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Utilisation of Wadden Sea salt marshes by geese in relation to livestock grazing

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Summary

To arctic breeding geese, the salt marshes of the International Wadden Sea are important spring staging areas. Many of these marshes have always been grazed with livestock (mainly cattle and sheep). To evaluate the influence of livestock grazing on composition and structure of salt-marsh communities and its consequences for habitat use by geese, a total of 17 pairs of grazed and ungrazed marshes were visited both in April and May 1999, and the accumulated grazing pressure by geese was estimated using dropping counts. Observed grazing pressure was related to management status and to relevant vegetation parameters.

The intensity of livestock grazing influences the vegetation on the marsh. Salt marshes that are not grazed by livestock are characterised by stands with a taller canopy, a lower cover of grasses preferred by geese, and a higher cover of plants that are not preferred.

Overall goose-dropping densities are significantly lower in ungrazed marshes compared to marshes grazed by livestock. Some ungrazed marshes had comparatively high goose grazing pressure, and these were all natural marshes on a sandy soil, or artificial mainland marshes with a recent history of intensive livestock grazing. Goose grazing is associated with a short canopy. The plant communities with short canopy, dominated by *Agrostis stolonifera*, *Festuca rubra* and *Puccinellia maritima*, together account for 85% of all goose droppings in our data.

The sites that were not visited by geese differed very little from those that were visited, in the parameters we measured. This might indicate that there was no

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shortage of available habitat for spring staging geese in the Wadden Sea, in the study period.

Introduction

Goose grazing and salt-marsh management

Salt marshes in the International Wadden Sea serve as feeding grounds for spring staging geese, preparing for migration to breeding areas in the Arctic. Barnacle Geese (*Branta leucopsis* (Bechst)) utilise the marshes mainly from February to April, with an increasing number present during May (Stock & Hofeditz, 2000; Engelmoer, Taal, Wymenga E & Kuipers, 2001), while Brent Geese (*Branta bernicla bernicla* (L.)) are mainly present from March until the end of May (Ebbinge et al., 1999). Feeding conditions during this period are crucial for future reproductive success, as reproductive output of geese is strongly related to the amount of fat and protein reserves accumulated during spring (de Boer & Drent, 1989; Ebbinge, 1989; Prop & Black, 1997). To a large extent, these feeding conditions will be determined by the vegetation composition and canopy height of the marsh, because plant species and plant parts differ in their palatability for geese. Vegetation composition is strongly related to the management of salt marshes, for example grazing with livestock (Beeftink, 1977; Jensen, 1985; Bakker, 1989; Esselink, Zijlstra, Dijkema, & van Diggelen, 2000; Gettner, Heinzel, & Kohlus, 2000).

Salt marshes that have never been grazed by livestock are found at some Wadden Sea islands. Under ungrazed conditions, salt-marsh vegetation changes due to natural succession, i.e. succession in the absence of livestock grazing (Roozen & Westhoff, 1985; Westhoff & van Oosten, 1991; Bakker, Esselink, van der Wal, & Dijkema, 1997; Leendertse, Roozen, & Rozema, 1997). Continual input of nitrogen by sedimentation is put forward as the major factor driving natural succession. The rate of sedimentation depends on the frequency and duration of tidal inundation (van Wijnen & Bakker, 1997), strongly determined by soil elevation. Increasing availability of nitrogen, favours the growth of the later successional tall grass *Elymus athericus* (Kerguelen) at high marsh elevation and the tall forb *Atriplex portulacoides* (L.) at the lower marsh (Olff et al., 1997; van Wijnen & Bakker, 1997). Both plant species are not preferred by geese and outcompete the preferred forage species *Plantago maritima* (L.), *Triglochin maritima* (L.), *Puccinellia maritima* (Parlatore) and *Festuca rubra* (L.) (Prop & Deerenberg, 1991, van der Wal, van Wijnen, van Wieren, Beucher, & Bos, 2000b). Subsequently, goose grazing decreases when marshes become too productive (van de Koppel, Huisman, van der Wal, & Olff, 1996). Grazing by hares (*Lepus europaeus*, Pallas) has been shown to retard vegetation succession (van der Wal et al., 2000b) to a certain extent.

