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## Effects of herbivorous birds on intertidal seagrass beds in the northern Wadden Sea

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**Abstract** During autumn migration (September to December), brent geese (*Branta b. bernicla*) and wigeon (*Anas penelope*) feed on the seagrass *Zostera noltii* in the nearshore, upper tidal zone leeward of the island of Sylt (eastern North Sea). To graze on leaves and shoots above the sediment and on rhizomes and roots below, these birds reworked the entire upper 1 cm layer of sediment eight times within this 3-month period. In addition, brent geese excavated pits 3–10 cm deep by trampling in order to feed on below-ground phytomass. About 12% of the seagrass beds became pitted to an average depth of 4.5 cm. Using net enclosures, it was estimated that birds removed 34 g dry weight m<sup>-2</sup> of above-ground and 28 g of below-ground phytomass. This corresponds to 45% of the phytomass in September. Of the overall loss of phytomass from September to December, 63% was caused by birds. Roughly half of the leaves fell off anyway until December and the other half were taken by the birds. Below the ground, phytomass remained almost constant where birds were excluded, while with birds phytomass of rhizomes and roots was halved. In spite of this strong effect, in the next vegetation period the blade density was lower at former enclosure sites compared to the ambient seagrass bed. The underlying process seems to be a self-inhibition of dense overwintering seagrass by mud accretion. Assuming our experimental results can be scaled up to the entire seagrass bed, we hypothesize that in the sheltered upper intertidal zone, seasonal erosion caused by herbivorous geese and ducks is necessary for the persistence of *Z. noltii*.

**Key words** Seagrass · Herbivorous birds · Grazing · Bioturbation · *Zostera noltii*

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### Introduction

In autumn, large numbers of dark bellied brent geese (*Branta bernicla bernicla* L.) and wigeon (*Anas penelope* L.) rest in the Wadden Sea to build up their body reserves for the winter. From September to December, the intertidal seagrasses *Zostera noltii* Hornem and *Z. marina* L. are their main food source (Madsen 1988; Meltofte et al. 1994). Both brent geese and wigeon rework the sediment by grubbing and pecking for seagrass plants with their beaks (Jacobs et al. 1981; Madsen 1988). In addition, to graze on the rhizomes and roots of the seagrass, brent geese create trampling pits by paddling in the sediment submerged under 5–10 cm of water. Collectively, these species cause considerable biogenic sediment reworking (bioturbation), simultaneously dislodging rhizomes and roots of the seagrass.

In the southern Wadden Sea, a dramatic decrease of intertidal *Zostera* beds has occurred since the 1960s/1970s (den Hartog and Polderman 1975; de Jonge et al. 1993; Kastler and Michaelis 1997). The cause of this decline is still under discussion and there seem to be several factors involved, i.e. light limitation, indirect effects of anthropogenic eutrophication and physical disturbances by the cockle fishery (Giesen et al. 1990; de Jonge and de Jong 1992; Philippart 1994, 1995a,b). Seagrass beds have also been shown to be strongly affected by different kinds of bioturbation. In shallow tropical lagoons, the burrowing shrimp *Callinassa* spp. negatively influences the seagrass *Thalassia testudinum* (Suchanek 1983). Philippart (1994) demonstrated that bioturbation by lugworms (*Arenicola marina*) severely affects density and biomass of *Z. noltii* on tidal flats of the Dutch Wadden Sea. Bioturbation pits in mixed *Z. marina* and *Halodule wrightii* beds in North Carolina are considered to impair the growth of seagrass bed margins and cause a fragmented pattern of seagrass cover (Townsend and Fonseca 1998). Orth (1975) documented the total extinction of a *Z. marina* bed in the Chesapeake Bay by the pit-creating activities of the cownose ray *Rhinoptera bonasus*.

Increases in the number of wintering brent geese and wigeon in the Wadden Sea since the 1980s (Poot et al. 1996) raise the question, whether a potential negative effect of bioturbation and grazing by these birds on the seagrass may also contribute to the general decline of intertidal *Zostera* beds in the Wadden Sea. The aim of this study was to (1) assess the extent of bioturbation by brent geese and wigeon during their autumn stay in the *Z. noltii* beds near the island of Sylt, (2) quantify the seagrass consumption by these wildfowl during this period, using bird enclosure cages, (3) evaluate the effect of brent geese and wigeon on seagrass density by revisiting former enclosure sites in the following summer.

## Materials and methods

### Study site

The study was conducted on the tidal flats of the north-eastern side of the island of Sylt (North Sea). This area is part of the Sylt-Rømø tidal basin in the northern Wadden Sea. With 15.6 km<sup>2</sup> or 12% of the tidal flats, this basin has a relatively high share of seagrass beds in comparison to the more southern Wadden Sea, but otherwise the composition of the benthos is rather similar (Reise and Lackschewitz 1998). These seagrass beds are restricted to the intertidal zone. Former subtidal stands were extinguished by the so-called wasting disease in the 1930s.

