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Long-term changes of salt marsh communities by cattle grazing

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Abstract

Over a period of 9 years a grazing experiment was carried out in the mainland salt marsh of the Leybucht (Niedersachsen) with three stocking rates, namely, 0.5 ha^{-1}, 1 ha^{-1}, and 2 cattle ha^{-1}. These were also compared with an abandoned area. The results are based on sampling of the invertebrates in 1980, 1981, 1982, and 1988, and of the vegetation in 1980 and 1988. The rate of sedimentation is highest in the *Puccinellia maritima*-zone and decreases with the increase of stocking rates. The *Elymus pycnanthus* vegetation type becomes dominant in the higher salt marsh in the abandoned site. The canopy height decreases with increasing stocking rate, whereas a gradient in the structure of the vegetation develops with the lowest stocking rate. The population densities, the species-richness and the community diversity of invertebrates increases after the cessation of grazing. The high rate of sedimentation in the abandoned site promotes the immigration of species from higher salt marsh levels and adjacent grasslands, and eventually halotopophilous species and communities may disappear. On the other hand grazing reduces numerous species living both in or on upper parts of the vegetation or being sensitive to trampling by cattle. The community structure shows that the salt marsh ecosystem changed from a food web dominated by plant feeding animals to a food web dominated by animals foraging on detritus. The salt marsh management has to be differentiated into both ungrazed and lightly grazed areas (each 50%) or an overall grazing in large areas with less than 0.5 cattle ha^{-1}.

Nomenclature: Plant species according to Van Der Meijden *et al.* 1983. Flora van Nederland. Groningen. Spider species according to Wiehle (1960), Locket *et al.* (1951–1974) and Roberts (1985–1987); beetle species according to Freude *et al.* (1964–1983).

Introduction

The undisturbed succession of salt marsh communities is governed by the tidal inundation frequency and sedimentation. Human interference is superimposed on these natural processes. Salt marshes have been grazed and cut for hay for a long time. Hay-making hardly occurs anymore, but grazing is still commonly practiced in north west Europe (Dijkema 1984). Heavy grazing for agricultural purposes results in a short turf with hardly any differences in the structure of the vegetation. About 74% of the salt marsh area along the North Sea coast is considered to be very intensively grazed, particularly in Niedersachsen and Schleswig-Holstein (Wesemüller & Lamp 1987; Prokosch & Kempf 1987). Abandoning salt marshes, often after their acquisition by nature conservation organizations, eventually results in tall forb communities with accumulated litter and a decrease in plant species diversity (Bakker 1987; 1989). The invertebrate fauna shows, however, an increased biomass and diversity after 3 years of abandoning (Irmler & Heydemann 1986; Irmler *et al.* 1987b). The effects of grazing in salt marshes has been under critical discussion for several years (Heydemann 1980; 1987; Dijkema 1984; Irmler & Heydemann 1986; Irmler *et al.* 1987a; Rahmann *et al.* 1987; Bakker 1987; 1989).

Many studies on the effects of grazing on salt marsh communities compare grazed and ungrazed areas at a given time and are restricted to either the effects on plant or animal communities. This study's aim was the comparison of the long-term effects of different stocking rates and abandoning on the rate of sedimentation and the structure and species composition of plant and invertebrate communities on a salt marsh.

Materials and methods

Study area

The study area is located in the Leybucht (Northern Germany, Niedersachsen, 53° 31′ N, 7° 08′ E). Since the last embankment in 1950 a new salt marsh of 800 m width has been formed by land reclamation techniques. Surface level rises from + 1.1 m NN (German Ordnance Level) (annual inundation frequency 450–500) at the lowest parts to + 1.9 m NN (annual inundation frequency 40–60) at the highest part near the dike. The Leybucht is characterized by a strong sedimentation, namely 2 cm yr^{-1} (Homeier 1974). This high rate of sedimentation can be attributed to the special hydrological conditions (Homeier 1955; Luck 1965) and the extremely high sediment load of 1667 mg l^{-1} in the flood stream (Müller 1960). As a result the salt marsh is very clayish and nutrient-rich. It features a narrow pioneer community, the *Salicornia stricta*-zone, a broad lower salt marsh community, the *Puccinellia maritima*-zone and a narrow higher salt marsh community, the *Festuca rubra*-zone (Dahl & Heckenroth 1978).

The study site has been heavily grazed (2 cattle ha^{-1}). In 1980 three exclosures of 10 ha each were established with 0.5 cattle ha^{-1}, 1 cattle ha^{-1} and zero grazing, and compared with the heavily grazed control area. The drainage furrows had not been maintained since 1980.

Field methods

In 1982 90 sediment plates were exposed in the four sites, of which 40 could be found again in 1988.

The vegetation was recorded in September 1988 by a map with a 1:1000 scale. The vegetation types were distinguished according to the typology used for the vegetation map of 1980 by Gross (in Dahl & Heckenroth 1978). The types were verified by means of relevés (2 × 2 m) in 1988. Species abundancy was quantified by point quadrat analysis in each site along the gradient from the dike to the tidal flats. Fifty hits were made every 50 m. The number of hits per species was grouped in frequency-classes: class 1 = 1–5 hits, class 2 = 6–10 hits, class 3 = 11–15 hits, etc. The vegetation can be subdivided into a high canopy with flowering *Aster tripolium* plants and an understorey formed by the remainder of the vegetation which consists mainly of grasses. The height of the canopy of both layers was measured (n = 20) at 50 m intervals along the gradient in each site.

