Estuaries and Coasts (2020) 43:298–315
https://doi.org/10.1007/s12237-019-00680-5

Long-Term Effects of Sheep Grazing in Various Densities on Marsh Properties and Vegetation Dynamics in Two Different Salt-Marsh Zones

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Received: 29 November 2018 / Revised: 22 October 2019 / Accepted: 17 December 2019 / Published online: 29 December 2019

Abstract

For conservation management of grassland ecosystems, an important question is under which conditions large grazers induce compositional and structural variation in plant communities, which is a prerequisite for high biodiversity. Here we used two long-term projects on the mainland salt marshes of the Wadden Sea to test the hypothesis that long-term grazing management with different stocking densities results in plant communities with distinctively different plant species composition and vegetation structure. The two projects took place on a low clayey and a high sandy salt marsh with different stocking densities of sheep: 0, 1.5, 3.5, 4.5 and the initially 10 sheep ha^{-1}, where measurements were collected 11, 15, 19 and 23 years after the start of the project. Moreover, grazers affect abiotic conditions by reducing soil-redox potential and surface elevation, thereby driving composition and structure of salt-marsh vegetation. On the low salt marsh, a continued high stocking density (10 sheep ha^{-1}) resulted in succession from the early-successional *Puccinellia maritima* community to the late-successional *Atriplex portulacoides* community. On the high salt marsh, the early-successional *Festuca rubra* community was maintained under all stocking densities. Cessation of grazing resulted in succession to the *Elytrigia atherica* community in both salt-marsh types. Intermediate stocking densities (1.5, 3 or 4.5 sheep ha^{-1}) resulted in a mosaic of tall vegetation and patches of lawn, i.e. short-grazed vegetation, where *Puccinellia maritima* lawn occurred interspersed with patches of the *Festuca rubra* and tall *Elytrigia atherica* communities in both salt-marsh types. Effects of grazers were influenced by the presence of watering points near the sea wall. To conclude, our results show how joint interactions between grazers and abiotic conditions drive vegetation diversity and heterogeneity, with implications for ecosystem functions and services such as wildlife biodiversity and coastal protection.

Keywords Grazing lawn · Long-term vegetation dynamics · Plant-herbivore interaction · Soil-redox potential · Surface elevation · Tall vegetation

Communicated by Stijn Temmerm

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s12237-019-00680-5) contains supplementary material, which is available to authorized users.

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Introduction

The interaction between grazers and vegetation has traditionally been studied from the grazers' perspective, i.e. how animals select forage of different qualities in various plant communities (Grant et al. 1985). The vegetation perspective, particularly how grazing and different grazing regimes affect both composition of plant communities over time and spatial variation in vegetation structure, has received considerably less attention (see, however, Rook et al. 2004). For conservation management, an important question is under which conditions large grazers induce compositional and structural variation in grassland plant communities, as this appears to be a prerequisite for high biodiversity (Milchunas et al. 1988). Answering this question may allow managers to apply adequate management tools for maintaining a high diversity of plants and animals and a variety of ecosystem functions and services (Hector et al. 1999; Schröter et al. 2005; Hautier et al. 2018).

Effects of grazers on vegetation dynamics are usually studied by comparing the vegetation of grazed and ungrazed sites by excluding grazers from previously grazed plant communities. The general pattern of such long-term studies (4–40 years) is a high above-ground standing crop with homogeneous tall vegetation in grazer exclosures versus continuously grazed plots dominated by lawn, i.e. homogeneous short-grazed vegetation, under high grazing pressure (see review by Milchunas and Lauenroth 1993). Similar patterns have been found in coastal salt marshes, natural grassland ecosystems occurring on both mineral and organic substrates worldwide. A recent global meta-analysis (Davidson et al. 2017) showed that plant species richness was higher in grazed than in ungrazed salt marshes. The problem with this type of comparisons is that the intermediate outcome, where grazers create a landscape with a high degree of structural heterogeneity typical for most naturally grazed ecosystems, is lacking as a result of a paucity of studies that investigate this phenomenon. Such patchy grassland ecosystems with high levels of spatial heterogeneity can develop as a result of selective grazing when vegetation productivity is higher than utilization (i.e. biomass loss to both grazing and trampling). In areas that remain ungrazed for a longer period, vegetation harbours taller tillers and accumulates litter and becomes less attractive to grazing animals. As a result, vegetation structure develops into lawns (i.e. homogeneous short-grazed vegetation) alternating with patches of taller stand, thus featuring spatially heterogeneous vegetation, as demonstrated in both grazed pastures in Argentina (Cid and Brizuela 1998) as well as on grazed salt marshes in NW Europe (Berg et al. 1997). Grazers play a role in soil compaction and bioturbation of soil organisms (Howison et al. 2017). In the long run, when other species establish in such tall patches, the initial plant community may be replaced. It is currently not known, however, which grazing conditions induce homogeneous or heterogeneous vegetation and eventually different plant communities at the landscape scale.

Here, we use salt-marsh ecosystems of North West Europe to better understand the effect of grazer densities on the development of plant communities and particularly on the development of structural spatial heterogeneity. Salt marshes represent excellent sites to explore these effects as they represent natural ecosystems except for a long history of livestock grazing. In fact, livestock grazing has been the most common land use of European salt marshes in the last millennia (Davy et al. 2009). Besides Europe, livestock grazing is the most common resource use of salt marshes in China, South America, whereas it is less common nowadays in North America, but not in the previous centuries (several authors in Davidson et al. 2017).

The first global meta-analysis of 89 studies on effects of livestock grazing in salt marshes included 89 studies (Davidson et al. 2017). This analysis was dominated by European studies (75 of which 62 from the Netherlands, Germany and the UK). There was a limited power to detect different effects across continents due to the small number of American studies (12 of which 4 from Argentina), no study from Australia, and only one from China, despite large areas of salt marsh. Besides positive effects of grazing on plant species richness, further positive effects were found on salinity and on bulk density, but conflicting effects were found on vertical accretion or surface elevation change. Negative effects were found on plant cover, above-ground biomass, soil-redox potential, litter biomass and vegetation height. Moreover, a negative relationship was found between stocking density and vegetation height. Differences in marsh zone and sediment type were not tested due to a lack of data. Effects over time, i.e. vegetation dynamics, were not recorded as duration of grazing was reported as the period of grazing or no grazing in single sites, ranging between a few weeks and 100 years. The same holds for the negative effect of duration of grazing on vegetation height. In their meta-analysis, Davidson et al. (2017) included plant species richness, i.e. presence/absence of species, without taking into account their abundance in plant communities. They also introduced vegetation height as average height, which does not take into account spatial heterogeneity. Certain stocking densities can, however, result in small-scale different grazing intensities within a paddock, or on a larger scale related to the position of watering points (Adler and Hall 2005). Hence, there are knowledge gaps with respect to effects of stocking densities on long-term vegetation dynamics, on the relationship between bulk density and vertical accretion, on vegetation height and structural heterogeneity in the vegetation, i.e. patterns of lawn and tall vegetation.

In this study, we investigated the relation between abiotic conditions, stocking densities, vegetation dynamics and vegetation heterogeneity on two salt marshes with long-term projects on the German Wadden Sea coast. Both sites experienced different stocking densities for over 20 years. We used these two sites to explore the (1) interaction effects of grazing and abiotic parameters (surface elevation, and soil-redox potential), (2) vegetation dynamics, especially the establishment of the tall late-successional plant communities by repeated vegetation mapping and (3) vegetation structure by recording vegetation height. We hypothesise that increasing stocking density results in increasing bulk density (as a result of increased soil compaction), hence lower surface elevation, reduced soil-redox potential (as a result of reduced soil aeration) and decreasing average vegetation height (as a result of decreasing area of late-successional plant communities). We further hypothesise that intermediate stocking density results in highest spatial variation of both plant communities and vegetation height (Fig. 1).

Methods

Study Area and Ecological Setting

Natural succession on salt marshes is characterized by the interaction of plants and sediment trapped during tidal inundation (Nolte et al. 2013). The resulting surface elevation change in NW European salt marshes drives succession from the short species-poor pioneer *Salicornia* forb and tall *Spartina* grass communities on intertidal flats via the short species-rich, early-successional *Puccinellia maritima* grass community to the tall species-poor, late-successional *Atriplex portulacoides* shrub community on the low salt marsh. On the high marsh, early successional communities, characterized by short, species-rich *Festuca rubra* grass, are followed by tall species-poor mid-successional *Artemisia* shrub communities and eventually by tall species-poor, late-successional *Elytrigia atherica* grass communities. After several decades, the late-successional community with the tall grass *E. atherica* occurs on most of the gradient from low to high salt marsh (Petersen et al. 2014; Wanner et al. 2014). In the short term, *Elytrigia atherica* cannot cope with the salt stress at the low marsh (Bockelmann and Neuhaus 1999). A large-scale study covering the German Wadden Sea coast of Schleswig-Holstein revealed that moisture and elevation were the main factors affecting species richness on salt marshes (Suchrow et al. 2015). Surface elevation, and hence inundation, seems to be related to salinity. Over a 13-year period six plant communities at various elevations showed a synchronous pattern in peak biomass. Year-to-year variation in peak biomass of these communities could be explained by the rainfall deficit during the growing season, while inundation frequency did not contribute to the regression model (De Leeuw et al. 1990). Surface elevation and soil-redox potential are independent important predictors for plant species distribution in ungrazed salt marshes (Davy et al. 2011). Mid and low salt-marsh species occur higher in the elevation gradient with grazing than without grazing, related to locally and temporally higher salinity of the top layer in the grazed area (see also Davidson et al. 2017). Not only the position with respect to inundation with salt water matters, but also competition with taller species may be more important (Bakker et al. 1985). Higher soil salinity with grazing may be due to compacted soil with lower leaching of salt and higher evaporation of more open soil (Olff and Ritchie 1998). Along an elevation and inundation gradient species, associations within salt marsh communities were strongly affected by grazing, not by the underlying stress gradient. In ungrazed areas, light competition was the likely dominant process (Howison et al. 2015). Livestock grazing sets back the successional clock: the late-successional communities are replaced by the *Puccinellia maritima* community in the lower marsh and the *Festuca rubra* community or the short, species-rich *Agrostis*