The seagrass beds of the study area consist of several small beds in Königshafen and one larger area north of the village of Kampen (Fig. 1). Except for one small *Z. marina* stand in the

western part of Königshafen, they were pure *Z. noltii* stocks on sand and muddy sand. Due to their position leeward of the island of Sylt, these seagrass beds are sheltered from onshore winds and surf. The seagrass beds emerge for 4–6 h in a semi-diurnal tidal cycle with an average amplitude of 1.8 m. Salinity is close to 30‰. A general description of the Sylt-Rømø Wadden Sea and its biota is given in Reise and Lackschewitz (1998). For more detailed information about benthos and sediments of Königshafen see Reise (1985) and Austen (1992).

### Field observations

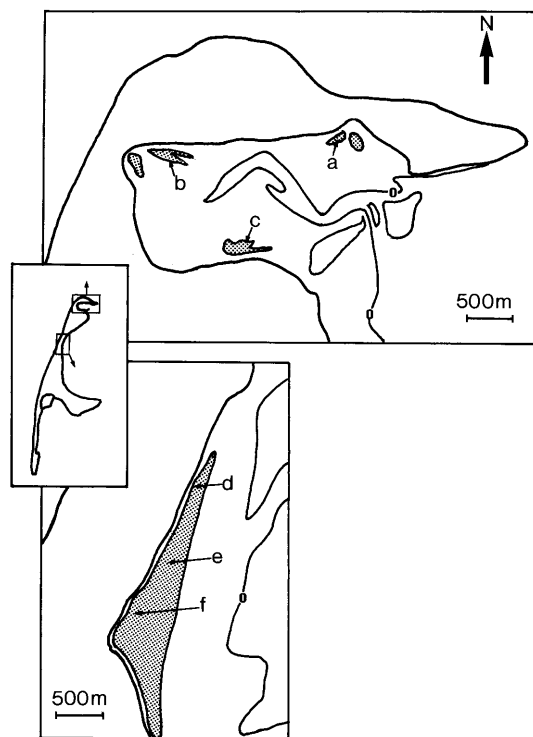
Feeding traces of brent geese and wigeon were separated into (1) pits caused by trampling of the geese and (2) surficially reworked patches caused by both brent geese and wigeon when pecking for leaves and searching for below-ground parts of the seagrass with their beaks. The trampling and digging intensity of birds was assessed by counting the number and measuring the size and depth of pits and the surficially reworked patches in six plots of 10×60 m about every 2 weeks from 25 September to 4 December 1997. These areas were spread over the seagrass beds (*Z. noltii*) along the north-eastern shore of Sylt (Fig. 1, sites a–f). When pit density was very high, counts were restricted to 10 randomly chosen subareas of 10 m<sup>2</sup> within the 10×60 m plots. Mean diameter and mean depth of newly created brent goose pits were determined by measuring 100 pits. The formation of these pits immediately prior to the measurements was directly observed in the field.

At most counts in the 10×60 m plots, pits were already partly levelled by the tidal currents. They were only counted and measured when ≥2 cm deep and had a clearly visible outline. Since the pit diameter decreased only slightly during the sediment refilling process (Table 1), the volume of reworked sediment by pit formation could be evaluated using the mean diameter of all pits per count and the average depth of newly created pits (4.5 cm). Calculations of pit volumina were made using the formula for the volume of spherical segments:

$$V = (\pi h/6) \times (3d^2/4 + h^2)$$

where  $d$  = mean diameter of pits per count;  $h$  = mean depth of newly created pits.

Measurements of pits with an oval shape were converted into circular diameters and then treated as above. The amount of surficially reworked sediment by digging without leaving holes was determined by conservatively assuming a digging depth of 1 cm. The black, anoxic sediment at the surface of surficially reworked patches indicated that the digging reached at least into the depth of the sulfide-horizon, which was below 0.5–2.5 cm in the *Z. noltii* beds at the study site. Surficial reworking of sediment also occurred inside pits, when birds grazed in already existing excavations. This additional bioturbation of pits could not be included into the above calculation, because it was not always possible to dis-



**Fig. 1** Intertidal seagrass beds (shading) on the leeward side of northern Sylt, aerial survey in September 1997; 10×60 m plots for surveys of brent goose and wigeon feeding traces (a–f). Site of bird enclosure experiment (f)

**Table 1** Changes in the dimensions (cm) of individually marked brent goose pits during their refilling with sediment. Different plots were observed during different time periods. Values are means of pit diameter/pit depth ( $n=6$ )

Days	Site f	Site b	Site b	Site c
0	34.2/4.0	30.2/4.3	30.2/6.5	37.5/4.5
1	34.2/4.0	30.2/4.3	29.8/4.7	–
2	32.3/3.3	–	27.7/4.5	39.3/4.3
3	32.8/2.5	30.5/4.0	–	–
4	Not visible	–	Not visible	39.5/3.8
6	–	30.0/3.2	–	38.0/3.8
8	–	–	–	39.8/3.7
10	–	Not visible	–	39.3/3.2
12	–	–	–	33.3/2.0
13	–	–	–	Not visible

tinguish between newly excavated pits and those that were reworked subsequently.