The invertebrate fauna was sampled in 1980–1982 and in 1988 in the period from April to October. Five pitfall traps were established within the inundation gradient in each of the 4 sites. Additionally 3 quadrat samples (0.1 m^2) were collected every two weeks in 1980 and 1981 and at the beginning of September in 1982 and 1988. Spiders and carabid beetles were determined to the species level in the four years of investigation, and the diversity of these groups was calculated according to Shannon & Weaver (1963). Spiders can be caught easily with pitfall traps because of their high activity and rapid reaction to environmental changes.

Results

Influence of cattle grazing on the rate of sedimentation

The highest sedimentation rates were found in the *Puccinellia*-zone at about + 1.4 m NN (Fig. 1). Moreover, in this zone the highest differences of the sedimentation rates between the sites with various stocking rates were observed with the highest rates in the abandoned sites (2.3 cm yr^{-1}) and the lowest rates in the heavily grazed sites (1.7 cm yr^{-1}). No differences were found in the *Festuca*-zone (+ 1.7–1.9 m NN) and the *Salicornia*-zone (+ 1.1 m NN) with regard to the various stocking rates.

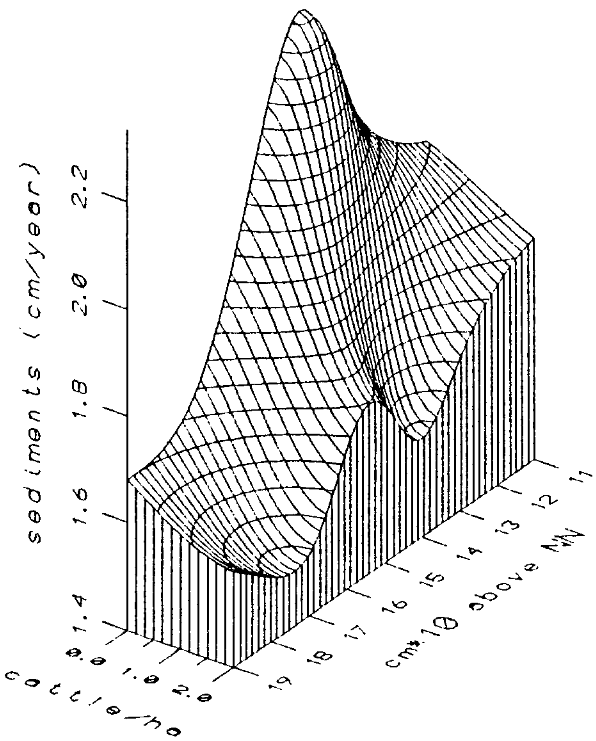

Fig. 1. Mean annual rates of sedimentation in the salt marsh of the Leybucht in relationship to the stocking rates.

Distribution of vegetation types and plant species

The species composition and abundancy in the discerned types of vegetation is given in Table 1. Figure 2 shows the simplified vegetation map of the study area in 1988. The pioneer vegetation bordering the tidal flats consisted mainly of a type of *Salicornia stricta* and locally a type of *Spartina anglica*. Somewhat higher on the salt marsh the type of *Puccinellia maritima* with *Salicornia stricta* was found. This type of vegetation also occurred higher on the salt marsh in depressions on the

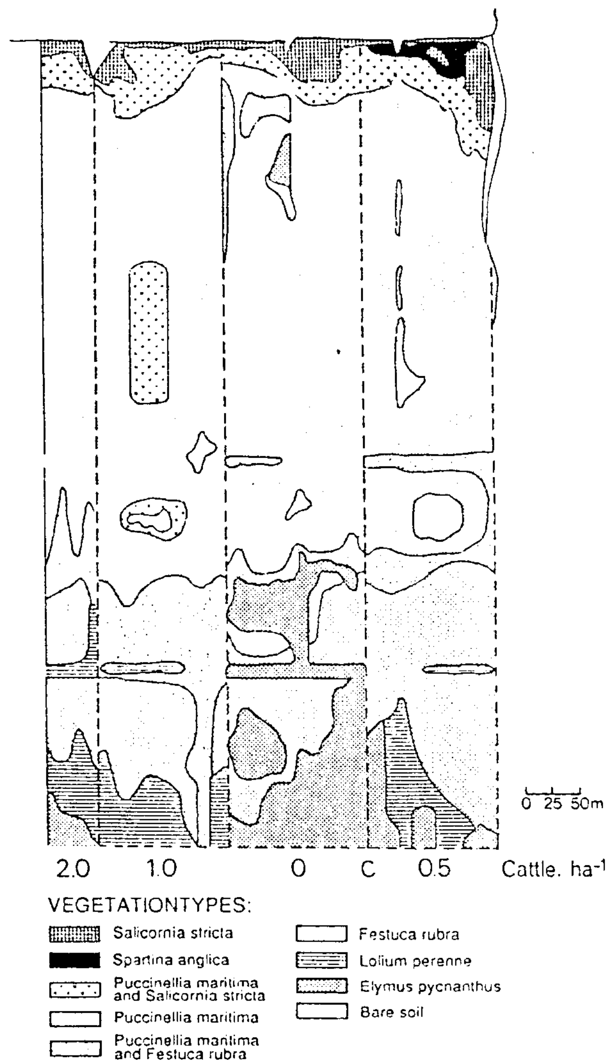

Fig. 2. Simplified vegetation map after 8 years of grazing with different stocking rates.

