare intertidal sand bottoms. A sink function for autochthonous detritus was also suggested for *Z. marina* beds in a low current regime (<53 cm s^{-1}) (Fonseca et al. 1983), which is comparable to the flow regime of the seagrass beds in this study. Using indirect measurements [e.g. isotopic dating of cored material (Boudouresque et al. 1980; Thommeret 1985) or lepidochronology (Pergent and Pergent-Martini 1990)], only sedimentation rates over longer periods are available. Direct measurements of particle fluxes in seagrass beds are rare. In Mediterranean *Posidonia* beds the retention capacity for particles was 15 times higher than in bare sediments (Gacia et al. 1999). The highest accumulation rates of suspended matter were found during the winter months (Dauby et al. 1995), since *Posidonia* leaves are developed throughout the year and the particle load is higher in winter than in summer. In the Sylt-Rømø Bay, seagrass leaves are developed only during the vegetation period, and particle trapping could be measured only during this time. During the ebb tide, seagrass beds retained more suspended solids than unvegetated mudflats did, because resuspension of material is inhibited in seagrass beds (Bulthuis et al. 1984).

Dense seagrass beds are situated in sheltered parts of the Sylt-Rømø Bight, and during the vegetation period they mediate hydrodynamic energy. In general, different types of seagrass beds have the potential to reduce currents and waves (Gambi et al. 1990; Fonseca and Calahan 1992; Worcester 1995). Because the particle

load of the tidal water increases during storms by a factor of ten (Ward et al. 1984), the sedimentation rate between the seagrass leaves also increases. This phenomenon was also observed in Chesapeake Bay, where wave energy was attenuated by vegetation, suppressing resuspension and enhancing deposition (Ward et al. 1984). Probably at a higher wind speed than the 7 Beaufort measured in this study and a subsequent more intensive water movement, a dense seagrass bed may switch to being a particle source (Fonseca et al. 1983; Dauby et al. 1995; Koch 1999). Sparse seagrass beds are particle sources on calm days, because they are situated in very shallow and turbulent water. Unfortunately we do not have comparable measurements from stormy days in sparse seagrass beds. The difference between a stormy situation and a calm situation is obvious regarding the exchange pattern of the total intertidal ecosystem, which shows a high release during storms and a slight uptake during calm days (Asmus R and Asmus H 1998). Dense seagrass beds are therefore important sinks in the intertidal habitat, and they may play an important role as particle sinks at the ecosystem level.

Dense seagrass beds in the Sylt-Rømø Bay are significant sinks for DIN (Asmus et al. 1994), but show only a tendency to take up PN and to release TN. Sparse seagrass beds are sources for TN and PN and are only small sinks for DIN.

The source function for TN is surprising and the reason for this may be a significant release of dissolved organic N (DON) from seagrass beds, which exceeds the sink function for PN and DIN. Because the counteracting uptake of DIN is much higher in dense seagrass beds than in sparse seagrass beds, the net release of TN is higher in sparse seagrass beds. A three times higher TN content in the sediments of seagrass beds compared to bare mudflats was reported from tropical seagrass beds dominated by *Syringodium isoetifolium* (Ascherson) Dandy (Yamamuro et al. 1993). At the same site the DON content was found to be higher in the water within the seagrass canopy compared with other areas (Yamamuro et al. 1993). Earlier studies suggested an increase in bacterial activity in seagrass beds, probably due to the exudation of organic matter by seagrass roots and rhizomes during photosynthesis (Moriarty et al. 1986). The origin of the efflux probably from DON from seagrass beds is not clear, but these processes are definitely associated with the seagrass, because other communities do not show a DON efflux. This imbalance between the fluxes of the N compounds may be a consequence of an increased sedimentation of N-containing particles following single irregular events (storms). This would keep the organic N pool in the sediment at a higher level, and intensify the remineralisation processes (indicated by a release of DON) and the bacterial activity for a longer time period. Hemminga et al. (1991) emphasised the role of such imbalances of net losses and net gains of nutrients for the fluctuations of seagrass productivity. This may be especially important in dynamic environments such as the Wadden Sea.