Since brent goose pits were recognizable for an average period of 7 days (see Table 1) and counts were carried out every 2 weeks, approximately half of the feeding pits could be recorded. Therefore, to estimate the area covered by pits throughout the whole grazing period, the measurements of counted pits were summarized and doubled. The superficially reworked patches vanished during each following tide. Thus, the total amount of replaced sediment was estimated by scaling up the observed digging traces to the number of tides (134) during the investigation period. The depth below sediment surface at which the sediment turned black was measured within pits 29 and 56 tides after their first appearance and compared with six undisturbed plots.

#### Bird enclosure experiment

The enclosure experiment was carried out on a dense and uniformly vegetated part of the seagrass bed close to site f (see Fig. 1). Enclosures were set up on 19 September 1997, prior to the arrival of the geese and ducks at the study site, and removed on 8 December, when most of the birds had already left, and the above-ground parts of *Z. noltii* were almost depleted.

Experimental exclusion of birds was achieved with cages, which covered an area of 1.6×1.6 m with a 15 mm meshed nylon net at 0.35 m height (Fig. 2). Six cages were arranged in two rows, alternating with control plots. Inter-cage distances were 20 m, which did not prevent the birds from grazing between the enclosures. The experimental site was visited weekly to clean the cages of drifting algae and seagrass material. The seagrass biomass was determined by taking samples of 100 cm<sup>2</sup> surface area and 15 cm depth in September and December. Within each enclosure and each control plot, one sample was taken at random. In the laboratory, the sediment was gently washed off over a 1.5-mm mesh and



**Fig. 2** Bird enclosure during low tide in September when most of the sediment was overgrown by seagrass

shoots and leaves were separated from rhizomes and roots. Samples were dried for 48 h at 85°C and weighed.

In August 1998, the former enclosure sites and control plots were revisited and mapped. Within the plots the cover of *Z. noltii* was estimated for every 20×20 cm square, using three categories of leaf cover: <30%, 30–60% and >60%.

## Results

### Field observations on bird bioturbation

Observations during this study confirmed that only brent geese create pits in the seagrass bed by trampling. Both brent geese and wigeon were grazing in the shallow water at ebbing tide. The latter were pecking and grubbing for seagrass plants with their beaks and showed no trampling like the geese. When the seagrass bed emerged, trampling stopped, but existing pits were often visited by both species. Birds were standing in the pits and grazed at the edges of these depressions. This indicates that wigeon can use the geese pits subsequently to get a better access to the below-ground parts of the seagrass.

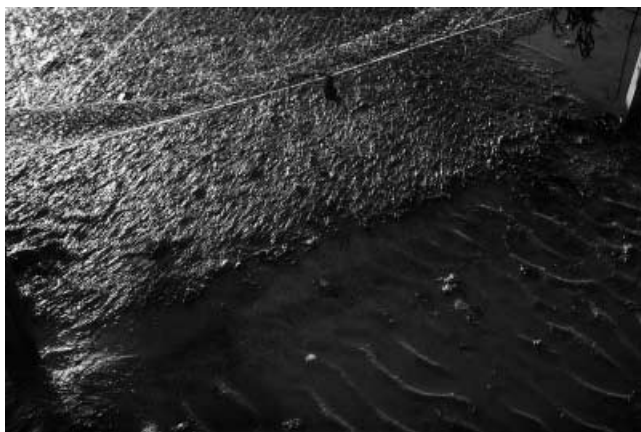
The mean circular diameter of newly created brent goose pits was 31 cm with a range from 15 to 56 cm ( $n=100$ ). Newly excavated pit depth was 3–10 cm (average: 4.5 cm;  $n=100$ ). Circular diameters of superficially dug-up patches ranged between 5 and 56 cm. Feeding traces of brent geese and wigeon turned out to be very patchy between the six plots at most counts. There were always some plots with no feeding traces at all.

Peak numbers of pits occurred in October, with a maximum of 59 pits per 100 m<sup>2</sup> on 23 October (Table 2). These pits covered 3.2% of the seagrass beds. The volume of reworked sediment at this date amounted 75.8 dm<sup>3</sup> per 100 m<sup>2</sup>. The highest local pit density observed during the whole study was 420 per 100 m<sup>2</sup> (22 October, close to site f). This corresponds to 23% of the area covered by pits (pits were relatively small), and a volume of reworked sediment of 550 dm<sup>3</sup> per 100 m<sup>2</sup>. During the entire autumn grazing period, roughly 12% of the seagrass beds became pitted by trampling holes of brent geese. The total volume of reworked sediment was 342.4 dm<sup>3</sup> per 100 m<sup>2</sup>.