Most of the salt marshes in the Wadden Sea have traditionally been grazed by livestock (Esselink, 2000). Cattle and sheep prevent accumulation of biomass, and create a short canopy and high cover of plant species preferred by geese and hare (Bakker et al., 1993; Olff et al., 1997), thus positively affecting the feeding conditions for geese (Aerts, Esselink, & Helder, 1996). Depending on the stocking rate (animals ha^{-1}) a homogeneous short sward results at high stocking rate, dominated by few species, or a diverse vegetation pattern with alternating patches of short and tall swards at low stocking rate (Dijkema, 1983; Aerts et al., 1996; Berg, Esselink, Groeneweg, & Kiehl, 1997; Kiehl, 1997). In the past decade, however, there has been a reduction in agricultural use along the coast of Niedersachsen, Germany (Potel & Südbeck, 1994) and livestock grazing stopped on 42% of the mainland marshes in Schleswig–Holstein, Germany (Stock & Kiehl, 2000), as a result of policies promoting natural development of the marsh ecosystem (Kempf, Lamp, & Prokosch, 1987; Stock, Kiehl, & Reinke, 1997; Stock & Kiehl, 2000). In the Netherlands and Denmark about 40% and 10% of the salt marsh area is ungrazed, respectively (Kempf et al., 1987; de Jong et al., 1999).

Other factors affecting succession and goose grazing

There is a difference between artificial mainland marshes and the natural marshes on the barrier islands of the Wadden Sea, as these differ in soil composition. The barrier marshes, or barrier-connected marshes according to de Jong et al. (1999), have a relatively thin layer of clay on top of a sandy sub-soil. In contrast, the artificial mainland marshes with sedimentation fields feature a thick layer of clay and salt marsh maturation is to a large extent driven by the change in elevation as a result of sedimentation (de Leeuw, de Munck, Olff, & Bakker, 1993). This has important consequences for the availability of nitrogen and drainage, the rate of vegetation succession, and presumably also for the final stages of succession. Marsh type is thus an important source of variation for vegetation composition and hence also for the feeding conditions of geese. Human-related disturbance may have negative consequences for geese, potentially rendering areas entirely unsuitable as habitat (Madsen, 1995; Bos & Stahl, 2003). Disturbance effects may hypothetically be more pronounced where there are many people (Stock & Hofeditz, 1996), or where marshes are small and people may approach the animals more readily.

Objective

In this study we evaluate the importance of livestock grazing for habitat use by geese. Our basic hypothesis is that livestock grazing affects the habitat choice of Brent and Barnacle Geese, via the impact on foraging conditions. Evidence to support this hypothesis has been derived from local studies (Aerts et al., 1996; Stock & Hofeditz, 2000), but the finding has not been generalised for the entire Wadden Sea in a comparative survey. We indirectly assess the foraging conditions using parameters of vegetation composition, canopy height and tiller density. Other factors examined are the availability of freshwater for drinking, the presence of hares and human disturbance, as each of these may hypothetically affect the suitability of the marsh for geese.

Methods

We established 63 transects, divided over 38 study sites (see Appendix A), based on the following criteria. Sites chosen were restricted to those with a stable and clearly defined management for at least the 6 preceding years. Only marshes with sufficiently large surface area (>5 ha), such that a flock of geese could land without inhibition, were included. The sites were distributed over the entire Danish ($n=11$), German ($n=17$) and Dutch ($n=10$) Wadden Sea. Twenty-two sites harboured transects in marshes with at least two different grazing regimes at similar abiotic conditions, a situation we specifically aimed at in order to be able to eliminate confounding effects. Seventeen sites with paired transects were visited twice, once in April and once in May 1999, and so were some of the unpaired transects (Appendix A). The remainder were only visited once. In 14 cases this was because of the lack of a paired comparison, which made them less useful for our purpose, but logistical reasons also played a role. Management was subdivided in 'long-term ungrazed' (>10 years), 'short-term ungrazed' (6–10 years), 'lightly grazed', i.e. with low stocking rate ($\leqslant 4.5$ sheep ha^{-1} or $\leqslant 1$ cow ha^{-1}) and 'intensively grazed', i.e. with high stocking rate. 'Short-term ungrazed' transects are those transects that had a relatively recent change in management from high stocking rate to ungrazed (6–10 years before). Grazed marshes were classified as being sheep- or cattle grazed. The transects on barrier marshes in our study are, with one exception, only visited by Brent Geese, while most transects on mainland marshes are utilised by Brent and Barnacle Geese. Barrier marshes feature natural drainage by creeks, while mainland marshes are artificially drained by ditches.