DIN was found to be low in water ebbing from seagrass beds as well as from mudflats (Bulthuis et al. 1984). Also, in the present study, the difference in DIN flux during ebb tide between mudflats and seagrass beds on mud showed a lower level of significance ($P<0.1$) compared to the differences in P flux ($P<0.005$). During the total tidal cycle, DIN differed significantly between vegetated and unvegetated areas. Seagrass communities are able to reduce ammonium concentrations (which contribute most to DIN in this study) in the water column considerably (Short and McRoy 1984; Short and Short 1984). They also intensify the turnover of the ammonium pool of sediments by a factor of 2–3 (Boon et al. 1986). This information from the literature as well as that from the comparison between the seagrass lane and the control lane of the flume suggests that a considerable amount of inorganic N remineralised within the seagrass bed and released by the sediments seems to be taken up by the seagrass leaves before an export out of the community occurs (Prieto and Corredor 1984; Hemminga et al. 1991; Asmus et al. 1994). DIN uptake in sparse seagrass beds is, therefore, smaller than in dense beds.

Dense *Zostera* beds were distinct sinks for TP and DIP, whereas sparse *Zostera* stocks release TP which could be explained by a release of DIP from the sediment. A sink function of seagrass beds for P compounds has been demonstrated by several authors. Bulthuis et al. (1984) showed that total and soluble reactive P concentrations did not increase significantly in water ebbing from intertidal seagrass beds, but increased by 30–100% in drainage from unvegetated flats. Also, in this study, a significant difference in DIP flux between vegetated (uptake) and unvegetated (release) lanes of the flume was only observed during ebbing. In the Sylt-Rømø Bay, TP is dominated by soluble inorganic compounds, but also dissolved organic P (DOP) compounds are found to be important P sources for *Zostera* plants (Lapointe 1989; Tomasko and Lapointe 1991). This is made available by alkaline phosphatase activity (APA) found especially in leaves and probably also epiphytes of *Posidonia oceanica* and *Cymodocea nodosa* during low nutrient availability (Pérez and Romero 1993). In contrast, in *Z. noltii* APA was found to be independent of external concentrations (Hernández et al. 1994). The contribution of particulate organic P (POP) to TP uptake can be explained by the sink function for particles mentioned above.

Seagrass beds may depend on an import of POP, which enriches the interstitial water via remineralisation, especially during low phosphate concentrations in summer (Hemminga et al. 1991; Asmus et al. 1994). This remineralised P is rapidly taken up by the roots (Pérez-Lloréns et al. 1993) and, therefore, P concentrations in the interstitial water of seagrass beds were significantly lower than those in adjacent muddy sediments, where all vegetation had been experimentally removed (Asmus et al. 1994). The complex pattern of P cycling within a seagrass bed is characterised by a dominance of DIP sinks such as roots and leaves of seagrass plants as well as benthic diatoms, epiphytes and associated macroalgae.

At the ecosystem level, the storage of P in below-ground organs of seagrasses is estimated to shift 1–15% from the P input due to planktonic primary production to a large sink with low turnover (Romero et al. 1994). On the other hand, the role of seagrasses as a P pump from the sediment to the water is variable due to the relation of nutrient concentration in sediments to that of the water column. The translocation and leaching of P was found to be negligible in *Z. marina* and *Z. noltii* (Brix and Lyngby 1985; Pérez-Lloréns et al. 1993). There is some evidence that in temperate zones seagrass leaves take up a large amount of P from the surrounding water (Brix and Lyngby 1985), but the difference between vegetated and denuded sediments in this study showed that a large amount of the DIP taken up by seagrass beds was released directly by the sediments rather than imported by tidal water transport. This also explains the dominant release of DIP from sparse seagrass beds, which was consistent with the release of unvegetated sediments.