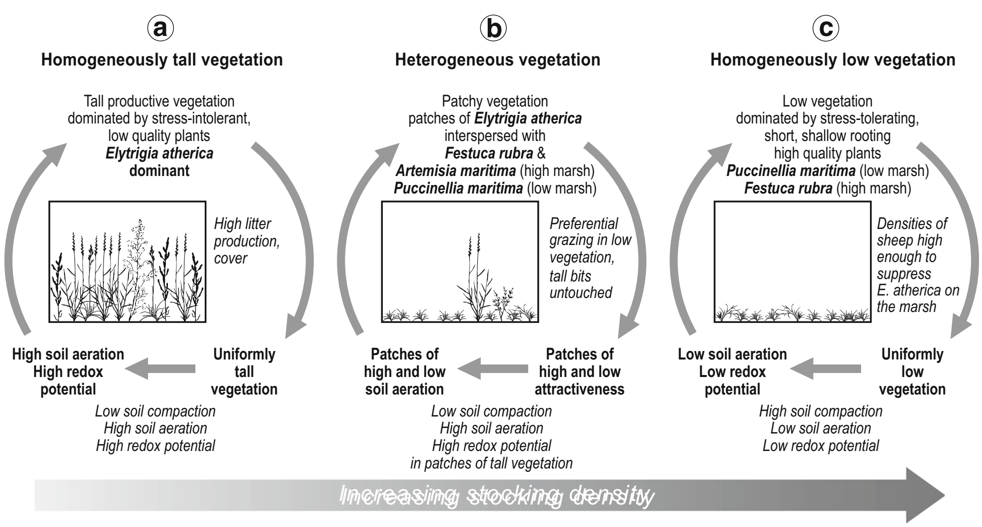


Fig. 1 Hypotheses on ecological processes between salt marshes that are not grazed, grazed at intermediate and high stocking density

stolonifera community in the higher marsh (Jensen 1985; Olff et al. 1997).

Study Area and Pilot Project

The study was conducted on a low (clay content 30%) (54° 38′ N 8° 50′ E) and a high (clay content 10%) salt marsh (54° 02′ N 8° 54′ E), about 65 km apart with roughly the same tidal regime (about 3 m) in Schleswig-Holstein, Germany. Both salt marshes were developed from coastal-engineering works. Their existence largely depends on the continued maintenance of the network of brushwood groynes, which enhances sedimentation and prevents salt-marsh erosion. They are characterized by collector drains and the evenly distributed drainage pattern of small ditches (Fig. 2). Initially, the engineering works aimed at coastal protection, land claim and exploitation by grazing. Nowadays, these artificial salt marshes are also regarded as having nature conservation interest featuring characteristic plant and animal life, and large areas are designated nature reserve (Bakker et al. 2002). Intensive sheep grazing (10 sheep ha^{-1}) between March and November occurred on approximately 95% of the salt marshes along the Schleswig-Holstein mainland coast of Germany. The salt marsh featured a ‘green’ of very short homogeneous vegetation without flowering plants (Stock 1993) (see photograph in Suchrow et al. 2015). Characteristic salt-marsh species such as *Atriplex portulacoides* were considered endangered (Dierssen et al. 1988), and halobiontic insects depending on

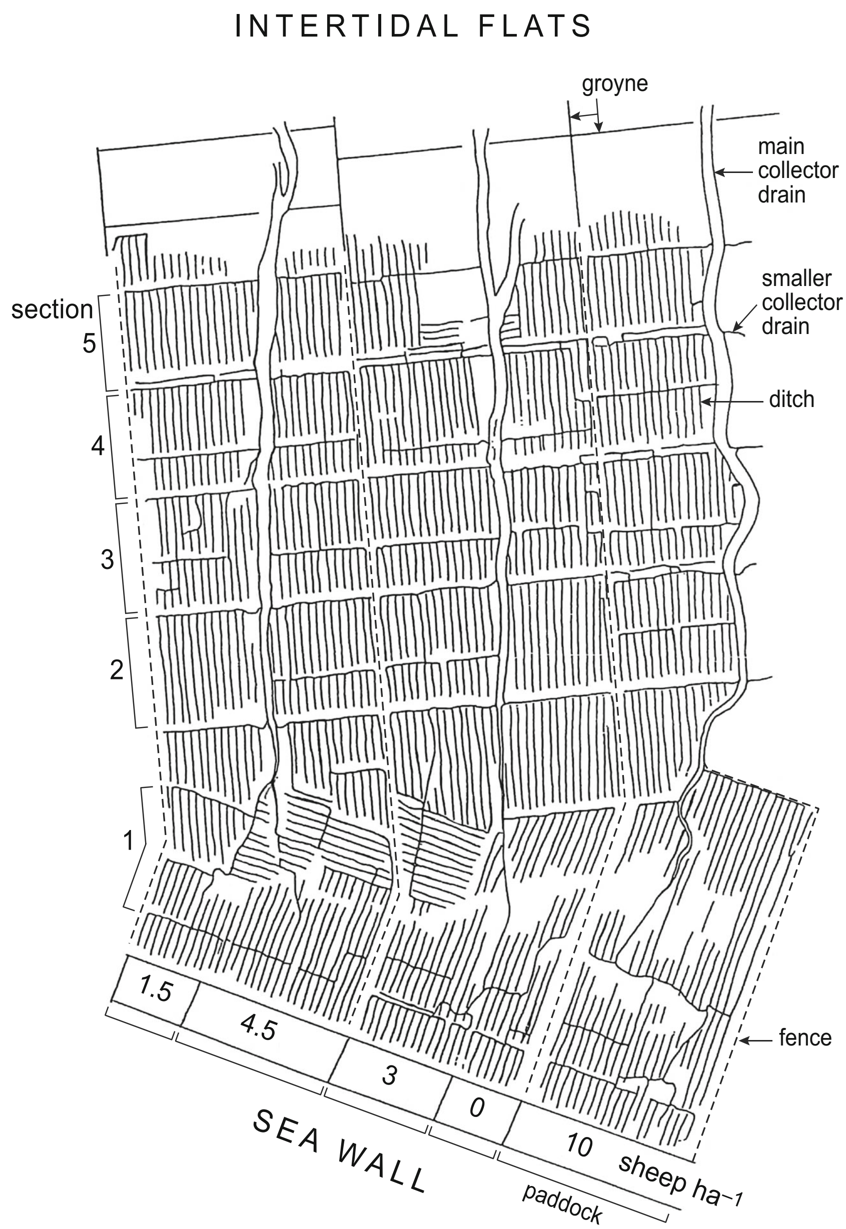


Fig. 2 Salt marsh developed from coastal-engineering works, including brushwood groynes, main collector and smaller collector drains and ditches. Indication of paddocks and fences with various stocking densities, subdivided in sections

fully developed flowering plants were absent (Heydemann 1985). In 1985, the National Park 'Schleswig-Holstein Wadden Sea' was established, and management changed by abandoning grazing on about 50% of the salt marshes to promote natural succession (Stock 1993; Esselink et al. 2017). In two sites, a pilot project was started with different stocking densities. In both sites, five adjacent paddocks (ranging from 6 to 19 ha) were established in 1988: a treatment with cessation of grazing, three paddocks with intermediate stocking densities of 1.5, 3 and 4.5 sheep ha^{-1} and a paddock with continuation of the initial high density of 10 sheep ha^{-1} (Fig. 2). Paddocks were separated by a collector drain or a fence perpendicular to the seawall. Each paddock was subdivided into five sections by smaller collector drains that ran parallel to the seawall (Fig. 2). Watering points were available close to the seawall. The project created the possibility to monitor long-term vegetation dynamics and record some vegetation parameters and abiotic conditions at one moment in time by the University of Groningen, the Netherlands.

The Low Salt-Marsh Site

The polder Sönke-Nissen-Koog was embanked in 1924. Thereafter, a new salt marsh developed is induced by the construction of sedimentation fields and will be referred to as 'low salt-marsh' (clay content 30%) in the remainder of the manuscript. Low salt marsh is defined as the area with flooding frequency > 100 times $year^{-1}$ (Erchinger et al. 1996). Here, it amounts to 80–200 times $year^{-1}$ (Kiehl et al. 1997). Surface elevation ranged from seawall to intertidal flats between 28 and 48 cm above mean high tide (MHT). Vegetation was dominated by the *P. maritima* community (Kiehl et al. 1997). The marsh was intersected with deep collector drains 100 m apart that could not be crossed by sheep. The collector drains allow sediment input onto the marsh, resulting in an alternating pattern of levees alongside the collector drains with depressions in between. Because of sediment accumulation within the drains, sediment was regularly removed from the collector drains before the start of the project in 1988, and twice during the project. The main channels separating the paddocks were dug out in 2009. Ditching enhanced the elevation differences between levees and depressions. The treatments with 1.5 and 4.5 sheep ha^{-1} were discontinued in 2003, 15 years after the start of the project.