Table 1. Synoptic table of the vegetation types including the frequency of abundance, lowest and highest percentage of cover (*after Gross in Dahl & Heckenroth 1978).

Vegetation types	Spartina *anglica*	Salicornia *stricta*	Puccinellia *maritima* + Salicornia stricta	Puccinellia *maritima*	Puccinellia *maritima* + Festuca rubra	Festuca rubra	Elymus *pycnanthus*	Lolium *perennie*
Number of relevés	8*	9*	4	7	3	5	2	3
Spartina anglica	100(50–90)	50(2)	100(4–10)	14(1)	–	–	–	–
Salicornia stricta	70(2)	100(50–90)	25(1)	–	–	–	–	–
Suaeda maritima	–	–	75(1)	43(1)	–	–	–	–
Halimione portulacoides	–	10(1)	–	–	–	–	–	–
Puccinellia maritima	–	–	100(20–80)	100(40–80)	100(2–50)	80(1)	50(1)	100(1)
Aster tripolium	–	30(2)	100(10–30)	100(4–30)	100(2–10)	100(1–2)	50(1)	100(1)
Spergularia salina	–	–	100(1)	29(1)	67(1)	40(1)	–	33(1)
Triglochin maritimum	–	–	25(1)	–	–	–	–	–
Atriplex prostrata	–	–	75(2–10)	86(1–4)	100(1)	100(1–2)	–	100(1)
Cochlearia danica	–	–	–	14(1)	67(1)	20(1)	–	–
Festuca rubra	–	–	–	14 (1)	100(1–10)	100(30–80)	50(30)	100(1–30)
Agrostis stolonifera	–	–	–	29(10–30)	100(30–80)	100(20–60)	50(1)	100(1–20)
Elymus pycnanthus	–	–	–	–	33(1)	40(1)	100(50–90)	–
Artemisia maritima	–	–	–	–	–	20(2)	–	–
Glaux maritima	–	–	–	–	–	20(1)	–	–
Cirsium arvense	–	–	–	–	–	20(20)	–	–
Taraxacum spec.	–	–	–	–	–	20(1)	50(1)	–
Plantago major	–	–	–	–	–	20(1)	50(1)	–
Lolium perenne	–	–	–	–	–	20(4)	50(10)	100(20–80)
Poa annua	–	–	–	–	–	–	50(1)	–
Poa pratensis	–	–	–	–	–	–	–	33(40)
Ranunculus sceleratus	–	–	–	–	–	–	–	33(1)
Polygonum aviculare	–	–	–	–	–	–	–	67(1)

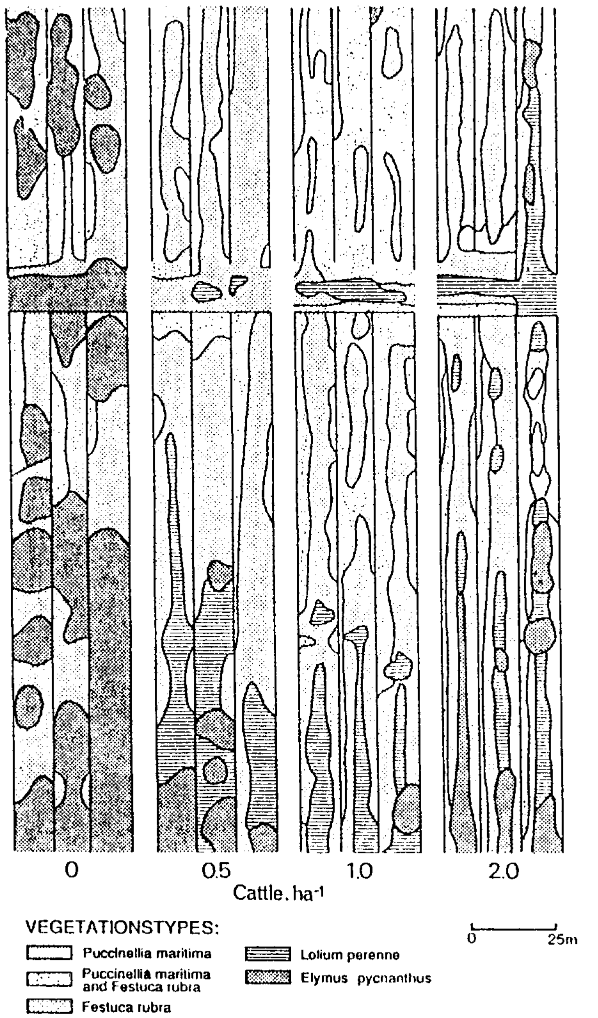

Fig. 3. Detailed vegetation map of parts of the study area after 8 years of grazing with different stocking rates.

grazed sites. The major part of all the sites was covered with a type of *Puccinellia maritima*. The type of *Puccinellia maritima* with *Festuca rubra* occurred at the transition of the low and the higher salt marsh. This type was also found locally at the lower salt marsh in the abandoned and lightly grazed sites. At the higher salt marshes the type of *Festuca rubra* was found and adjacent to the dike the type of *Lolium perenne*. The latter type was restricted to the grazed sites. The type of *Elymus pycnanthus* was also found on the higher salt marsh and dominated the abondoned site, whereas it was not found at the beginning of the experiment in 1980.