For each management regime at each site, one transect was placed perpendicular to the seawall and the coastline, along the entire extent of the marsh. Transects were thus variable in length and included high-, mid- and lower marsh sections in proportion to presence. Transects ranged from 0.1 to 1 km. Twenty plots of 4 m^2 were sampled per transect, with plots distributed equally over the length of the transect. The accumulated number of goose and hare droppings in these plots were counted. Goose-dropping densities are a good measure of grazing intensity, as geese defecate very regularly (Owen, 1971). We could not discriminate between droppings of Brent or Barnacle Geese. Dropping densities and grazing pressure by hare are also correlated (Langbein, Hutching, Harris, Stoate, & Tapper SC & Wray, 1999). Hare droppings were distinguished from rabbit droppings by shape and size. For three transects at one site, the results of the dropping counts were likely to have been affected by spring tide during the preceding 14 days, as assessed using tide tables and observations in the field. These transects have not been included in the data set. For the other transects, there were no indications that the results were compromised by high tides over this time period.

The vegetation at each plot was assigned to a plant community using a key based upon the salt-marsh typology from de Jong et al. (1998) (see Appendix B). Nomenclature of species follows van der Meijden (1990). Vegetation composition was described using five parameters: (1) percentage cover of preferred grasses (*Lolium perenne* (L.), *Poa* sp., *A. stolonifera* (L.), *Puccinellia maritima* and *F. rubra*), (2) percentage cover of tall plant species (*E. athericus, A. portulacoides, A. maritima*, *Spartina anglica* (H & J Groves) and standing dead remnants of *Aster tripolium* (L.)), (3) joint abundance of *Plantago maritima* and *T. maritima* (absent, present and abundant ($>3\%$ cover)) and (4) canopy height. Canopy height was measured five times per plot to the nearest 0.5 cm using a styrofoam disc (20 cm ∅, 24 g), sliding along a graduated stick, randomly dropped on the vegetation. Finally, we measured (5) tiller-density in the *F. rubra* and *Puccinellia maritima* communities using a quadrat of 25 cm^2. A tiller was defined as a group of leaves with one meristem, often surrounded by senescing leaves. Additional plots were randomly placed in *F. rubra* and *Puccinellia maritima* communities at each transect, and sampled for the parameters mentioned above, to arrive at a minimum sample size of five for these communities. Hereby we obtained a more balanced set of data for these communities to study effects of livestock grazing at the level of the plant community.

For each transect, an index of disturbance was assessed covering three classes: undisturbed, moderately disturbed or heavily disturbed (see Appendix A). This index was based on our field impression, the distance to nearest roads, towns and recreational pressure. Distance to a fresh water source (km) was assessed in the field, aided by a topographical map. Transect length was used as the measure for lateral extent of the marsh.

Statistical analyses

Observed goose-dropping densities were related to factors at two levels of explanation and three levels of aggregation (transect-, plant community- and plot-level). At a high level of aggregation, the transect level, we averaged the dropping density and vegetation parameters over the 20 plots per transect and related them to livestock grazing regime, salt-marsh type (mainland versus barrier marsh) and month of sampling as fixed factors in a General Linear Model (GLM). The incidence of plant communities per transect (%) was calculated as the proportion of observations of each community on the total of 20 plots sampled per transect. In the analysis of dropping densities, we limited the selection of transects to those sites where two contrasting management regimes were sampled in both months. Transect length (lateral extent), the index of disturbance, freshwater availability and average hare dropping densities were included as covariates, while site and the interaction between month of sampling and grazing regime were included as factors in the GLM. Dropping density was also directly related to vegetation parameters (vegetation composition, canopy height, tiller density and combined abundance of *Plantago maritima* and *T. maritima*) using GLM, after the correlations between vegetation composition, canopy height and tiller density were examined using Pearson's correlation test. We applied contingency tests in order to examine whether differences existed in the proportion of grazing regimes or marsh types that had no signs of goose grazing at all.

At a lower level of aggregation, the level of individual plant communities, all data were averaged per plant community and per transect, and differences between plant communities were tested using the Kruskal–Wallis test (K–W test). The additional plots that we had sampled were included in these analyses. Within the plant communities dominated by *Puccinellia maritima* and *F. rubra*, we also studied the effect of livestock grazing regime, salt-marsh type, average hare-dropping density and month of sampling in a GLM. For the analyses of goose-dropping densities at the plant community level, only those sites were selected where geese had been observed in any of the months. Canopy height and dropping density at the plot level were related to distance from the seawall for each grazing regime separately, while correcting for site, using GLM.