Newly created pits were visible for an average duration of 7 days. After 4–13 days, they were level with the surrounding sediment (Table 1). This high temporal variability was apparently related to different levels of wave

**Table 2** Brent goose and wigeon bioturbation in six plots of 600 m<sup>2</sup> spread over seagrass beds at the leeward side of Sylt. Plots were mapped about every 2 weeks from 25 September to 4 December 1997

	25 Sept	15 Oct	23 Oct	8 Nov	22 Nov	4 Dec
Mean number of pits per 100 m <sup>2</sup>	6.5	21.8	59.3	1.4	13.1	1.8
Percentage of the area covered by pits	0.3	1.4	3.2	0.07	0.8	0.1
Mean volume of reworked sediment (dm <sup>3</sup> /100 m <sup>2</sup> )	6.5	33.0	75.8	1.7	19.1	2.6
Mean number of superficially reworked patches per 100 m <sup>2</sup>	242.6	23.8	19.5	16.8	2.3	0
Percentage of the area covered by superficially reworked patches	5.2	0.5	0.5	0.2	0.04	0
Mean volume of superficially re-worked sediment (dm <sup>3</sup> /100 m <sup>2</sup> )	5.2	0.5	0.5	0.2	0.04	0



**Fig. 3** Caged area with a dense cover of seagrass and adjacent bare and rippled sediment in December 1997, at the end of the experiment

action. Pit diameters remained almost constant during the refilling time. Occasionally, pits were even enlarged subsequently. This may be due to sediment erosion at pit margins or additional bioturbation. The latter has been investigated by marking pits at different sites and different times, indicating that between 0 and 47% of previously marked pits were revisited by the birds during one tide. There were no significant differences in pit diameters between sites.

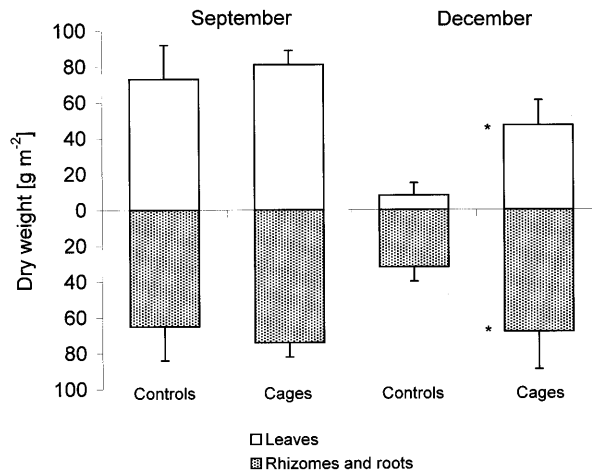
The trampling of brent geese caused a significant lowering of the black oxygen-deficient horizon. Fifteen days after the pits were formed, the mean depth of the reduced sediment layer was  $4.33 \pm 0.61$  cm at former pit sites and  $1.58 \pm 0.38$  cm in undisturbed sediments (Mann and Whitney U-test:  $P < 0.01$ ). After 29 days it was still  $2.83 \pm 0.68$  and  $1.92 \pm 0.38$  cm, respectively, but no longer significantly different.

Surficially reworked patches from brent geese and wigeon were most frequent just after wigeons and brent geese had arrived on 24 September and decreased during the autumn months (Table 2). On 25 September, the highest digging activity was found with 30% of the area covered by surficially reworked patches (site f). During the entire period, the seagrass beds were bioturbated eight times by means of these digging traces.

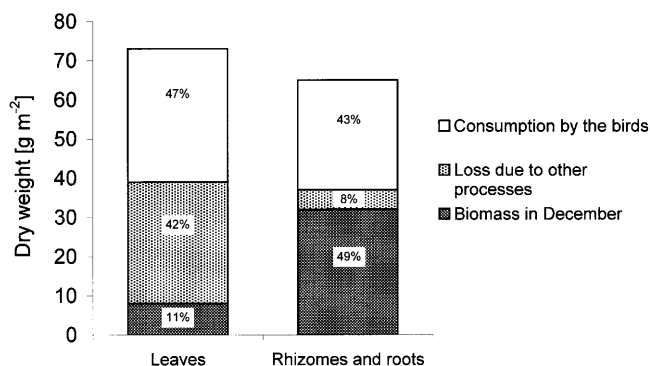
#### Enclosure experiment

In December 1997, when the enclosure experiment was finished, coverage by *Z. noltii* at the site was less than 1%. Fine sediments were washed away by the tidal currents, and sand-ripples had formed. The still densely vegetated caged plots and the ambient flat were separated by a sharp boundary (Fig. 3).