The High Salt-Marsh Site

The polder Friedrichskoog was embanked in 1854. Also here, a salt marsh started developing after embankment and will be referred to as 'high salt-marsh' (clay content 10%) in the remainder of the manuscript. High salt marsh is defined as the area with flooding frequency < 100 times $year^{-1}$. It amounts to 40–50 times $year^{-1}$. From seawall to the intertidal flats, surface elevation ranged between 44 and 84 cm above MHT. Vegetation was dominated by the *F. rubra* community (Kiehl et al. 1997). Because of low sediment input, maintenance of the collector drains was not carried out at a regular interval before the start of the project. Differences in surface elevation between levees and depressions were small. The shallow collector drains in this site could easily be crossed by sheep. The intermediate grazing treatments could not be maintained until the end of our study period but were discontinued in 2005, 17 years after the start of the project.

Surface Elevation

Surface elevation above MHT at both sites was measured in 2005, 17 years after the start of the project using a levelling instrument (Spectra precision® laser LL500 and laser receiver HR500 by Trimble). We measured only the three sheep densities that had been maintained since the start of the project in 1988. In both sites, in each of the five sections of all paddocks with a grazing treatment (sheep densities 0, 3 and 10 sheep ha^{-1}, in the high salt marsh 3 sheep ha^{-1} only partly), we measured surface elevation in 3–4 locations between the small ditches (Fig. 2) at intervals of 25 m in a line perpendicular to the seawall, resulting in 30–50 points in each section, depending on the size of the section.

Soil-Redox Potential

As a proxy for the saturation of oxygen in the soil, we determined soil-redox potential in September 2011, 23 years after the start of the project. Each set of measurements was composed of the average measurement of five electrodes with a platinum tip of 1 mm and a Ag/AgCl calomel reference electrode (Cole-Palmer®), all of which were connected to a Graphtec GL200 Datalogger (Graphtec GB) and were read out 2 min after the electrodes were placed. In both salt-marsh sites, measurements were recorded at three different depths (2, 5 and 10 cm depth) in stocking densities 0 and 10 sheep ha^{-1}, being the densities consistently maintained since the start of the project. We recorded 10 sets of measurements, at spots at 10 m distance from the levees where oxygen content is generally higher. Instantaneous measurements on redox may not necessarily reflect absolute values but allow comparisons between treatments (Van Bochove et al. 2002).

Vegetation Dynamics

Vegetation dynamics were assessed by repeated vegetation mapping at 11 years (1999), 15 years (2003), 19 years (2007) and 23 years (2011) after the start of the project. Plant nomenclature follows Van der Meijden (2005). Plant communities were assigned according to the standardized typology of Trilateral Monitoring Assessment Programme

(TMAP) (Petersen et al. 2014) which was especially developed to monitor dunes and salt marshes in the Wadden Sea region. This plant-community typology is based on the presence of characteristic or dominant plant species. Patches larger than 5 m × 5 m were mapped. Patches were assigned to a single community in case of homogeneity or when they were intermingled with another community when it covered less than 50%. In case both communities covered 50%, the patch was mapped as a mixture of both communities and accounted for 50% each in calculations of surface percentage. Surface areas of the different plant communities, taking into account mixtures, were assessed in ArcGIS (ArcMap 10.3) and subsequently converted to percentage cover.

Vegetation Structure

Vegetation structure was determined by recording vegetation height in September 2001, 13 years after the start of the various treatments, and the last year that all five grazing treatments could be compared between both sites. Vegetation height was recorded with a calibrated stick and a styrofoam disc (20 g, diameter 30 cm), once every two metres along transects from the watering point near the seawall to the fence at the very wet parts of the low salt marsh, and to the intertidal flats at the high salt marsh. Measurements were carried out along four to six transects (length between 350 and 600 m for each of the treatments). Within each paddock, individual transects were spaced at least 20 m apart.

Statistical Analyses

Surface Elevation

Differences in surface elevation between grazing regimes after 17 years were tested with a two-way ANOVA analysis with grazing (3 levels, the three sheep densities that had been maintained since the start of the project in 1988, namely, sheep densities 0, 3 and 10 sheep ha^{-1}) and section (5 levels, five sections in all paddocks with a grazing treatment) as categorical predictors and distance as a continuous variable. A post-hoc Tukey test was performed to test for differences between grazing treatments. Low and high salt marsh were analysed separately. In order to meet assumptions of normality and homogeneity of variances, we tested for homogeneity of variances tested with the Bartlett chi-square test; normal distributions of residuals were tested using visual inspection (QQ-plot). Statistics were carried out in Statistica 14.0.

Soil-Redox Potential

Averages of the five platinum electrodes were used for graphs and statistics, after correction for reference electrode (+ 192 mV), temperature and soil pH. To examine how grazing affected soil-redox condition, we ran a two-way ANOVA, with soil-redox potential as a dependent variable and grazing treatment (grazed at highest density of 10 sheep ha^{-1} vs ungrazed), depth (2, 5, 10 cm) and electrode number (1–5) as categorical predictors.

Vegetation Height

Differences in mean vegetation height between grazing treatments were tested using multiple pairwise comparisons of means adjusted for multiplicity with the Tukey-Kramer method. In order to relate vegetation height across the gradient from the watering point to the different stocking densities, we used a linear regression model that included vegetation height every two metres from the watering point. This analysis was done both for the low and the high salt marsh. The model included linear and quadratic terms of both stocking density and the distance from watering point as continuous variables. Since the model contained both linear and quadratic terms in stocking density and distance from watering point, we used sequential F tests to account for the dependence of the quadratic or the linear term. The models were fit using ordinary least squares. The ungrazed paddock on the low salt marsh contained dense stands of the tall-growing grass species *E. atherica* that were flattened. As a result, low vegetation heights were recorded that were considered to be not representative for the actual vegetation height in this paddock. Hence, we only used the mean measured vegetation height computed over all transects within one paddock in the analyses, and excluded the ungrazed paddocks in the statistical analyses on vegetation height. We used *glm* package in R (R Development Team 2010).

Results

Surface Elevation

In 2005, 17 years after the start of the project, surface elevation was significantly lower in grazed versus ungrazed paddocks, on both the low and the high salt marsh ($F_{(2,\ 64)} = 53.523$, $P < 0.001$ and $F_{(2,131)} = 22.6$, $P < 0.001$; Fig. 3). The irregular pattern in section 5 close to the intertidal flats may be related to trampling the soft substrate with *Salicornia* spp. (see Fig. 6). There was also a significant negative effect of distance to the nearest collector drain levee, but only on the low salt marsh ($F_{(5,\ 64)} = 23.979$, $P < 0.001$; Fig. 3). The ungrazed marsh had the highest surface elevation and the intermediate stocking density showed intermediate elevation in 2005, 17 years after the start of the project, but were not significantly different from each other on the low salt marsh (Tukey HSD; $P = 0.18$). Lack of replication on the high salt marsh