The vegetation types built a finer pattern with increasing stocking rates, which can be seen on the detailed vegetation map (Fig. 3). The vegetation types of *Elymus pycnanthus*, *Lolium perenne* and *Festuca rubra* retreated to the central part of the area between two furrows with increasing stocking rates, whereas the types with *Puccinellia maritima* were found higher with respect to NN.

Puccinellia maritima dominated the lower salt marsh in all sites (Fig. 4). It was hardly found at the higher salt marsh in the abandoned site. *Aster tripolium* occurred more frequently at the higher salt marsh with increasing stocking rates. *Festuca rubra* and *Agrostis stolonifera* were found more frequently at the higher, grazed salt marsh than elsewhere. Bare soil was hardly found in the abandoned site, but its frequency increased with increasing stocking rates, particularly at the lower salt marsh. The occurrence of lower salt marsh- and annual species, namely *Salicornia stricta*, *Suaeda maritima*, *Spartina anglica*, *Spergularia salina* and *Cochlearia danica* in the grazed sites seems to be related to the occurrence of bare soil.

Structure of the vegetation

The canopy height of the flowering *Aster tripolium* layer increased from the dike towards the tidal flats in the grazed sites (Fig. 5), which indicates a decrease of grazing impact towards the tidal flat. This trend was not found in the abandoned site. Non-flowering *Asters* were only found at the higher salt marsh with the highest stocking rate. The height of the *Aster* canopy measured over the whole gradient decreased significantly ($P < 0.01$, *t*-test) with increasing stocking rates.

The canopy height of the understorey was significantly higher ($P < 0.05$) in the abandoned site than in the grazed sites along the major part of the gradient (Fig. 6). The differences in the stocking rates were small, especially at the higher salt marsh. The canopy height in the lightly grazed site was significantly ($P < 0.01$) higher than in the heavier grazed sites at the lower salt marsh, which indicates stronger influences at the lower salt marsh with increasing stocking rates.

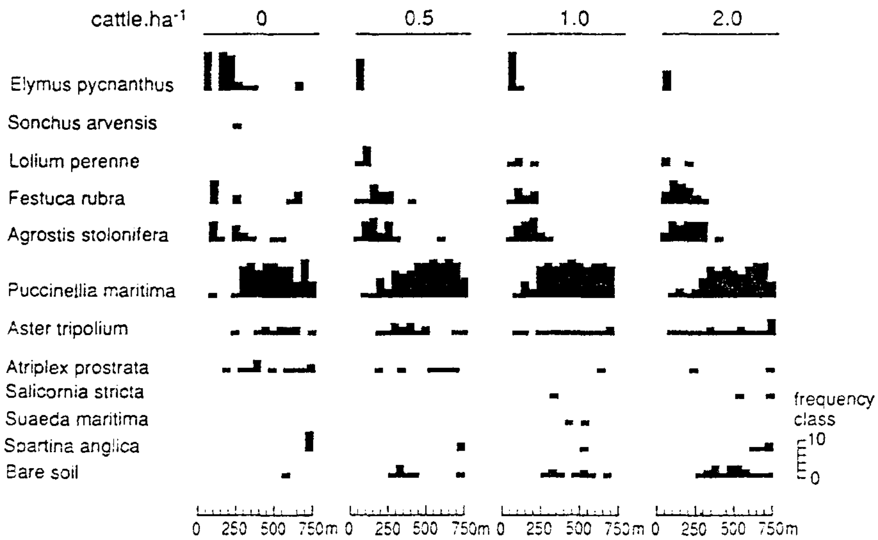

Fig. 4. Frequency classes of the plant species at 50 m intervals along the gradient from the dike towards the tidal flats after 8 years of grazing with different stocking rates.

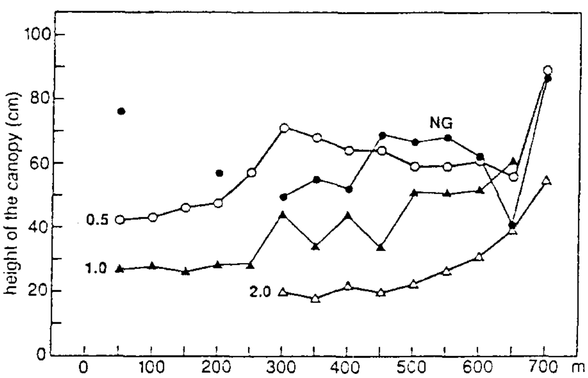

Fig. 5. Height of the canopy from the dike towards the tidal flats after 8 years of grazing with different stocking rates. NG: not grazed.

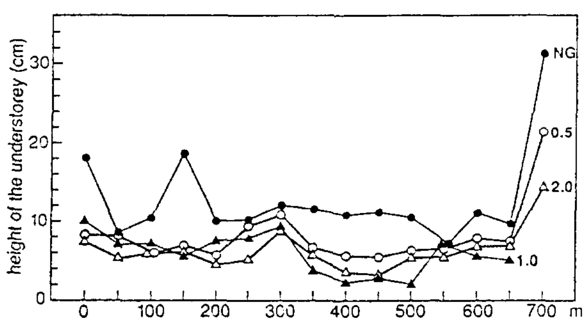

Fig. 6. Canopy height of the understorey from the dike towards the tidal flats after 8 years of grazing with different stocking rates. NG: not grazed.