Arcsine and log-transformations were used for percentage values and canopy height, respectively (Zar, 1996). The non-parametric K–W test was employed where the statistical assumptions of normality and homogeneity of variances were not appropriate.

Results

Effects of livestock grazing on marsh vegetation

The vegetation composition was significantly related to livestock grazing on mainland marshes (Fig. 1), but these differences were less pronounced on barrier marshes. Incidence of communities characterised or dominated by short grasses (*Puccinellia maritima, F. rubra, A. stolonifera* and *Juncus gerardi* (Loisel.)) was higher at intensively grazed marshes and decreased with reduced stocking rates (GLM factor grazing, $F_{3,58} = 23.9$, $P < 0.001$). The incidence of communities dominated by tall plants (*E. athericus* , *A. portulacoides* and *A. maritima*) increased with lower stocking

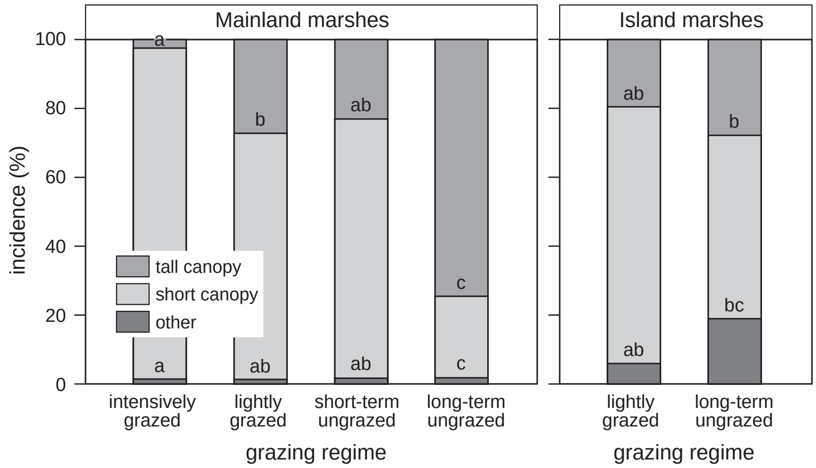

Figure 1. Incidence of communities on salt marshes, grouped by height of the canopy, in relation to livestock grazing regime and marsh type. The group with short canopy includes the communities *Puccinellia maritima, Limonium vulgare*, *Juncus gerardi*, *Agrostis stolonifera* and *Festuca rubra*. The group with tall canopy includes *Elymus athericus*, *Atriplex portulacoides* and *Artemisia maritima*. See Appendix B for a key to identification of the communities in the field. Grazing regimes that do not share the same letter within a class of communities differ significantly from each other ($P < 0.05$).

Table 1. Pearson correlation coefficients for vegetation parameters at the community level. All correlations are significant at the 0.01 level

	TP	PG	CH	TD
Cover of tall plants (TP)		−0.67	0.86	−0.30
Cover of palatable grasses (PG)			−0.61	0.39
Canopy height (CH)				−0.39
Tiller density (TD)				

rates of livestock (GLM factor grazing, $F_{3,58} = 19.7$, $P < 0.001$).

The vegetation parameters canopy height, cover of edible grasses, cover of structural elements and tiller density were strong and significantly correlated to each other at all levels of aggregation (Pearson's correlation, all $P < 0.01$, Table 1). For this reason only the data for canopy height will be further analysed. The canopy height of marsh vegetation strongly differed between communities (Fig. 2A, K–W test, $\chi 2 = 75.4$, $P < 0.001$). Communities dominated by *Puccinellia maritima*, *F. rubra* and *A. stolonifera* had significantly lower canopy than communities dominated by *E. athericus*, *A. portulacoides* and *A. maritima*. But even within plant communities, a relationship was found between livestock grazing and relevant habitat parameters for small herbivores. Under ungrazed circumstances, the communities dominated by *Puccinellia maritima* and *F. rubra* on mainland marshes, had taller canopies (Fig. 3A, GLM, $F_{3,84} = 21.3$, $P < 0.001$). Barrier marshes had a lower canopy height for a given livestock grazing regime (Fig. 3A, GLM, $F_{1,84} = 5.4$, $P = 0.022$). The index of combined abundance of *Plantago maritima* and *T. maritima* was higher for barrier marshes (K–W test $\chi^2 = 9.3$, $P < 0.005$) than for mainland marshes. We were unable to detect differences in the vegetation parameters studied for the two species of livestock (sheep or cattle). Canopy height significantly increased with distance from the seawall in 33% of the marshes (GLM, interaction of distance and site significant), while in 54% there was no relationship.