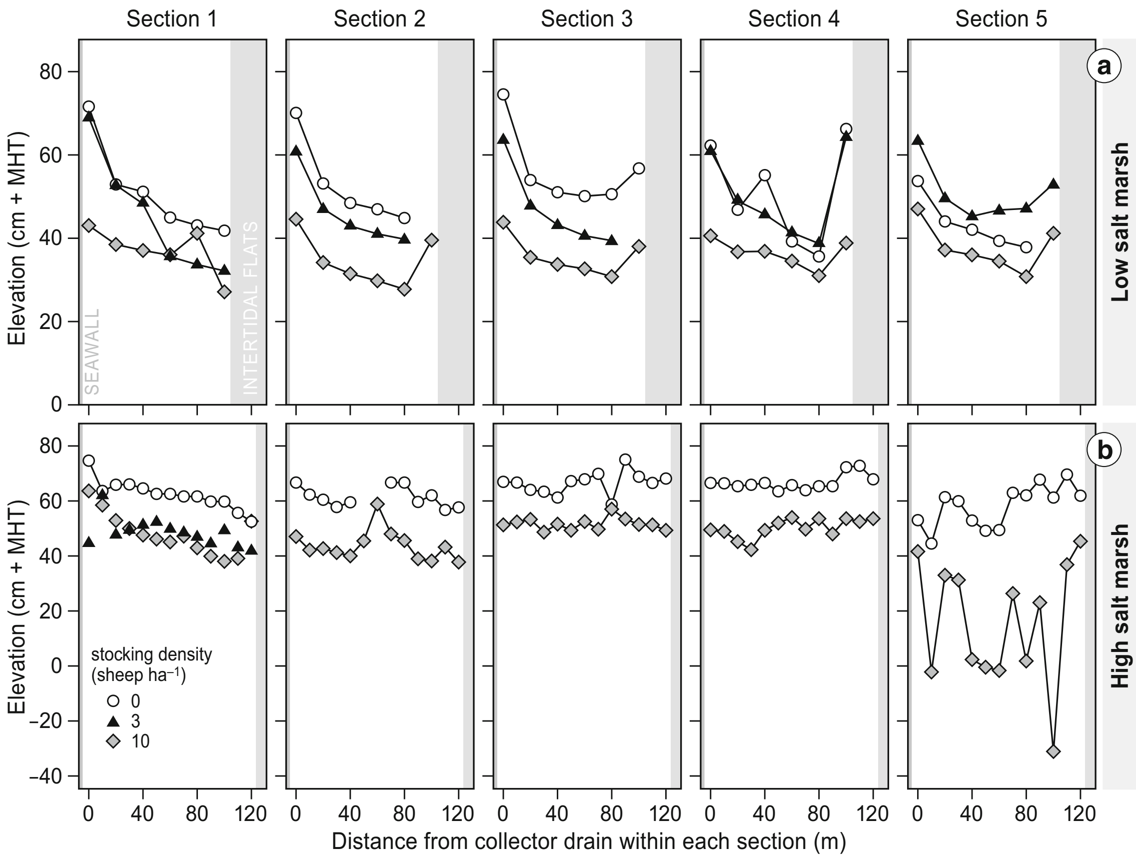


Fig. 3 Differences in surface elevation between different grazing treatments in **a** low and **b** high salt marsh in sections from seawall to intertidal flat in 2005, 17 years after the start of the grazing project. Statistics are mentioned in the text

did not allow us to test this for the intermediate treatment. On both salt-marsh types, we found the lowest surface elevation in the treatment with 10 sheep ha^{-1} compared to treatments with 3 and 0 sheep ha^{-1} (low salt marsh: Tukey HSD; $P < 0.001$, high salt-marsh: Tukey HSD; $P < 0.001$; Fig. 3). Differences in elevation between 10 sheep and 0 sheep ha^{-1} were larger on the low than on the high salt marsh. A sharp elevation decrease from the collector drain levees can be clearly distinguished on the low marsh but not on the high marsh (Fig. 3).

Soil-Redox Potential

Soil-redox potential in the grazed treatment was significantly lower in 2011, 23 years after the start of the project, both for the low ($F = 2957$; $P < 0.0001$), and the high salt marsh ($F = 111.8$; $P < 0.0001$) (Fig. 4). Grazing had, however, a much stronger effect on the low than on the high salt marsh. There was no interaction effect between grazing and soil depth on the high salt marsh. Here, both grazed and ungrazed treatment showed a marked decrease in soil-redox potential at greater depth. In the low salt marsh, stronger negative soil-redox potentials with depth were found only in the grazed treatment ($P = 0.023$).

Vegetation Dynamics

The low salt-marsh site was initially dominated by the *P. maritima* community. The tall *A. portulacoides* community had established in 1999, 11 years after cessation of grazing only at great distance from the watering point, whereas the tall *E. atherica* community established over the entire paddock, and later replaced the *A. portulacoides* community. This phenomenon also occurred at intermediate stocking densities, although the tall *E. atherica* community became less dominant, and the *P. maritima* community lawn persisted longer. Particularly, in 2003 and 2007, 15 and 19 years after the start of the project, small-scale mixtures of different plant communities were found with intermediate stocking densities. The *P. maritima* community maintained most optimally with stocking density of 10 sheep ha^{-1}, although it became infiltrated by the *Salicornia* community. In 2011, after 23 years, this community was also taken over by the tall *A. portulacoides* and *E. atherica* communities, particularly further from the watering point (Figs. 5 and 7; Table S1).

The high salt-marsh site was initially dominated by the *F. rubra* community. It became gradually overgrown by the tall *E. atherica* community after cessation of grazing, first as a small-scale mixture of the *F. rubra* and the *E. atherica*

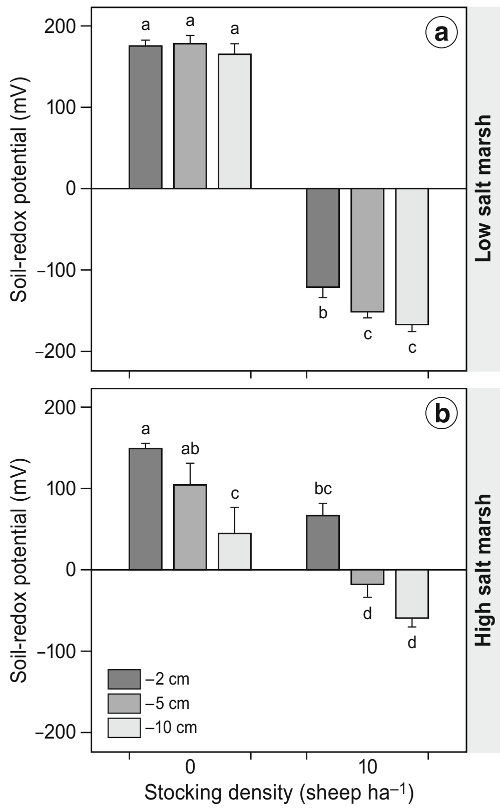


Fig. 4 Effect of grazing treatment (stocking density 0 vs 10 sheep ha^{-1}) on soil-redox potentials in **a** the low and **b** the high salt marsh in 2011, 23 years after start of the grazing project. All measurements were conducted at levees along the collector drains. Different letters indicate significant differences at $P < 0.05$

community, later as a homogeneous *E. atherica* community. The *F. rubra* community maintained in the paddock with intensive grazing, although it became infiltrated as a small-scale mixture by the *P. maritima* community near the watering point, particularly during later years. The tall *E. atherica* community did not establish. The *F. rubra* community maintained in 2003, after 15 years of grazing with lower stocking density. Unfortunately, no data are available for longer-term effects of low-intensity grazing (Figs. 6 and 7; Table S1).

Vegetation Structure

In the low salt marsh, vegetation height in 2001, 13 years after the start, revealed a striking pattern of regular peaks in the paddocks with intermediate stocking densities (Fig. 8). The peaks were situated just before the deep collector drains parallel to the seawall, which sheep could only pass close to the fence separating the treatments. Vegetation heights showed a gradual increase to a peak before a creek, dropping to a lower height just after the creek. Such patterns of peaks in vegetation height could not be detected in the high salt marsh with only shallow drains that were easily crossed by the sheep.

Mean vegetation height was significantly higher ($P < 0.001$) in the low than in the high salt marsh, except for 3 sheep ha^{-1}. In the ungrazed paddock of the low salt marsh, the vegetation height was lower due to the flattened stands of the tall-growing *E. atherica* compared to the paddock in the high salt marsh (Fig. 9).

Overall, tall vegetation (> 20 cm) dominated at both the low and high salt marsh in the ungrazed treatments in 1988, after 13 years of abandonment (Fig. 10). The treatments with intermediate stocking densities revealed the highest variation in height classes from lawn to tall vegetation (> 20 cm), except for the paddock in the high salt marsh with 4.5 sheep ha^{-1}. Treatments with the highest stocking density had only 10% vegetation < 6 cm in the low salt marsh, whereas this was 50% in the high salt marsh.

Stocking density and distance to watering point interactively affected vegetation height in both low and high salt marsh, but this effect varied among the two types of salt marsh (Table 1; Fig. S1). Vegetation height was higher and more sensitive to increasing stocking density on the low than on the high salt marsh. Overall, on both low and high salt marshes, stocking density seemed to exert a stronger influence on vegetation height than distance to watering point (Table 1).

Discussion

The aim of this study was to determine to what extent long-term management with different stocking densities drives species abiotic conditions, plant species composition and heterogeneity in vegetation structure. We hypothesised that increasing stocking density would result in increasing bulk density, hence lower surface elevation, and reduced soil-redox potential, decreasing average vegetation height with spatial variation in plant communities and vegetation height at intermediate stocking density. Our results showed that grazed areas on both low and high salt marshes, which previously experienced high stocking densities (10 sheep ha^{-1}), can be transformed from homogeneous lawn into heterogeneous vegetation, especially at intermediate stocking densities (1.5–4.5 sheep ha^{-1}). Cessation of grazing, however, resulted in tall, homogeneous vegetation, much in line with our hypotheses. Again, this effect was found on both the low and high salt marsh. The ecological mechanisms underlying the observed changes in vegetation were strongly affected by interactive effects of grazing and abiotic conditions at the various sites. These interactions will be addressed in greater detail below and are illustrated in Fig. 11.