Influence of cattle grazing on the immigration of the soil fauna

Spiders are the most important predators on the soil surface of salt marshes and there are sometimes extremely high population densities (Heydemann 1969; Irmler & Heydemann 1985a). *Erigone longipalpis* is the most important spider species in the *Puccinellia*-zone, it is a halotopobiontic species. Other species occur mainly in the *Festuca*-zone and cannot be considered as halotopobiontic, namely, *Oedothorax retusus*, *Pardosa agrestis* (= *purbeckensis*) and *Pachygnatha clerki*.

Whereas *Erigone longipalpis* still occurred in high abundance in the *Festuca*-zone at the beginning of the experiment, it has, since 1982, moved to the lower *Puccinellia*-zone and the *Salicornia*-zone in the abandoned site. The other species spread into the lower salt marsh with different rates. *Oedothorax retusus* occurred in 1980 up to about + 1.6 m NN, in 1982 up to + 1.4 m NN and in 1988 up to 1.1 m N (Fig. 7). In 1982 *Pachygnatha clerki* could already be found over the whole gradient of the salt marsh with highest abundancies at + 1.5– + 1.4 m NN. The area of the highest abundancy still shifted seawards to + 1.4– + 1.2 m NN in 1988. Similar zonations

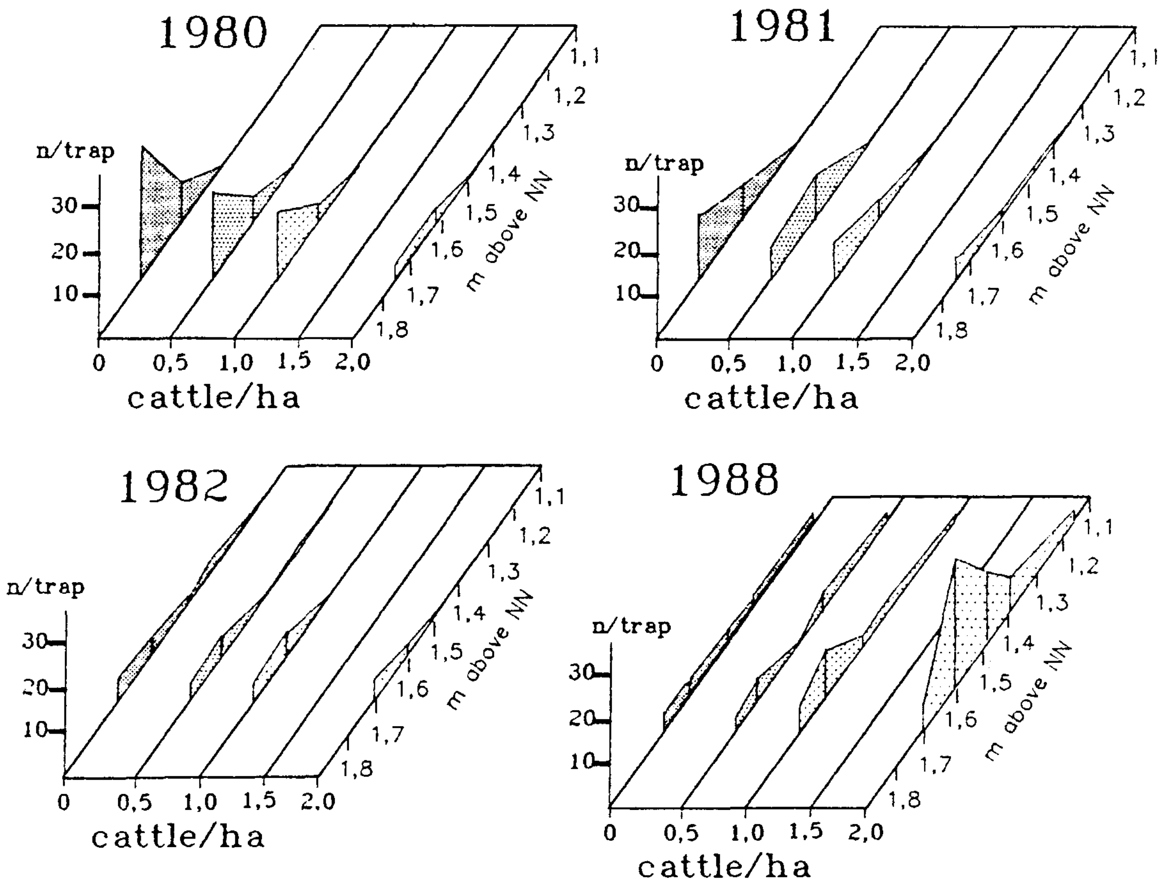

Fig. 7. Distribution of the dwarf spider (Micryphantidae) Oedothorax retusus during the four years of investigation.

were observed for *Pardosa agrestis* with somewhat higher abundancies than for *Pachygnatha clerki*. Since 1982 two species, *Allomengea scopigera* and *Robertus lividus*, have immigrated into the salt marsh.

In the period 1980–1982 relationships between stocking rate and abundancy of most of the spider species had been found, featuring highest abundancies in the abandoned area. In the case of most species these relationships had disappeared in 1988. The newly immigrated species *Allomengea sopigera* and *Robertus lividus* showed, however, higher abundancies in the abandoned site than in the grazed areas.