Dense *Zostera* stocks acted as sinks for silicate, but this was not significant over the whole growing season. This is explained by the occurrence of benthic and epiphytic diatoms, whereas seagrasses are probably not able to use silicate as a nutrient, because no stimulating effect for seagrass growth could be found in experiments where seagrasses were exposed to increasing silicate levels (Kamermans et al. 1999). In sparse seagrass beds as well as in unvegetated control areas of both seagrass types this effect is probably surpassed by the bioturbating infauna which significantly release silicate from the bottom to the water column (Asmus 1986). Bulthuis et al. (1984) found that both vegetated and unvegetated mudflats released silicate during ebb time. He explained this by an efflux of interstitial water. However, in bare mudflats the silicate level was significantly higher than in vegetated mudflats, possibly because the loss of seagrasses increases the efflux of interstitial water. On the other hand, a release of silicate from the bottom could be diminished by the uptake of epiphytic diatoms growing on the seagrass leaves.

Material fluxes at the ecosystem level

If we extrapolate the flux rates to the total area of the seagrass beds and compare this with the material exchange of the total intertidal region (Fig. 10a, b), it becomes evident that seagrass beds contribute a significant part to the material turnover of the total intertidal system, although seagrass beds cover only 12% of the intertidal area. The seagrass beds act as particle sinks in accordance with the total intertidal ecosystem, and they counteract the general trend of nutrient release on calm days (see Fig. 10a). The seagrass beds become nutrient sources if the stormy days are included in the material budget (see Fig. 10b). The coastal ecosystem, Banc d'Arguin, is dominated by seagrasses covering 84% of the intertidal area. Here a distinct sink effect for nutrients as well as particulate organic matter was observed for the total ecosystem (Wolff et al. 1993). Com-
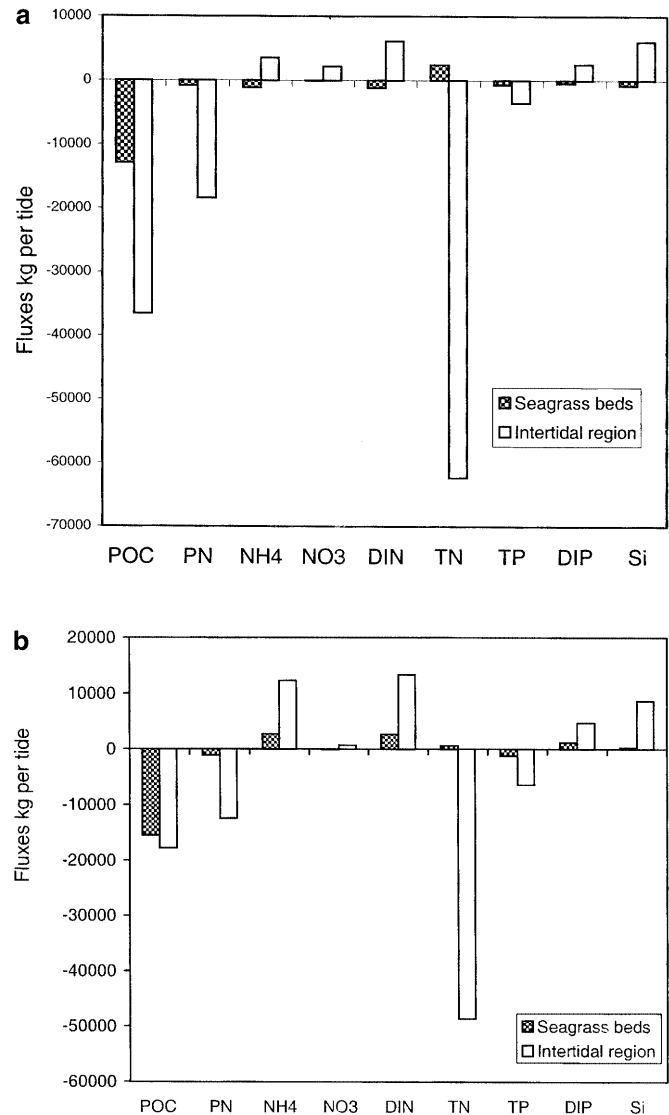
Fig. 10 Material turnover in kg per tide and total area of intertidal seagrass beds in the Sylt-Rømø Bight (16 km[2]) (*chequered columns*) compared with the the material turnover of the total intertidal region of the bay (135 km[2]) (*white columns*) and either without stormy situations (**a**) or with storms included (**b**)