Higher Stocking Densities Are Associated with Lower Surface Elevation

On both salt-marsh types, we found lower surface elevation with increasing stocking density, whereas vegetation

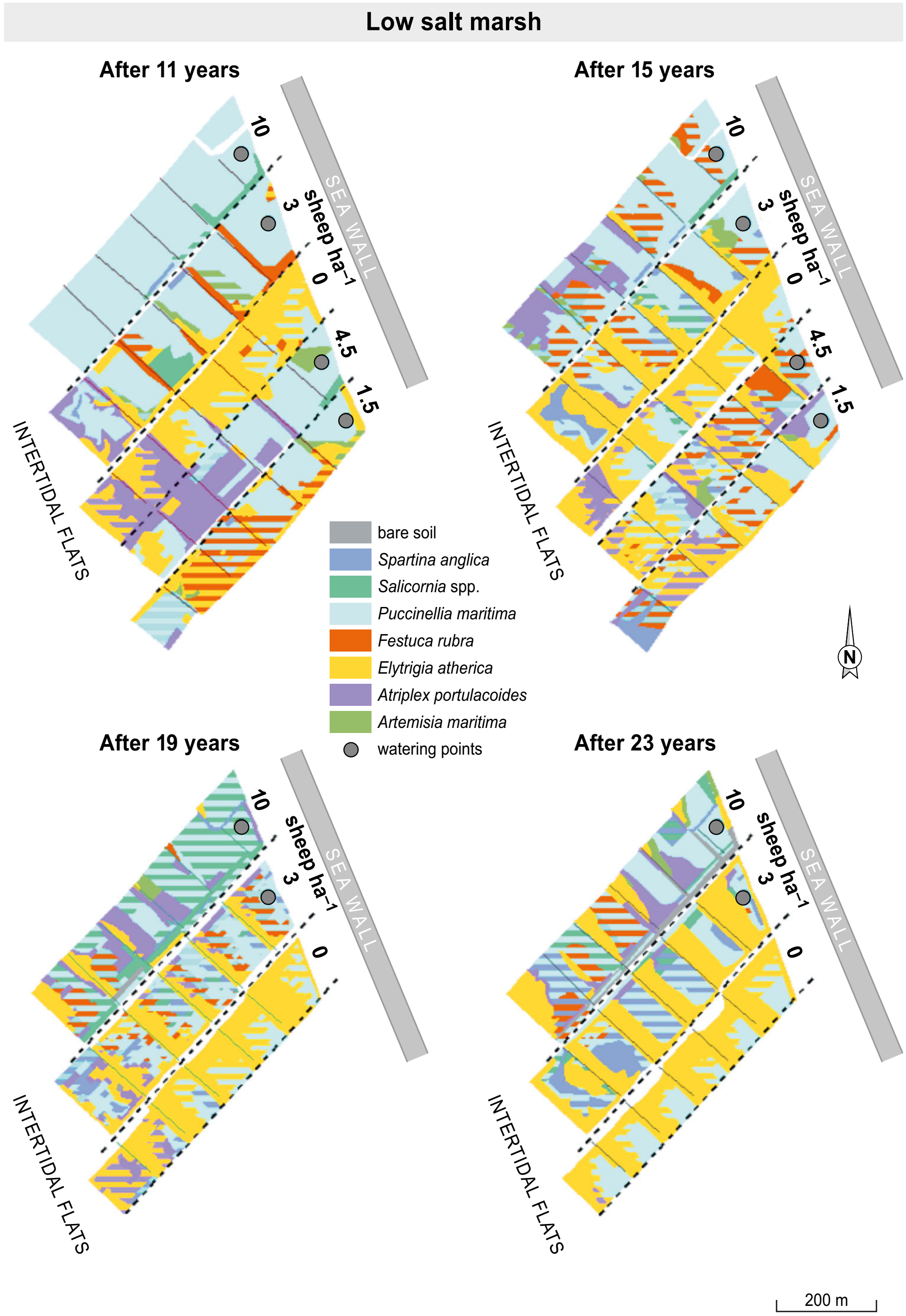
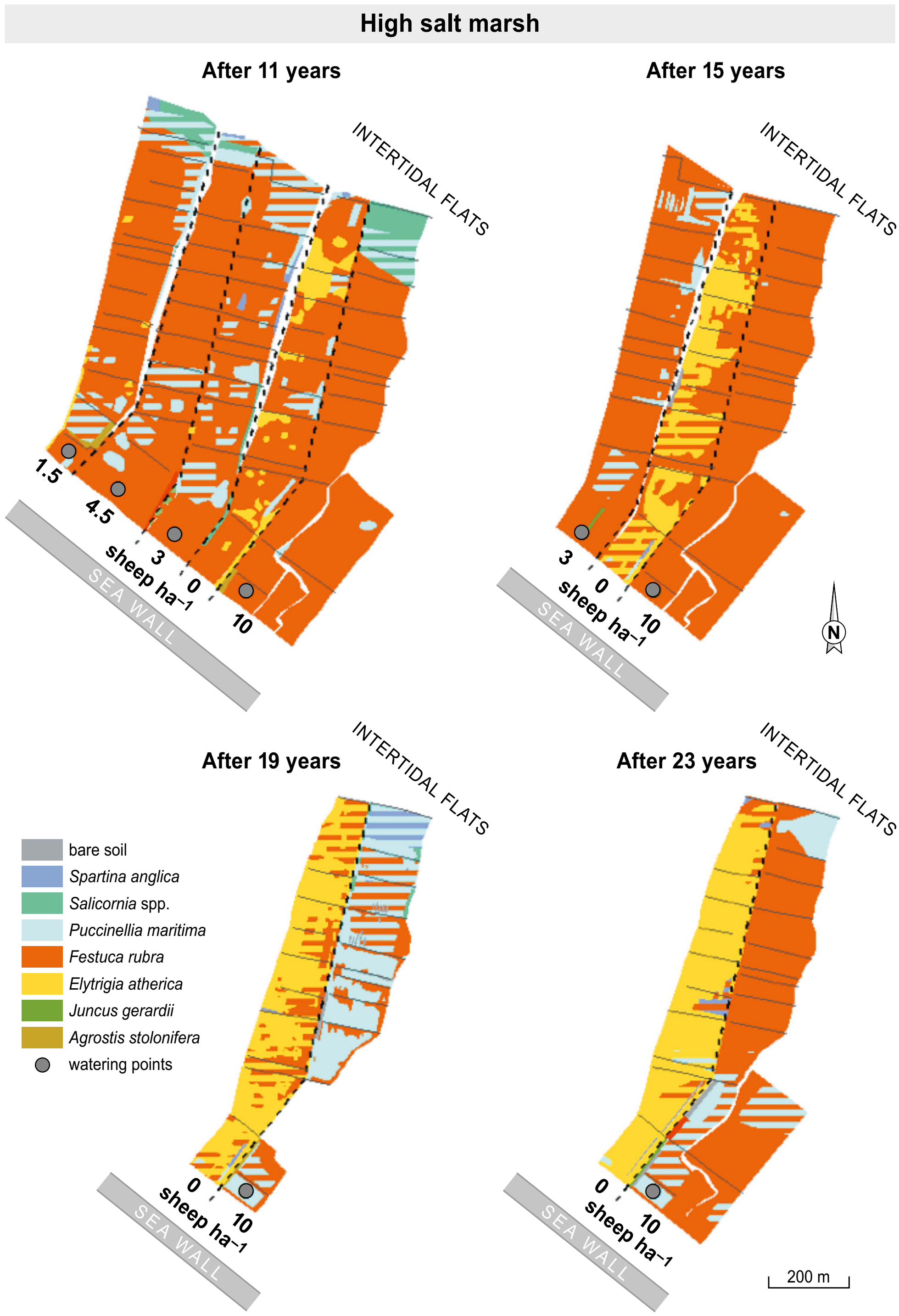


Fig. 5 Vegetation map 11, 15, 19 and 23 years after the start of grazing treatments in 1988 in the low salt marsh. Note that two treatments were discontinued after 15 years. The regular pattern of the vegetation is caused by deep smaller collector drains which could only be passed by the sheep at one point along the fence. Grazed treatments had a watering point close to the seawall (Online version in colour)

height decreased. In line with these observations is the result from our low salt-marsh study site that treatments without grazing revealed higher surface elevation change (SEC) for the period 1990–1993 compared to the grazing treatment with 10 sheep ha^{-1}. Intermediate stocking densities generally showed intermediate SEC values (Dierssen et al. 1994). Our own observations confirm this: 7 years after the start of the project, SEC was higher in ungrazed treatments (15–20 mm) than in grazed treatments (10 mm) in both our low and high salt-marsh study sites (Neuhaus et al. 1999). These elevation differences had increased 17 years after the start of the project. Larger differences between 10 sheep and 0 sheep ha^{-1} on the low than on the high salt marsh might be related to the more clayey soil in the low salt marsh (Schrama et al. 2013). This was also confirmed in a 5-year grazing trial in the Leybucht salt

Fig. 6 Vegetation map 11, 15, 19 and 23 years after the start of grazing treatments in 1988 on the high salt marsh. Note that the three intermediate treatments were discontinued after 11–15 years. Grazed treatments had a watering point close to the seawall (Online version in colour)



marsh, Germany, where different stocking densities of cattle revealed SEC 16 mm year^{-1} with 1 and 2 head of cattle ha^{-1}, 20 mm year^{-1} with 0.5 head of cattle ha^{-1} and 21 mm year^{-1} in ungrazed treatment (Erchinger et al. 1996). Unfortunately, we were not able to determine the area-specific absolute surface elevation change over the total 17-year period, because the elevation data at the start of the project could not be matched with our detailed measurements. Hence, we could not conclude a causal relationship between stocking density and elevation change in this study. Although it is possible that some of the differences in initial surface elevation were already present at the onset of the project, salt marshes emerged from sedimentation fields are generally very homogeneous and, as such, there is no reason to think that this situation was otherwise for our study area. To conclude, our observations