The observed behaviour of the soil spiders suggest that their occurrence, in particular, shows a relationship with the flood gradient. The zonation of the spiders was, therefore, calculated for a height gradient after correction, namely, by adding the annual sedimentation to the soil level of 1980. This calculation resulted in a characteristic zonation, which indeed showed no relationship with the stocking rate. The highest abundancy for *Erigone longipalpis* is found at + 1.52 m NN, for *Pachygnatha clerki* at + 1.61 m NN, for *Pardosa agrestis* at + 1.69 m NN, for *Centromerita bicolor* at + 1.73 m NN, for *Oedothorax retusus* at + 1.74 m NN, for *Allomengea scopigera* at + 1.75 m NN, and for *Robertus lividus* at + 1.77 m NN.

A distinct zonation of the animal communities was observed in the first three years of the experiment (Fig. 8). The community diversity was highest in the abandoned site, since communities of the higher salt marshes spread into the lower salt marsh. During dry summers the community of the higher salt marsh extended also in the grazed areas as shown in 1982. In 1988 the com-

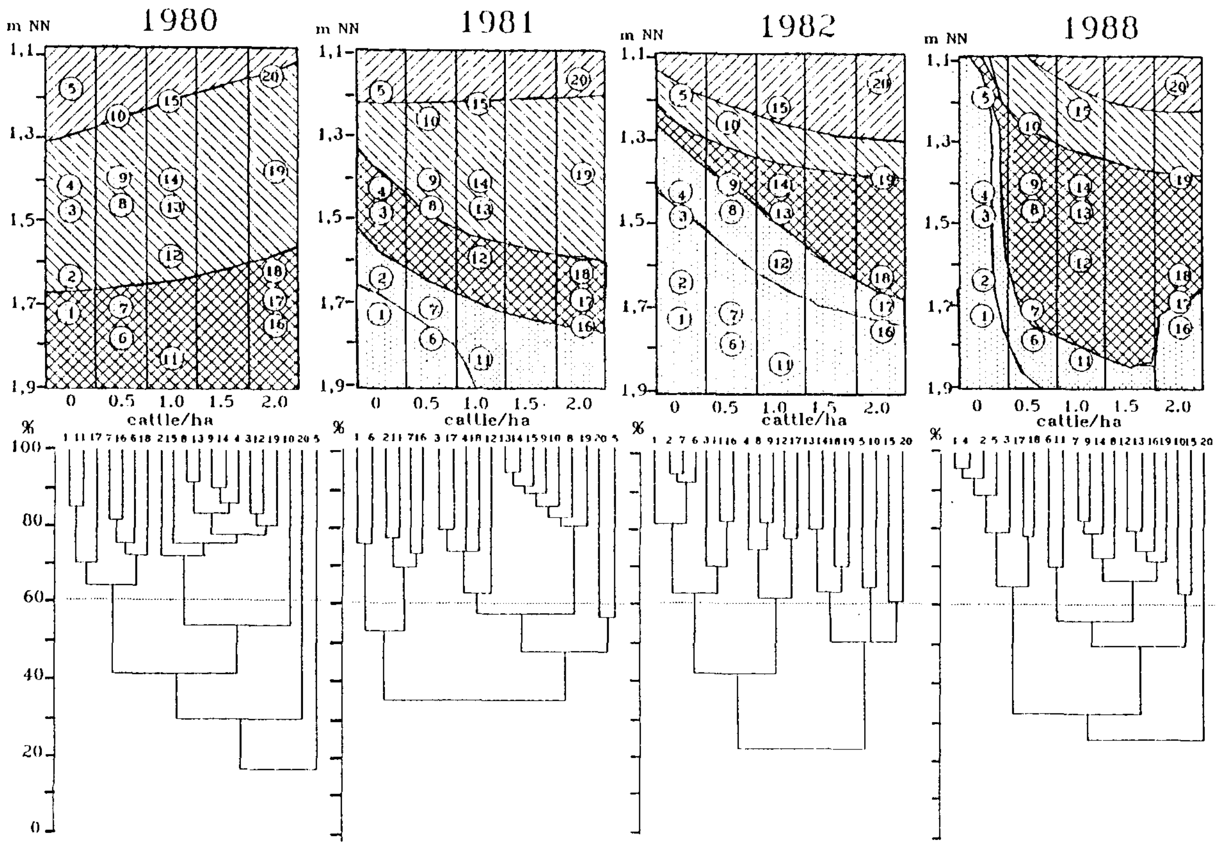

Fig. 8. Differentiation of the 20 pitfall sites by cluster analysis (according to the Renkonen index) for the different stocking rates in the salt marsh gradient. Clusters with higher similarity than 60% are considered as communities.

munity of the higher salt marsh, however, spread over the whole gradient and almost entirely replaced the communities of the lower salt marsh nearly completely in the abandoned site. The community diversity was, therefore, eventually lowest at the abandoned site.

Influence of cattle grazing on the community structure

A high amount of litter is produced in the abandoned site, which gives rise to an increasing biomass of detritus feeding animals. Hence, the population density of *Collembola* (springtails) (Fig. 9) and *Orchestia gammarellus (Amphipoda)* increased from 1980 to 1988. *Orchestia gammarellus*, in particular, serves as an excellent indicator of the stocking rate, namely, its population density decreased with increasing stocking rates.

Spiders are the most abundant predators of detritus feeding animals. Although the species composition changed during the 8 year experimental period, the population density of spiders had already reached a steady state after 3 years (Fig. 9).