The average total phytomass of *Z. noltii* within control plots decreased between 19 September and 8 December from  $138$  to  $40$  g dry weight  $m^{-2}$  (Fig. 4). Assuming that differences in phytomass between control and caged plots are entirely due to bird grazing, the brent

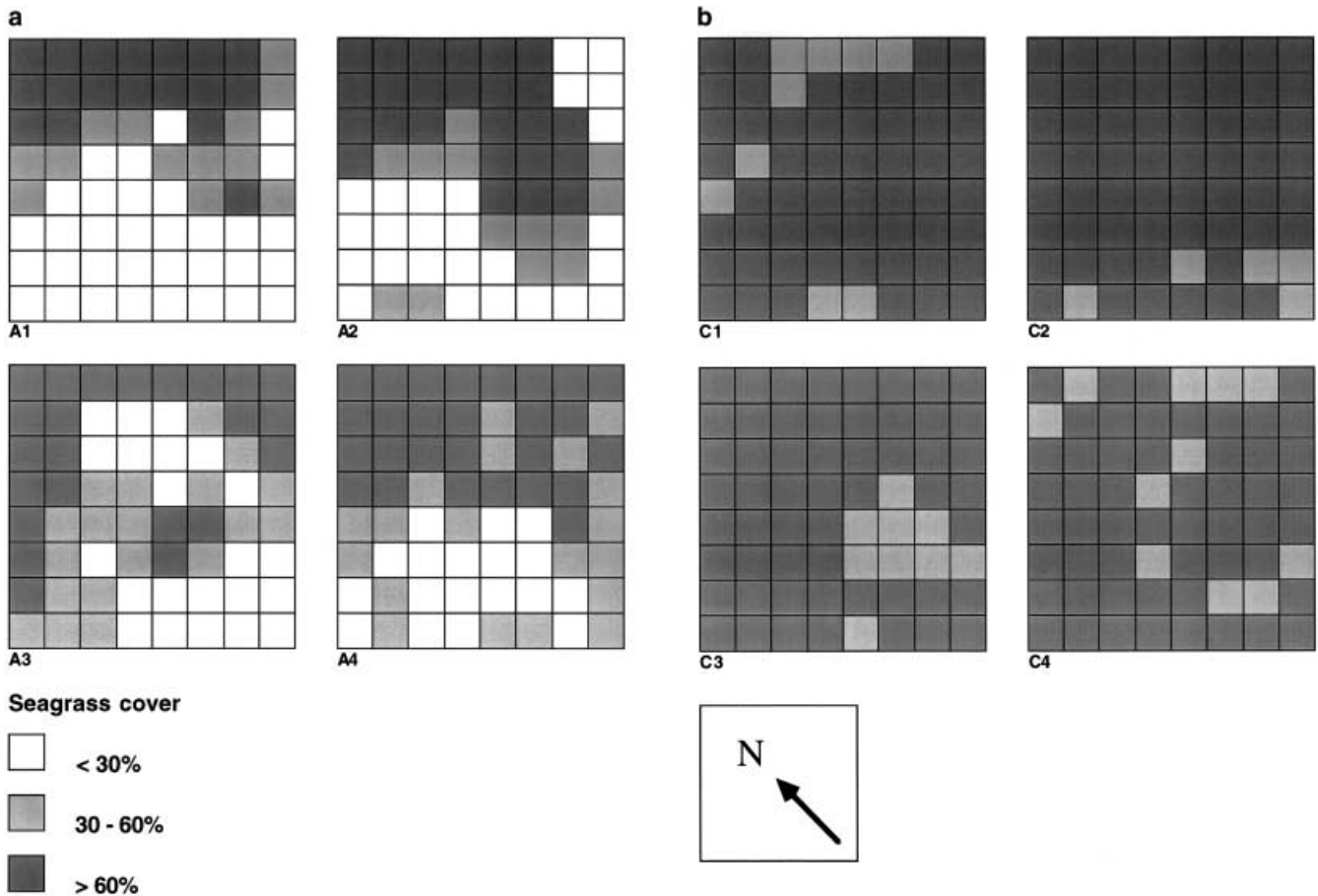


**Fig. 4** Biomass of *Z. noltii* leaves (open bars) and rhizomes/roots (shaded bars) prior to the impact of brent geese and wigeon (September) and after their grazing period (December). Significant differences between controls and cages are marked with asterisks (Mann-Whitney U-test,  $P < 0.05$ ;  $n = 6$ )



**Fig. 5** Above-ground (leaves) and below-ground (rhizomes and roots) biomass of *Z. noltii* in September 1997. Losses during autumn due to consumption by birds (open) and other processes (light shading) and the remaining biomass in December (dark shading) are given as percentages

geese and wigeon consumed  $62$  g dry weight  $m^{-2}$ . This amounts to 63% of the total loss of  $98$  g  $m^{-2}$  of phytomass, or to 45% of the standing stock in September removed by the birds from September until December. Losses of phytomass above- and below-ground differed substantially. Little of the shoots and leaves survived, while about half of the rhizomes and roots persisted. From September to December a loss of 89% occurred above and 51% below the ground on the control plots. Within the cages, however, only 42% of the above-ground and only 8% of the below-ground phytomass was lost (Fig. 4). From these differential losses we calculate that  $34$  g  $m^{-2}$  of shoots and leaves and  $28$  g  $m^{-2}$  of rhizomes and roots were consumed by the birds. Thus, the diet of the birds consisted for about 55% of above-ground and 45% of below-ground phytomass. Although these shares are rather similar, the survival of plant parts above and below the ground was very different (Fig. 5).