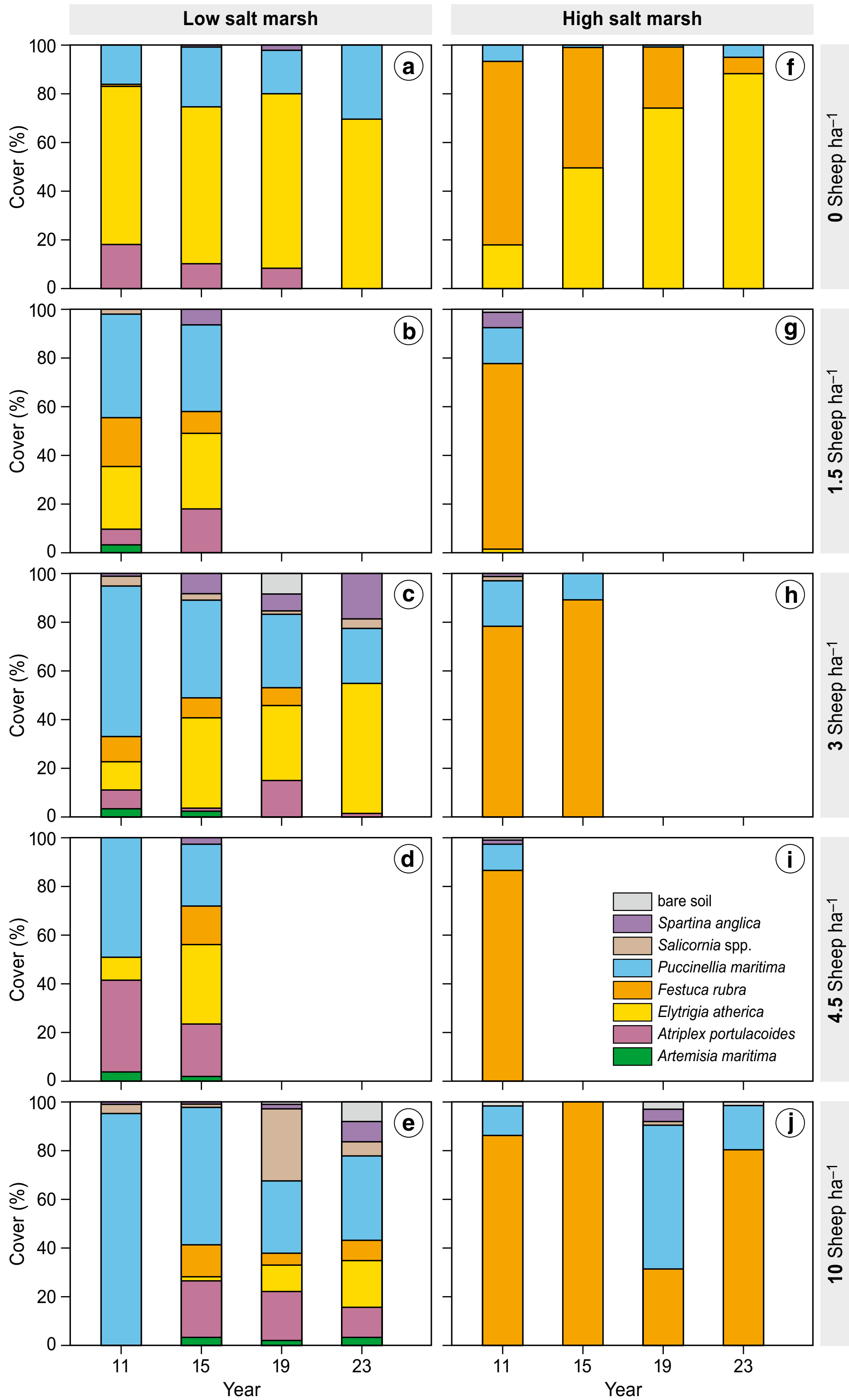
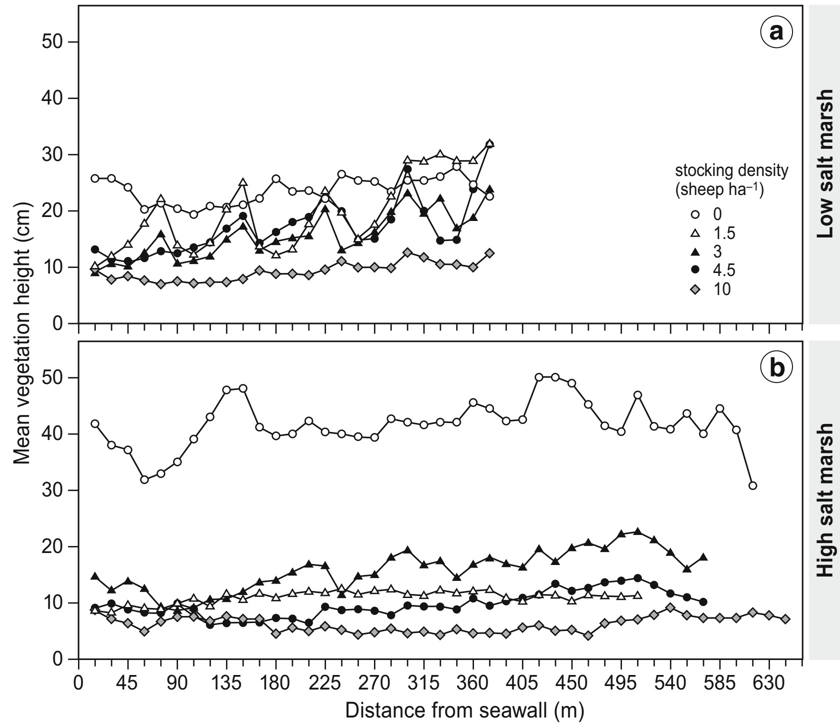


Fig. 7 Cover percentage of plant communities in individual paddocks of **a - e** in the low and **f - j** in the high salt marsh 11, 15, 19 and 23 years after the start of grazing treatments (**a, f**: 0 sheep ha -1, **b, g**: 1.5 sheep ha -1, **c, h**: 3 sheep ha -1, **d, i**: 4.5 sheep ha -1, *e, j*: 10 sheep ha -1) in 1988. Not all treatments could be maintained (Online version in colour)

are in line with the general idea that grazing leads to lower surface elevation change, but additional measurements in the study sites are needed to estimate the absolute effects for these salt marshes.

Fig. 8 Mean vegetation height (10 points pooled per 20-m stretches) at different stocking densities from the seawall to the intertidal flats in **a** the low and **b** high salt marsh in 2001, 13 years after the start of the treatments. The vegetation at the ungrazed low salt marsh was flattened; hence, the vegetation height was lower than could be expected based on vegetation composition



Higher Stocking Densities Are Associated with Lower Soil Redox Potentials

Our results indicate a significant decrease in soil-redox potential in the grazed versus the ungrazed treatments, likely reflecting differences in soil bulk density as a result of herbivore trampling. This is in line with measurements indicating that soil-shear strength, thus soil compaction, increased with subsequent low soil-redox potential with increased stocking density in our low salt-marsh site (Zhang and Horn 1996).

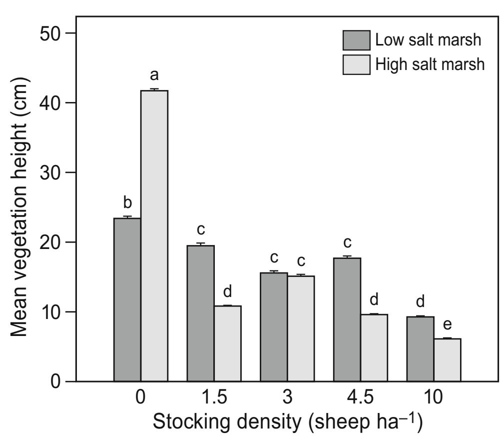


Fig. 9 Mean vegetation height with SE for different stocking densities in the low and the high salt marsh in 2001, 13 years after the start of the project. Different letters indicate significant differences at $P < 0.001$. Note: in the ungrazed low salt marsh, vegetation stands were flattened, and consequently, vegetation height was lower than could be expected based on vegetation composition

Such changes in soil-redox potential affect vegetation composition (Davy et al. 2011). Higher bulk density and an

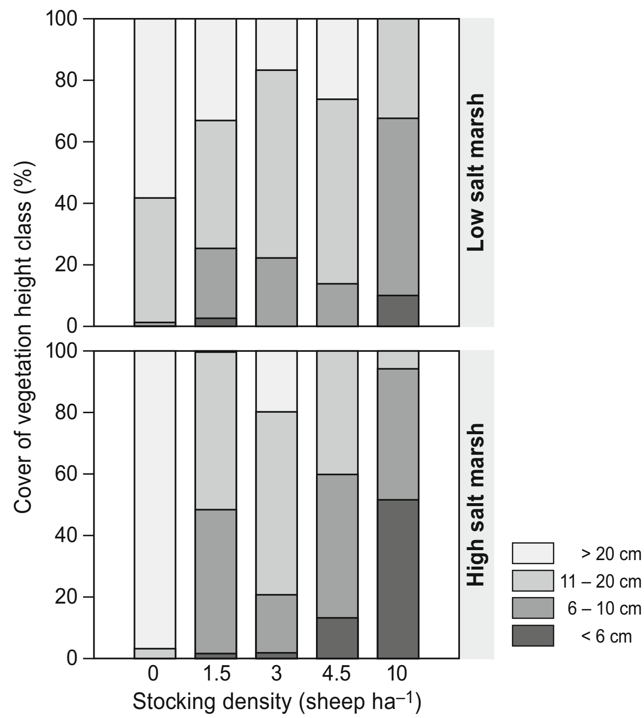


Fig. 10 Cover percentage of vegetation heights per treatment in the low and high salt marsh, 13 years after the start of the project in 1988, expressed as percentages of total number of measurements (925 in low and 1420 in high salt marsh). Frequency class > 20 cm low salt marsh is lower than could be expected based on vegetation composition with flattened vegetation at the ungrazed low salt marsh (see Fig. 8)