The number and diversity of species was highest in the intensively grazed area with 27 species and a diversity H(s) of 1.25 at the start of the experiment in 1980. During the 8 years of succession both number and diversity of species increased in all sites. The species number increased to the highest values, namely, 39 species and a species diversity of 2.5 in the abandoned area, whereas the species diversity amounted to 2.3 and 2.4 in the grazed areas (Fig. 10).

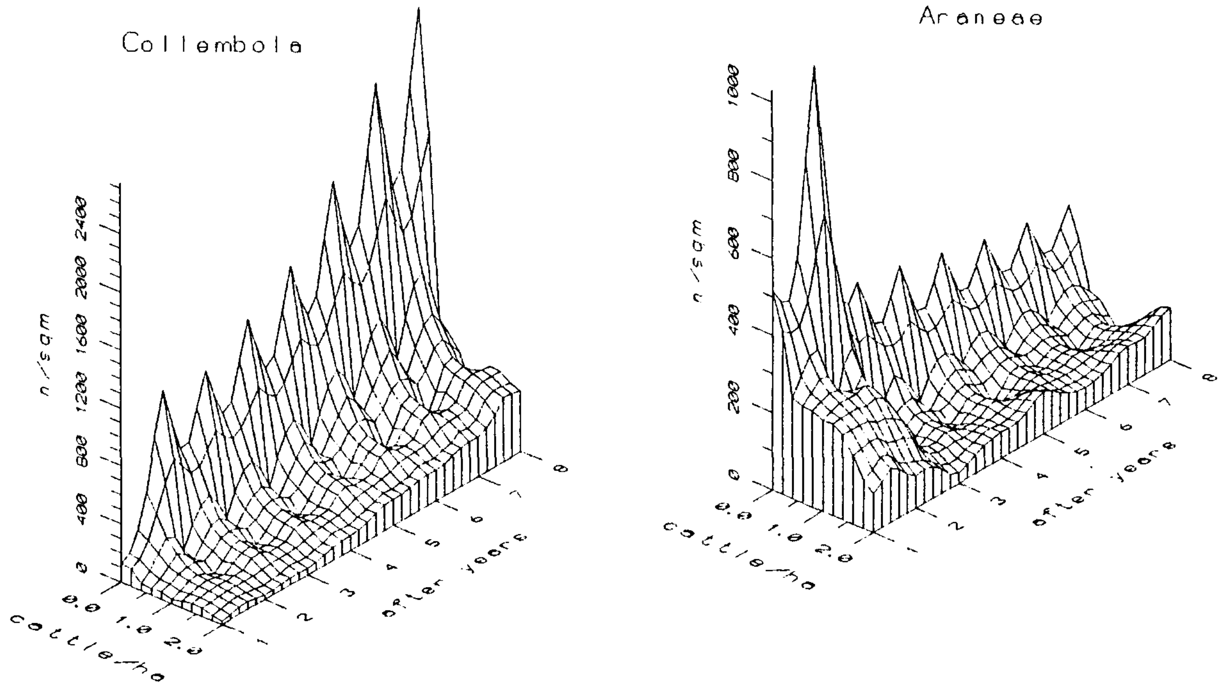

Fig. 9. Long-term development of population densities for springtails (Collembola) and spiders (Araneae) in relationship to the stocking rates.

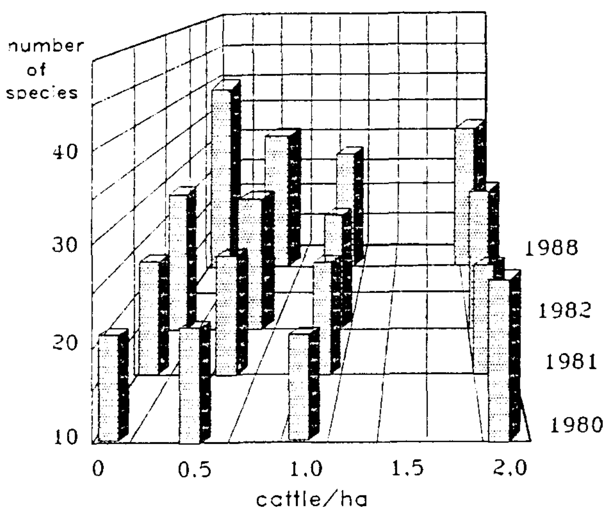

Fig. 10. Development of the species number in pitfall traps for spiders and carabids in relationship to the stocking rates.

Discussion

Successional dynamics

The observed rate of sedimentation in the Leybucht area is in agreement with the high figures of the range of 0.6 to 2.5 cm yr^{-1} for Schleswig-Holstein in Germany (Dieckmann 1988) and of 1.0 to 2.3 cm yr^{-1} for Groningen in the Netherlands (De Glopper 1981). The lower rates of sedimentation in the *Puccinellia*-zone in the grazed than in the abandoned area might be attributed to the higher turbulence of the flood water in the grazed area. The finding that these differences were not observed in the other zones, might be attributed to the low frequency of inundation in the *Festuca*-zone and the low grazing intensity in the *Salicornia*-zone. The sedimentation rate in the *Puccinellia*-zone in the ungrazed site was 0.6 cm yr^{-1} higher than in the heavily grazed site. Grumblatt (1987) found a difference of 0.8 cm yr^{-1} in a six year old exclosure as compared to a sheep-grazed control site at the transition of a *Pucçinellia*- and a *Festuca*-zone in the saltmarsh in front of Marienkoog.