parisons between benthic oxygen sulphide and nutrient fluxes of different macrophyte communities reveal that *Z. noltii* communities in Arcachon Bay had a stabilising effect on the benthic fluxes (Viaroli et al. 1996). Even these few studies show that the function of the ecosystem either as a source or a sink is influenced by the percentage cover of seagrass beds. In the present study, the seagrass cover was not high enough to control the direction of the ecosystem function, but it contributed significantly to the material budget and determined the material exchange rates.

Exclusion of seagrass beds

What would happen to the material flux of the intertidal area of the Sylt-Rømø Bay if all seagrass beds became
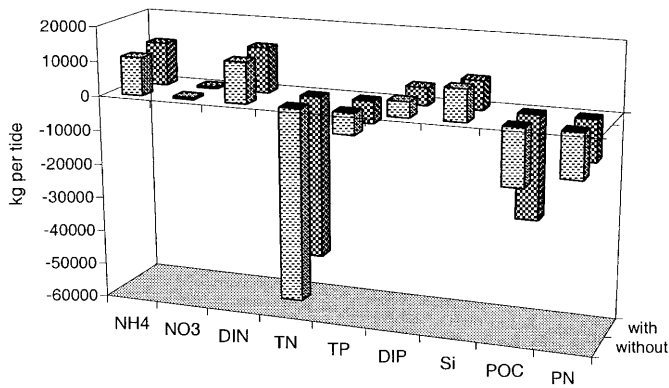
Fig. 11 Material turnover (kg per tide) of the total intertidal area of the Sylt-Rømø Bight with seagrass beds (*dark chequered columns*) and without, i.e. when seagrass beds were substituted by *Arenicola* – sandflats (*light chequered columns*)

extinct or disappeared. This scenario is illustrated in Fig. 11, where seagrass beds were replaced by *Arenicola* sandflats to simulate the loss of seagrass beds. This leads to two relevant alterations in the material budget at the ecosystem level: (1) the POC uptake is dramatically reduced if seagrass beds are absent and (2) the uptake of TN by the system increases. A dominant role of seagrass beds for intensifying organic matter exchange and bacterial production at ecosystem level was also observed by Middelboe et al. (1998) in Limfjorden. These fundamental alterations may have serious consequences for the ecosystem, because they may influence the further development and this may also have implications for the energy flow and the food web of the system.

If we exclude seagrass beds from the system, firstly the C or energy flow will show some important alterations. One important consequence is that the detritus input per year to the total system will be reduced by 32% of the value we find in intertidal areas with seagrass beds. This may well have fundamental consequences for the whole ecosystem (Table 2), because the loss of seagrass beds may reduce the benthic deposition of organic matter and at the same time may increase material turnover in the water column.

Other important components of the ecosystem would also be affected if seagrasses were lost. The aerobic microbial turnover would be reduced by 9%, while the anaerobic microbial turnover would be reduced by 7%. The importance of detritus import for bacterial activity in seagrass beds has been reported from different areas by several authors (Pollard and Kogure 1993; Yamamuro et al. 1993; Middelboe et al. 1998).

Seagrass beds in the present study have a high species richness but most species found in these intertidal seagrass beds are not specific to this community, but also occur in adjacent areas without macrobenthic vegetation (den Hartog 1983). Exceptions are the isopods *Idothea balthica* and *I. chelipes*, as well as the hydrozoon *Orthopyxis integra* (Reise and Lackschewitz 1998). The secondary production and biomass of macrofauna shows a value similar to the average of the total bight; but consumption in seagrass beds is slightly higher.