Table 1 Estimated coefficients and their standard errors (SE) for the regression of vegetation height on sheep stocking density and distance to the watering point in low and high salt marsh in 2001, 13 years after the start of the grazing project. Data of the ungrazed treatments were excluded from the analysis, because the tall vegetation was flattened (see text)

Site	Effect	Estimate	SE	*T*	*P* > |*T*|
Low salt marsh	Intercept	13.389	0.509	26.323	< 0.0001
	Distance from watering point	0.241	0.252	0.957	0.339
	Stocking density	1.172	0.173	6.769	< 0.0001
	(Distance from watering point)^2	0.45	0.045	10.066	< 0.0001
	(Stocking density)^2	− 0.162	0.013	− 12.069	< 0.0001
	Stocking density × distance from watering point	− 0.496	0.031	− 16.186	< 0.0001
High salt marsh	Intercept	11.703	0.339	34.48	< 0.0001
	Distance from watering point	1.092	0.061	17.778	< 0.0001
	Stocking density	− 0.977	0.174	− 5.626	< 0.0001
	(Distance from watering point)^2	− 0.001	0.002	− 0.322	0.747
	(Stocking density)^2	0.037	0.016	2.342	0.019
	Stocking density × distance from watering point	− 0.103	0.009	− 11.658	< 0.0001

associated decrease in soil oxygen as a result of grazing were previously reported for mainland salt marshes of the Wadden Sea region (Nolte et al. 2013; Chang et al. 2016), on the back-barrier salt marsh of Schiermonnikoog, the Netherlands (Schrama et al. 2013) and as well as in the meta-analysis by Davidson et al. (2017). Experimental soil compaction in a mainland salt marsh revealed increased bulk density and water logging, decreased soil aeration, soil-redox potential and cover of *E. atherica* after 2 years (Van Klink et al. 2015). Because *E. atherica* generally prefers oxygenated soils on ungrazed salt marshes (Davy et al. 2011; Sullivan et al. 2018), soil compaction through trampling and a decreased soil-redox potential may provide a mechanistic explanation for the low cover of *E. atherica* in grazed salt marshes (Schrama et al. 2013). In general, these effects were stronger on the low than the high salt marsh, which may be a result of

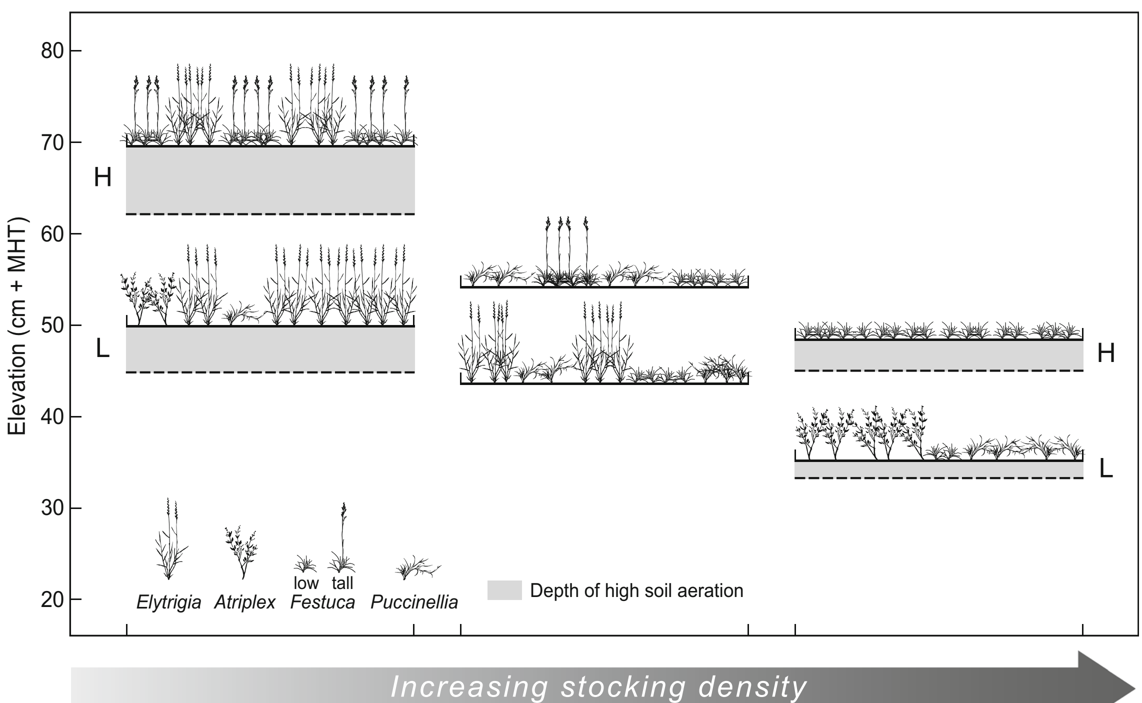


Fig. 11 Conceptual overview of the main ecological processes at play in high (H) and low (L) salt marshes that are grazed at different stocking densities after c.15 years. Differences between the start of the project and 15 years later are not indicated, as they are not recorded. The main variables include surface elevation, soil-redox conditions expressed as depth of aerobic layer, stocking density, spatial arrangement of plant communities and their structural variation

differences in clay content between both marshes. The low soil-redox potential in the grazed low salt marsh was associated with high clay content, whereas the higher soil-redox potential in the grazed high marsh was associated with low clay content, which is also in agreement with results in other salt marshes (Schrama et al. 2013). Overall, differences in soil-redox potential between high stocking density and ungrazed treatments revealed a strong effect of grazing on soils and thereby likely reflect differences in belowground oxygen stress, potentially driving some of the observed changes in community compositions.

Stocking Densities Control Vegetation Dynamics

The distribution and range of *P. maritima* in the north and *F. rubra* in the south is related to the continuum of lower lying salt marshes in the north to higher elevated salt marshes in the south (Suchrow and Jensen 2010). Establishment of the *E. atherica* community in the mid and higher elevated *F. rubra* community occurred in the southern region. Persistence of the early -successional *P. maritima* community in the salt marshes of the northern region suggests that large-scale gradients of salinity, inundation frequency and sedimentation lead to geographical variation in the pace of succession (Rupprecht et al. 2015).

The negative relation between stocking density and the concomitant increase of the *E. atherica* community in our study is in line with other salt marshes in the Wadden Sea area. At the mainland salt marsh of the Leybucht, Germany, spreading of *E. atherica* into a *F. rubra* community was observed already 8 years after cessation of cattle grazing, whereas establishment in the *P. maritima* community started after 15 years and covered the entire elevational gradient after 20 years. Spread of *E. atherica* hardly occurred in the treatments with 1 or 2 head of cattle ha^{-1}, whereas in the treatment with 0.5 head of cattle ha^{-1}, a considerable spread of the *E. atherica* community into the low and the high salt was observed (Andresen et al. 1990; Bakker et al. 2003).

Retrogressive succession under grazing regimes on the high salt marsh such as observed in this study, for example the establishment of the *P. maritima* community in the *F. rubra* community, might be explained by intensive grazing and trampling near the watering points. Overall, these results provide support for our hypothesis that grazing regimes are a major determinant of the distribution of plant communities on the salt marsh.

Vegetation dynamics in grazed salt marshes along the Wadden Sea are in line with salt marshes in other parts of the world. The rate of change in a salt marsh in the UK in which *Spartina anglica* is dominant to a predominantly *Phragmites australis* marsh (ungrazed) or to a *Puccinellia maritima* marsh (grazed by sheep) was estimated to be of the order of 8 and 10 years (Ranwell 1961). Mid-Atlantic organic salt marshes in America constitute almost complete monocultures of *Spartina alterniflora* when not grazed, while salt marshes that are grazed by horses have different plant communities (Furbish and Albano 1994). Grazing on the dominant grass *Spartina densiflora* resulted in decrease of light competition and increased the number of plant species in a South-Atlantic marsh in Argentina. It led to patch-to-patch dissimilarity by increasing spatial variability (Daleo et al. 2017). Cattle grazing in a Chilean salt marsh strongly reduced aboveground biomass and suggested an effect on species composition, This effect was, however, smaller than in European salt marshes as the plant communities in those marshes often have many more species than the Chilean marshes (Fariña et al. 2016). Coastal grassland species established in monocultures of *Phragmites australis* after resumption of cattle grazing in marshes along the Baltic (Sammul et al. 2012). Livestock is used to counteract spreading of the invasive wetland plant *Phragmites australis* in the USA (Silliman et al. 2014).