**Fig. 6** Seagrass cover at **a** former enclosure plots (A1–4) and **b** controls (C1–4). Grid size 20 cm, mapped 21 August 1998

Nearly half of the stems and leaves were grazed and nearly half was subject to natural die-off or mechanical break-off by waves and currents, leaving only one tenth of the above-ground plant material present in September to persist until December. Birds had a share of 52% in this 2-months loss of above-ground phytomass. In contrast, below the ground, half of the plant material persisted until December. Most of the loss within the 2 months was caused by the birds (85%).

During the following winter, the seagrass leaves at former enclosure plots also fell off, but the areas remained distinguishable from the surrounding flat as slight elevations. In the following vegetation period, seagrass growth at these sites was less than in the ambient seagrass bed. In August 1998, there was still a clearly visible difference in seagrass cover between former caged and control plots (Fig. 6). At the northern edge of each mapped enclosure plot, however, seagrass density was high.

## Discussion

The patchy occurrence of brent goose and wigeon feeding traces reflects the grazing behaviour of the birds.

Both species are known to graze in flocks (Bergmann et al. 1994; Brunckhorst 1996), and they frequently changed their feeding ground during the study period. This led to an equal exploitation of all *Z. noltii* beds during the autumn months. Most of the time, brent geese and wigeon were grazing in mixed flocks. For the wigeon, this provides the opportunity to profit from the trampling activity of the geese, using their pits to get easier access to the rhizomes and roots of the seagrass. Observations by Fog (1967) indicate that brent geese prefer feeding on *Zostera* in pools, where leaves are floating in water, even if the density of seagrass is higher at surrounding elevations. Possibly, the advantage in creating pits is not only to facilitate the access to below-ground parts of the seagrass, but also to be able to wash off sediment from plant material during low tide.

## Bioturbation

From September to December, a share of 12% of the seagrass beds became pitted by trampling brent geese. This is roughly in the same range as the annual area covered by trampling pits of black-headed gulls (30%) and shelducks (15%) on a tidal flat near the island of Texel in the southern Wadden Sea (Cadée 1990). This author estimated the bioturbation by gulls and shelducks to equal a sediment layer of about 1.0 cm and 1.5 cm per year, re-

spectively. Using percent cover and mean depth of pits for calculations, as Cadée (1990) did, our studies reveal a reworked sediment layer caused by brent geese of 0.5 cm. This leads to an overestimation of the amount of bioturbated sediment, since at least brent goose and shelduck pits have an approximate semi-spherical or conical shape. Estimations based on the volumina of spherical segments, as used in this study, resulted in a sediment layer reworked by means of brent goose pits only 0.3 cm thick. However, since the pit creating activity of brent geese is restricted to 2–3 months of the year, brent goose bioturbation intensity in these months is several times higher than that of gulls and shelducks all the year round, whereas during the rest of the year it is almost zero.

The surficially reworked patches of brent geese and wigeon may be quantitatively much more important than the conspicuous pits. During the investigation period, the seagrass beds studied were covered eight times by these shallow bioturbated patches. With a depth of surficially reworked patches of roughly 1 cm this equals a displaced sediment layer of 8 cm in about 2 months. This estimate may be too high, because nocturnal low tides were included in the extrapolations, and it is not certain whether brent geese also grazed at night time. Jacobs et al. (1981) observed that these geese left their feeding grounds at dusk, while Madsen (1988) gives a nightly share of brent geese feeding activity of 43%. On the other hand, wigeon prefer nocturnal feeding (Brunckhorst 1996). Thus our estimations seem to provide a good approximation. However, the fact that subsequent reworking of already existing pits was not included into our calculations, and that digging depth probably exceeded 1 cm very often, could have led to an underestimation of the total amount of bioturbation by geese and ducks.

Cadée (1976, 1979) measured the annual sediment reworking rates of the deposit-feeding polychaetes *Arenicola marina* and *Heteromastus filiformis* and the deposit-feeding bivalve *Macoma balthica*, which collectively reworked a sediment layer of 35 cm annually. Accordingly, bioturbation by gulls and shelducks (2.5 cm annually) appears to be less important than sediment reworking by these deposit-feeding infauna. In the seagrass bed, both rates may be of a similar magnitude. Based on data from Cadée (1976, 1979), we calculated that the amount of bioturbated sediment by *A. marina* and *M. balthica* (*H. filiformis* was not present) in our study area was 8 cm annually, the same amount as calculated for surficial digging by geese and ducks. With respect to the 2 months in autumn when geese and ducks were present, the reworking rates of deposit-feeders and wildfowl were in the ratio 1:6. However, it should be noted that the depth of bioturbation when excavating pits or cycling sediment through lugworm burrows may have more effects on the sediment biota than just overturning the upper 1-cm layer.