Therefore, if seagrass beds are excluded from the system, the sum of macrofaunal consumption may decrease slightly (by 1%), whereas secondary production seems to be less affected. This is in contradiction to other studies showing eelgrass beds to make a major contri-

Table 2 Alterations of ecological features after theoretical exclusion of seagrass beds: production, biomass and consumption at different trophic levels (g C m^{-2} a^{-1}) in the intertidal Sylt-Rømø Bay in the period 1990–1995

	With seagrass beds	Without seagrass	% Change	Reference
Primary production and detritus input				
Phytoplankton primary production	43	43	0	Asmus H et al. 1998
Microbenthic primary production	357	356	0	Asmus H et al. 1998
Seagrass gross primary production	30	0	−100	Asmus H et al. 1998
Seagrass biomass	3	0	−100	Asmus H et al. 1998
Detritus input	226	154	−32	Asmus H and Asmus R 1998
Total	659	553		
Small food web and microbial turnover				
Aerobic microbial metabolism	40	37	−9	Kristensen et al. 1998
Unaerobic microbial metabolism	94	88	−7	Kristensen et al. 1998
Macrobenthic secondary production				
Consumption (net)	98	97	−1	
Biomass	29	28	−1	Reise and Lackschewitz 1998
Production	54	54	0	
Predatory macrobenthos				
Shore crabs	0.4	0.1	−71	
Infaunal predators	4	4	0	
Birds (consumption)				
Carnivorous birds	5.05	5.05	0	Scheiffarth and Nehls 1997
Herbivorous birds	1.8	0	−100	Madsen 1988

bution to species richness (Orth et al. 1984; Zieman and Zieman 1989) and secondary production in shallow water communities (Baden and Pihl 1984; Fredette et al. 1990; Kalejta and Hockey 1991; Valentine and Heck 1993; Heck et al. 1995). The reason for this is that the former authors mainly described subtidal seagrass beds, where the second trophic step is enhanced and there are also many seagrass residents. This is also reported from early studies in the Sylt-Rømø Bight, where subtidal seagrass beds occurred before 1933 (Wohlenberg 1935). In the intertidal area of the Sylt-Rømø Bight, secondary production shows the following ranking at the community level:

mussel beds>muddy sands>seagrass beds>sandflats >mudflats>sandy shoals
<div align="center">(Asmus 1987; Asmus R et al. 1998).</div>

These small alterations at the consumer level of the ecosystem mask distinct qualitative alterations within the dominance of trophic guilds. The average biomass of benthic grazers such as the mud snails *Hydrobia ulvae* and *Littorina littorea* in the system is reduced to around 30% when seagrass beds are absent. With respect to biomass and secondary production of benthic grazers, the intertidal communities are ranked as follows:

seagrass beds>mussel beds>mudflats >muddy sands>sandflats>sandy shoals.

The dominance of benthic grazers in seagrass beds was found to be related to the epiphyte availability (Bologna and Heck 1999). Therefore, in intertidal *Zostera* beds (this study) and *Posidonia* beds, this group surpassed other trophic guilds in shallow seagrass associations compared with deeper ones (Gambi et al. 1992).

The reduction was not significant in other trophic guilds of the macrofauna such as suspension-feeders, detritus feeders and various other feeding types as far as they were permanently present. We do not yet have any information on the mobile epibenthos in intertidal seagrass beds of the study area. This group will be important because, as many authors have shown, this group prefers vegetation as a habitat (Edgar and Robertson 1992; Connolly 1994a, c, 1997). Therefore, changes for this group are probable.

In the higher trophic levels, there are no apparent differences in infaunal predators, but predation by shore crabs (*Carcinus maenas*) changed dramatically. A high degree of crab predation was also reported for eelgrass beds worldwide (e.g. Strieb et al. 1995). It is evident that herbivorous birds, which are the predominant direct grazers on seagrasses in the Wadden Sea (Madsen 1988), would not find food on the tidal flats if seagrass beds were missing; therefore a 100% decrease is assumed.