Stocking Densities Determine Vegetation Height and Induce Spatial Heterogeneity

At both the low and high salt marshes, mean vegetation height decreased with increasing stocking density. Although this pattern was broadly similar between sites, it was more pronounced in the low than the high salt marsh. The negative relationship between herbivore density and mean vegetation height accords with results of the meta-analysis by Davidson et al. (2017). It is also in line with higher soil shear strength near the seawall (Zhang and Horn 1996). Andresen et al. (1990) found increasing vegetation height of the *Aster tripolium* layer with increasing distance to the seawall on the mainland salt marsh of Leybucht, Germany. Intermediate stocking densities revealed the highest variation in vegetation height. These results coincide with a previous study in our high salt marsh-site that showed that high spatial variation between stands < 10 cm and ≥ 10 cm was found at scale of $10\ m \times 2\ m$ in paddocks with intermediate stocking densities, especially 3 sheep ha^{-1} (Berg et al. 1997). A similar phenomenon has also been demonstrated within a plant community at the plot scale ($< 100\ m^2$) in a pasture in Argentina (Cid and Brizuela 1998), which indicates that this may be a general pattern.

Besides a strong effect of stocking density on vegetation height and structure, there was also a significant impact of the position of watering points. Lawns dominated by *P. maritima* and *F. rubra* increased closer to the watering point and with increasing stocking density. Not only do these species have a high nitrogen content (Minden and Kleyer 2014), but also a high sugar content too. The latter explains why these species are selectively grazed (Fokkema et al. 2016). Both species also have a high regrowth potential (Kleyer et al. 2008). Tall vegetation dominated by superior light competitors such as

A. portulacoides and *E. atherica* increased further away from the watering points, which is likely caused by lower grazing intensity further away from the watering point. Adler and Hall (2005) modelled the effects of watering points on vegetation height with various stocking densities. According to this model, an increase in stocking density will increase the portion of the gradient affected by grazing, since animals will have to walk farther to meet their daily requirements. The significant interaction between stocking density and distance to watering point on vegetation height in our study may thus indicate that sheep in higher stocking densities removed more biomass and grazed further away from the watering point to meet their requirements. Overall, our results show that two major factors determine salt-marsh vegetation height and structure on grazed marshes: stocking density and the distance to watering points.

Management Implications for Coastal Protection and Wildlife

Implications for coastal protection As we show in this study, grazers decrease surface elevation compared to ungrazed sites through trampling, with subsequent negative effects on soil-redox potential, probably due to increased soil compaction and bulk density. Possible reduced surface elevation change (SEC) may render it difficult for salt marshes to cope with increased sea-level rise (SLR) and thereby threaten coastal protection efforts (Bouma et al. 2014). Furthermore, livestock grazing reduces vegetation height, which has negative effects on wave dissipation (Knutson et al. 1982; Möller 2006). Increased bulk density in grazed soils may, however, increase resistance to erosion by waves. In addition, higher below-ground biomass in grazed salt marshes (Davidson et al. 2017) may also increase resistance against wave action. Hence, livestock grazing might enhance coastal protection as long as SEC is higher than the 4.5 mm year^{-1} which is the scenario for SLR where emissions of greenhouse gases stabilize around 2100 (IPCC 2013). The resulting effect of these opposing forces on the vulnerability to SLR therefore depends on the local importance of each of these components. In general, marsh vulnerability tends to be overstated because assessment methods often fail to consider biophysical feedback processes known to accelerate soil building with SLR (Kirwan et al. 2016). How grazing affects the balance and trade-offs between SEC, vegetation height, bulk density erosion and wave action is likely dependent on the local context of a given salt march and, as such, requires further research.

Implications for Biodiversity Management Abiotic conditions such as surface elevation and soil-redox potential are important predictors for the occurrence of salt-marsh plant species and characteristic plant communities. Grazers in turn modify these abiotic conditions. Our results suggest that, together, they shape the ecological context of grazed and ungrazed salt marshes, with major implications for local salt marshes. High stocking density results in homogeneous lawn, whereas moderate stocking density creates salt marshes with heterogeneous vegetation including both lawn and tall vegetation. Plant communities, however, irrespective of being located on a low or high salt marsh, often converge to a similar community dominated by *E. atherica* after cessation of grazing. Hence, the number of plant communities (which takes into account abundance of species) at the landscape scale depends on grazing management. Total number of plant species (which implies presence of species) at landscape scale did, however, not differ between grazed and ungrazed salt marshes (Wanner et al. 2014). Grazing management did, however, affect plant species richness at the small scale. Lawn in salt marshes harbours relatively high plant species richness at the plot scale compared to tall vegetation (Bos et al. 2002). Domination of late-successional tall *E. atherica* can be prevented by high-intensity grazing, for instance 10 sheep ha^{-1} (this study), 1 head of cattle ha^{-1} (Bos et al. 2002; Van Klink et al. 2016) or 1 horse ha^{-1} (Van Klink et al. 2016). Species of grazers in salt marshes have different effects. Cattle as ruminants require less food per day, compared to horses as hind-gut fermenters (Duncan et al. 1990). Consequently, horses remove a higher amount of biomass per animal and may be less selective. Horses also travel longer distances per day and spend more time grazing than cattle. Horses more often forage on short *Puccinellia maritima*, where sheep and cattle diet contain more *Aster tripolium* (Kiehl et al. 1996; Nolte et al. 2017). Sheep select on *Aster tripolium*.

Long-term monitoring, like the one described in this study, is necessary to obtain a clear picture of the effect of stocking densities and indicates that management should take its time to evaluate changes in grazing management. Kiehl et al. (1996) previously reported that vegetation height showed the greatest variation in the treatment where grazing was discontinued after only 4 years of study on our low salt marsh. Our results covering 13 years revealed, however, very low variation in height classes in the ungrazed treatment compared to the various grazed treatments. Another salt marsh that was abandoned after it was previously intensively grazed produced a wealth of flowering plants and attracted many invertebrates in the first few years after abandonment (Irmler and Heydemann 1986). However, tall-growing plant species took over in the 10 years after abandonment, outcompeted low-statured plant species and their characteristic invertebrate species, apart from the treatments with high stocking density (Andresen et al. 1990).

Cascading Effects on Higher Trophic Levels It is well known that species richness of a single group of organisms may not serve as a useful proxy for overall biodiversity on salt marshes (Davidson et al. 2017). This implies that results of this study, which largely focused on the response of plant species richness and structure to stocking densities, might not be directly translatable to higher trophic levels. Nonetheless, previous studies have shown that grazing pressure has direct, cascading effects on higher trophic levels, most notably on insects (Evans et al. 2015; Van Klink et al. 2016) and spring-staging geese (Bos et al. 2005), which are hardly found on long-term abandoned salt marshes. Fishes are, however, more abundant in ungrazed marshes (Levin and Ellis 2002). Moreover, increased structural heterogeneity, as found in the intermediate grazing treatments of this study, has previously been shown to affect communities of higher trophic levels. Some breeding birds (Norris et al. 1997) and some invertebrates (Pétillon et al. 2005) prefer patches with taller vegetation. Also at our site, cascading effects on higher trophic levels have been subject of a number of studies. In 2010, 22 years after the start of the project in this study, 54 arthropod species were sampled in homogeneous lawn, homogeneous tall vegetation and in lawn and tall vegetation within heterogeneous vegetation (Van Klink et al. 2013). Most species showed a clear preference for either short or tall vegetation, but some species were most abundant in grazed mosaics. Arthropod richness and composition were similar in patches of lawn in plots with moderate and high stocking density, while patches of tall vegetation were similar to ungrazed plots. Grazed mosaics were not richer in species than homogeneous tall vegetation, despite the co-occurrence of species from homogeneous short or tall, and heterogeneous vegetation. Half of the species were salt-marsh specialists, and half were generalists (Van Klink et al. 2013). Several species of arthropods had been lost from the ungrazed plots, which had been present 2 years after the start of the grazing project (Meyer et al. 1995; Meyer and Reinke 1996). Nevertheless, the ungrazed marshes were still most species rich, which can mostly be attributed to an increase of non-habitat specialists (Van Klink et al. 2013). Following these results as well as results from other studies, we propose to preserve an optimum wildlife diversity at various scales, a large-scale mosaic of different grazing regimes (including no grazing and rotational grazing), inducing a maximum variety of different plant communities with flowering species (Wanner et al. 2014; Van Klink et al. 2016; Esselink et al. 2017).

Acknowledgements We thank the participants of the Coastal Ecology Expeditions 1999, 2003, 2005, 2007, 2009 and 2011 of the University of Groningen for their help in collecting data. Dick Visser enhanced the figures.

Authors' Contributions M.St. conceived the project, J.B., M.Sc. and R.V. designed the field sampling methodology, M.Sc., P.E., P.D., S.N., R.V., Y.V. and M.St. collected the data, N.B. analysed the data with input from P.D., M.Sc. and R.V., J.B. led the writing of the manuscript, all authors contributed critically to the drafts and gave final approval for publication.

Funding Information This study was partially supported by the 'Waddenfonds' (Project WF200451).

Data Availability Data will be uploaded and available from the University of Groningen Data Repository DataverseNL Dataverse Network (https://dataverse.nl/dvn/dv/GELIFES, permanent handle: https://hdl.handle.net/10411/34QBYP).

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