The future development of the soil level as a result of the observed sedimentation rates may be as follows. The soil level increases rapidly, especially in the abandoned *Puccinellia*-zone, and will eventually resemble that of the *Festuca*-zone.

Part of the observed invertebrate succession can be attributed to the overall rise of the soil level. As the soil level of the abandoned site showed more sedimentation than that of the grazed sites, the less flood tolerant species occurred first and in highest abundancies in the abandoned site. As the sedimentation continues at the grazed salt marsh these species also eventually become very abundant in the grazed salt marsh. The increase of the invertebrate species number and species diversity in all sites in the period of the experiment can be attributed to both the overall sedimentation and the immigration of species from adjacent grasslands. Nevertheless, a negative effect of cattle grazing on the population densities exists, as could be shown for *Erigone longipalpis* (Irmler *et al.* 1987b). Grazing effect also change the metabolism of the ecosystem. In the grazed salt marsh the main matter flow goes through the vegetation feeding cattle and some phytophagous insects sucking on grass like plantlice and cicads. Most of the species are, however, damaged by grazing (Tischler 1980; Irmler & Heydemann 1985b; Irmler & Heydemann 1986; Tulowitzki 1988; Stüning 1988). The community structure showed, that the salt marsh ecosystem developed from a food web dominated by plant feeding animals to a food web dominated by animals foraging on detritus. A negative effect of abandoning is the eventual disappearance of invertebrate communities characteristic for salt marshes.

Nine years after the cessation of grazing the higher salt marsh was dominated by the *Elymus pycnanthus* vegetation type, which had also established locally in the lower salt marsh. Dominance of a single plant species a few years after the cessation of grazing is well known in mainland and island salt marshes. Depending on the tidal inundation frequency various species can reach dominance, namely, *Puccinellia maritima* (Ranwell 1968), *Festuca rubra*, *Elymus repens* (Schmeisky 1977), *Phragmites australis* (Siira 1970; Jensen 1978); *Elymus pycnanthus* (Bakker 1987). The species-richness and the number of vegetation types will eventually decrease as a result of the high standing crop and the accumulation of litter (Bakker 1989).

In the grazed sites the lower salt marshes *Puccinellia maritima* types spread further into the higher salt marshes with increasing stocking rates. Four years after the beginning of the experiment already less *Salicornia europaea*, *Suaeda maritima* and *Spergularia maritima* were found in the ungrazed site (Scherfose 1989). The occurrence of lower salt marsh vegetation types higher with respect to NN at grazed than at abandoned salt marshes is also known from barrier island salt marshes in the Netherlands (Bakker 1987; 1989). It seems to be in contradiction with the overall sedimentation. Grazing and trampling, however, cause a reduction of the canopy height, open up the turf and locally bare the soil and create space for lower salt marsh species. Halophytic species require more light for seedling establishment and early growth than glycophytic species (Bakker 1987; 1989). The weak soil of the lower salt marsh is very susceptable to treading. It particularly causes severe destruction of the turf in the sites with higher stocking rates. This finding is in agreement with the reduction of species-richness at the lower salt marsh on a barrier island with a stocking rate of 1.6 cattle ha^{-1} (Bakker 1989).

Management

In order to evaluate the grazing management of salt marshes, the consequences for both nature reserve and coast-protection purposes have to be considered for long-term effects. Discussion of the effects has to be focussed on salt marsh successional dynamics under grazing and abandoning. The effects of grazing are:

1. the process of sedimentation is retarded,
2. the species-richness of plants decreases at the lower salt marsh with high stocking rates,
3. species and plant communities of the lower salt marsh spread into the higher salt marsh,
4. a pattern of different vegetational structures develops, especially with a low stocking rate,
5. litter production and both population density

of detritus feeding animals and their predators decreases,
6. immigration of animals from higher salt marshes into lower salt marshes is retarded,
7. the invertebrate community of lower salt marshes spreads to higher salt marshes,
8. the species-richness of plant feeding insect species decreases as a result of destruction of the higher vegetation canopy.

The effects of abandoning – apart from the opposite effects of grazing – are:
1. the species-richness of plants decreases,
2. the number of vegetation types decreases,
3. characteristic halophytic plant species and communities disappear,
4. the number of invertebrate communities decreases,
5. characteristic halotopobiontic invertebrate species and communities disappear.

The different effects of the successional dynamics should be evaluated with regard to the purposes of the management. A rapid sedimentation process is highly advantageous for the protection of the coast, and abandoning is, therefore, the proper management. It can be concluded, for nature conservation purposes, that intensive grazing promotes lower salt marsh plant communities with poorly developed invertebrate communities. Abandoning initially results in flowering plant communities with well developed, species-rich invertebrate communities, but within 10 years the characteristic salt marsh communities of both plants and invertebrate disappear.

It can be concluded that for nature conservation purposes light grazing by 0.5 cattle ha^{-1} is the best management practice. Light grazing on a large area (Beeftink 1977) enhances plant species diversity and differences in vegetational structure by creating a pattern of heavily grazed areas with short turf and lightly grazed patches with accumulated litter, and hence habitats for various evertebrate species and communities. Dijkema (1983) recommended spatial variation of management practices. It can be discussed, and it should be studied whether a differentiated management of 50% salt marsh abandoned and 50% grazing with low intensity or an overall grazing lower than 0.5 cattle ha^{-1} can be recommended.

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