Historical changes

The seagrass beds we recently found in the Sylt-Rømø tidal areas seem to be only relicts from a time when seagrass beds were more important to the ecosystem than today. There is evidence for the Königshafen, that former intertidal beds were different in size and distribution than the present ones (Nienburg 1927; Reise et al. 1989). In the 1930s (1932–1936) these seagrass beds were damaged by the parasitic slime mould *Labyrinthula*, which caused the wasting phenomenon (Wohlenberg 1935; den Hartog, 1987). In concert with unfavourable environmental conditions (e.g. increasing eutrophication, turbidity and erosion of areas in a suitable depth for seagrass growth), the subtidal stocks of seagrasses did not recover until recently. The loss of subtidal seagrasses must have led to dramatic changes in the ecosystem. In contrast to the intertidal seagrass beds, subtidal seagrass beds have a rich and specialised fauna (Orth et al. 1984; Zieman and Zieman 1989), and a loss of this community may have had a stronger impact on species diversity of the total system compared to a possible loss of intertidal seagrass beds. The loss of spawning grounds for herring *Clupea harengus* (Wohlenberg 1935) and the loss of sea sticklebacks *Spinachia spinachia* and the deep-snouted pipefish *Siphonostoma typhle* are only a few examples of losses reported from the Wadden Sea area.

In the tidal gullies the dense mat of rhizomes within the sediment may have counteracted erosion and, therefore, immediately after the loss of only one subtidal seagrass bed (about 80 ha) in Königshafen at least 40,000 m^3 of sediments were eroded (Wohlenberg 1935). Because of the important role seagrasses play in the material budget of the ambient ecosystem, it is possible to formulate the hypothesis that in historical times the loss of seagrasses may have led to fundamental changes in the material budget and has probably promoted the erosion of sediments in the whole of the Wadden Sea (Jespersen and Rasmussen 1994).

In the shallowest part of the subtidal area of the Sylt-Rømø Bight from low spring tide line to 5 m depth, changes of water volume show an increasing trend. This means that the shallow subtidal part has been extended over the last 100 years with a concomitant decline of the area (Higelke 1998). In the parts deeper than 5 m below low spring tide level, there is no significant trend. The period with low water volumes in the shallow subtidal areas (from 1879 to 1935) can be distinguished from the period after 1950 with high water volumes. In the period 1935–1950, a dramatic increase in water volumes was observed, which may indicate that in this time period a large amount of sediments has been eroded and tidal flats have probably been lost. This period is also characterised by substantial changes in the ecosystem (Reise 1982, 1998; Riesen and Reise 1982; Reise et al. 1989; Asmus H and Asmus R 1998). The hypothesis of a causal connection between the loss of seagrass beds and an increasing water volume in the tidal gullies due to erosion could not be verified or disproved until now. How-

ever, other possible causes of erosion in the Sylt-Rømø Bay may be the construction of the causeways from the mainland to the islands or the documented increase in tidal range.

Conclusions

Intertidal communities of the Sylt-Rømø Bight act as a particle sink and a nutrient source. Seagrass beds play a major role as important particle sinks which are significant also at the ecosystem level. The extinction of seagrass beds will lead to changes in the material budget of the total ecosystem. It will additionally affect the food web. The loss of subtidal seagrass beds in the past may have been accompanied by fundamental changes in the material budget of the total system and may have promoted erosion of the shallow subtidal areas. Historical changes in macrobenthic communities of the Sylt-Rømø Bight are correlated with changing water masses and building activities, but it is not known whether there is a causal connection. The example of the history of seagrass beds in the Wadden Sea may show that changes in single communities may have induced changes which are visible at the ecosystem level. It also illustrates that we urgently need further large-scale ecosystem analyses combined with thorough historical research in order to understand the fate of our coastal ecosystems.

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