On an unvegetated sandflat, bioturbation by dasyatid rays amounted to <1% of the sediment movement due to

tidal bedload transport (Grant 1983). During the summer maximum of ray disturbance, ray feeding pits covered roughly 30% of the area. This is in the same order of magnitude as the maximum cover of brent goose pits (23%) and wigeon feeding traces (30%) at our study site. In comparison to bare sand, seagrass beds represent relatively stable sediment conditions (Orth 1977; Reise 1985). Therefore, bioturbation by birds in this habitat is likely to play a more important role in relation to hydrodynamically induced sediment movement than does the above-mentioned ray disturbance on unvegetated sand.

Due to the high sediment stability in seagrass beds, oxygen transport into the sediment is low. Feeding on *Zostera*, brent geese and wigeon transport anoxic sediment to the surface, where it becomes oxidized during the following tide. For at least 15 days, a significantly deeper oxygen-deficient horizon was detected at former pit sites. This suggests that, particularly in seagrass habitats, bioturbation by birds is of high qualitative importance and contributes to an enhanced exchange of substances at the sediment–water interface as already proposed by Thiel (1981).

### Grazing

During the autumn grazing period of brent geese and wigeon in the seagrass beds, these birds consumed approximately 45% of the total *Z. noltii* phytomass in September. This estimate agrees with the estimates of Jacobs et al. (1981), who calculated from bird weight, standard metabolism and bird days, that the seagrass consuming geese and ducks at Terschelling in the southern Wadden Sea removed roughly 50% of the total maximum standing stock of *Z. noltii* from September to December. From our estimates, 55% of the seagrass material consumed by the birds was leaves and 45% consisted of rhizomes and roots. This result stresses the significance of the below-ground parts of the seagrass in the autumn diet of brent geese and wigeon and shows the importance of sediment reworking in the search for food by these birds.

Although the netting consisted of a very thin thread and a relatively wide mesh, possible cage-artifacts cannot be ruled out. If net enclosures had a current-reducing effect, the above-ground seagrass biomass inside cages could be biased upwards. Consequently, the estimated share of below-ground parts of *Z. noltii* consumed by the birds would be even higher than 45%. On the other hand, reduced loss of above-ground phytomass might entail higher survival of below-ground biomass (see Hemminga 1998). If that was the case, we overestimated the consumption of below-ground parts by the birds. Campbell (1946, cited in Charman 1977) determined from examinations of stomach contents of shot specimens, that brent geese feed on above- and below-ground parts of *Zostera* equally, whereas wigeon prefer the leaves of the seagrass. A preference for leaves in both species (between 58 and 91% for brent geese and 92 and 98% for wigeon)

is mentioned by Madsen (1988), who examined the droppings of the birds microscopically. Since numbers of wigeon at our study site were 3.4-fold higher than numbers of brent geese (own counts during the investigation period), and approximately half of the consumed seagrass material was rhizomes and roots, these results cannot be supported by the present study.

#### The year after

Exclosures were removed from the experimental plot in December 1997 because the birds had left the area. The high leaf cover underneath cages vanished until February/March 1998. In August 1998, slight elevations of sediment with low seagrass cover remained at former exclosure plots, although the density and homogeneity of the ambient seagrass bed were similar to the year before. Sediment stabilization at former exclosure plots was probably afforded by a prolonged period of leaf cover and by the dense root–rhizome system, that had been halved in the ambient seagrass bed by geese and ducks. The mechanisms leading to the reduced seagrass cover at patches without grazing were not investigated. Jacobs et al. (1981) speculate that the absence of the thinning out of roots and rhizomes by birds leads to higher intraspecific competition and thereby negatively influences seagrass growth. Other factors, such as changes in sediment chemistry (e. g. sulphide and nitrogen content) or burial of the rhizomes due to the absence of bioturbation and erosion, need to be investigated. Whatever the exact mechanism, the underlying process seems to be a self-inhibition of dense overwintering seagrass by mud accretion in a sheltered position. At our former exclosure plots, a high coverage of seagrass at the northern edge of each experimental plot is assumed to be an artifact caused by the small size of the elevated patches and their exposure to the prevailing hydrodynamic forces.

Due to the mild temperatures in winter 1997/98, our experimental results were not distorted by erosion owing to ice scour. Therefore, the effect by herbivorous birds on the *Z. noltii* beds seems to be responsible for maintaining the balance between silt accumulation during summer and erosion of sediment in autumn and winter. Jacobs et al. (1981) assume that without this effect, a raising of the seagrass beds above high-water level could, in the long run, lead to a decline in the seagrass. It is uncertain whether our experimental results can be extrapolated to the entire seagrass bed. However, our results imply that, even on an annual basis, bioturbation and grazing by geese and ducks is necessary for the persistence of *Z. noltii* where it grows under sheltered conditions such as on the leeward side of Sylt.

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#### References

- Austen I (1992) Geologisch-Sedimentologische Kartierung des Königshafens (List/Sylt). *Meyniana* 44: 45–52
- Bergmann HH, Stock M, Thoren B ten (1994) Ringelgänse. Ark-tische Gäste an unseren Küsten. Aula Verlag, Wiesbaden
- Brunckhorst H (1996) Ökologie und Energetik der Pfeifente (*Anas penelope* L. 1758) im Schleswig-Holsteinischen Wattenmeer. Dissertation, Universität Hamburg
- Cadée GC (1976) Sediment reworking by *Arenicola marina* on tidal flats in the Dutch Wadden Sea. *Neth J Sea Res* 10: 440–460
- Cadée GC (1979) Sediment reworking by the polychaete *Heteromastus filiformis* on a tidal flat in the Dutch Wadden Sea. *Neth J Sea Res* 13: 441–456
- Cadée GC (1990) Feeding traces and bioturbation by birds on a tidal flat, Dutch Wadden Sea. *Ichnos* 1:23–30.
- Charman K (1977) The grazing of *Zostera* by wildfowl in Britain. *Aquaculture* 12:229–233
- Fog M (1967) An investigation on the Brent Goose (*Branta bernicla*) in Denmark. *Dan Rev Game Biol* 5(1):3–40
- Giesen WB, Katwijk MM van, Hartog C den (1990) Eelgrass condition and turbidity in the Dutch Wadden Sea. *Aquat Bot* 37:71–85
- Grant J (1983) The relative magnitude of biological and physical sediment reworking in an intertidal community. *J Mar Res* 41: 73–689
- Hartog C den, Polderman PJG (1975) Changes in the seagrass populations of the Dutch Waddenzee. *Aquat Bot* 1:141–147
- Hemminga MA (1998) The root/rhizome system of seagrass: an asset and a burden. *J Sea Res* 39:183–196
- Jacobs RPWM, Hartog C den, Braster BF, Carriere FC (1981) Grazing of the seagrass *Zostera noltii* by birds at Terschelling (Dutch Wadden Sea). *Aquat Bot* 10:241–259
- Jonge VN de, de Jong DJ (1992) Role of tide, light and fisheries in the decline of *Zostera marina* L. in the Dutch Wadden Sea. *Neth Inst Sea Res Publ Ser* 20:161–176
- Jonge VN de, Essink K, Boddeke R (1993) The Dutch Wadden Sea: a changed ecosystem. *Hydrobiologia* 265: 45–71
- Kastler T, Michaelis H (1997) Der Rückgang der Seegrassbestände im niedersächsischen Wattenmeer. Niedersächsisches Landesamt für Ökologie, Forschungsstelle Küste, Norderney
- Madsen J (1988) Autumn feeding ecology of herbivorous wildfowl in the Danish Wadden Sea, and impact of food supplies and shooting on movements. *Dan Rev Game Biol* 13(4):1–32
- Meltofte H, Blew J, Frikke J, Rösner HU, Smit CJ (1994) Numbers and distribution of waterbirds in the Wadden Sea. IWRB Publication 34, Wader Study Group Bulletin 74 special issue. Wilhelmshaven
- Orth RJ (1975) Destruction of eelgrass, *Zostera marina*, by the cownose ray, *Rhinoptera bonasus*, in the Chesapeake Bay. *Chesapeake Sci* 16: 205–208
- Orth RJ (1977) The importance of sediment stability in seagrass communities. In: Coull BC (ed) *Ecology of marine benthos*. University of South Carolina Press, Columbia, pp 281–300
- Philippart CJM (1994) Interactions between *Arenicola marina* and *Zostera noltii* on a tidal flat in the Wadden Sea. *Mar Ecol Prog Ser* 111:251–257
- Philippart CJM (1995a) Effects of shading on growth, biomass and population maintenance of the intertidal seagrass *Zostera noltii* Hornem. in the Dutch Wadden Sea. *J Exp Mar Biol Ecol* 188:199–213
- Philippart CJM (1995b) Effect of periphyton grazing by *Hydrobia ulvae* on the growth of *Zostera noltii* on a tidal flat in the Dutch Wadden Sea. *Mar Biol* 122:431–437

- Poot M, Rasmussen LM, Roomen M van, Rösner HU, Südbeck P (1996) Migratory waterbirds in the Wadden Sea 1993/94. Wadden Sea Ecosystem 5. Common Wadden Sea Secretariat, Wilhelmshaven
- Reise K (1985) Tidal flat ecology. (Ecological studies, vol 54) Springer, Berlin Heidelberg New York
- Reise K, Lackschewitz D (1998) Benthos des Wattenmeeres zwischen Sylt und Rømø. In: Gätje C, Reise K (eds) Ökosystem Wattenmeer- Austausch-, Transport- und Stoffumwandlungsprozesse. Springer, Berlin Heidelberg New York, pp 55–64
- Suchanek TH (1983) Control of seagrass communities and sediment distribution by *Callianassa* (Crustacea, Thalassinidea) bioturbation. J Mar Res 41:281–298
- Thiel H (1981) Aviturbation – eine Hypothese oder die Ramsar Konvention von 1971 zum Schutze der menschlichen Umwelt. Seevögel 2: 69–74
- Townsend EC, Fonseca MS (1998) Bioturbation as a potential mechanism influencing spatial heterogeneity of North Carolina seagrass beds. Mar Ecol Prog Ser 169:123–132