Goose grazing in individual plant communities

Different plant communities had significantly different goose grazing pressure (Fig. 2B, K–W test, $\chi 2 = 38.1$, $P < 0.001$). The communities dominated by *Puccinellia maritima*, *F. rubra* and *A. stolonifera*, had higher utilisation by geese. These communities together accounted for 85% of all goose droppings in our data. Within plant communities, differences between levels of livestock grazing (Fig. 3B) were tested for the *F. rubra* and *Puccinellia maritima*, communities. Higher dropping densities were found with increased intensity of livestock grazing (GLM, $F_{3,85} = 3.6$, $P < 0.017$), with higher dropping densities at the barrier connected marshes (GLM, $F_{1,85} = 14.1$, $P < 0.001$) than at the mainland marshes.

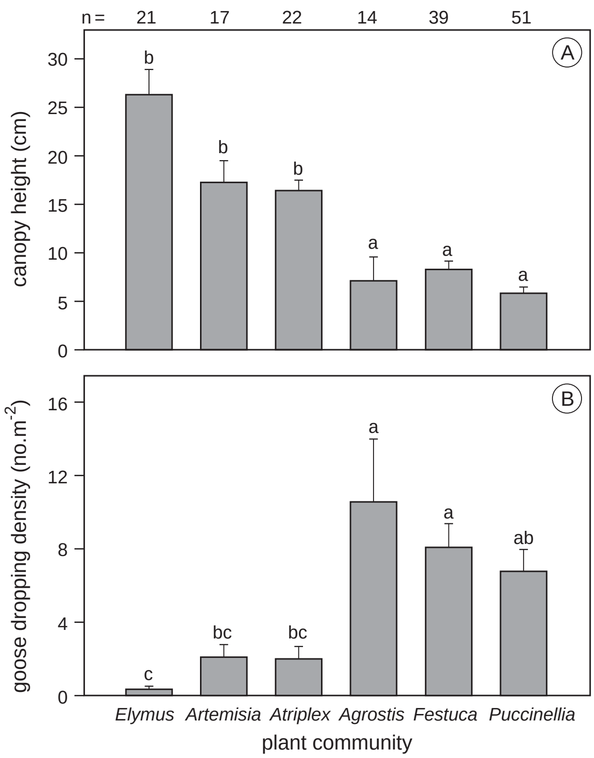

Figure 2. (A) Canopy height of salt marsh vegetation for the six plant communities that were most frequent in the dataset. Data refer to all transects. (B) Grazing pressure of geese per plant community. Only data for sites that were visited by geese are used. Bars that do not share the same letter differ significantly from each other ($P < 0.05$).

Goose grazing in transects

Grazing pressure by geese at the transect level increased significantly with the intensity of livestock grazing regime (Fig. 4, GLM, $F_{3,60} = 5.7$, $P = 0.002$), while transect length, month of sampling, marsh type and the interaction between grazing regime and month of sampling were not significantly related to grazing pressure by geese. In April, goose-dropping densities at the transect level did not differ between grazing regimes (GLM, $F_{3,21} = 1.7$, n.s.), while in May, livestock grazed marshes had significantly higher dropping densities than ungrazed marshes (GLM $F_{3,19} = 9.2$, $P = 0.001$). This finding still holds when the dataset is further limited to the 17 sites with paired transects that were visited in both periods or to the sites ($n = 14$) that are known to be visited by both species of geese. There were no significant differences in dropping densities by geese between transects that were grazed by cattle or sheep. When testing for the effect of marsh type separately within ungrazed transects, we found that long-term ungrazed transects on the mainland had much lower dropping densities than long-term ungrazed transects on barrier marshes (0.3 ± 0.2 versus 5.2 ± 0.7; t-test, $t = 2.7$, $P = 0.03$).

We summed per transect, the cover of all plant communities that are characterised by short canopy and grasses that are preferred by geese (the communities *Puccinellia maritima, Limonium vulgare*, *J. gerardi*, *A. stolonifera* and *F. rubra*, see Appendix B and Fig. 1). This variable was positively related to goose-dropping densities at the transect level (Fig. 5, linear regression $R^2 = 0.1$, $P = 0.037$). Goose-dropping densities at the transect level were negatively related to average canopy height ($F_{1,45} = 5.0$, $P = 0.029$) and positively related to the combined index of abundance of *Plantago maritima* or *T. maritima* ($F_{1,45} = 6.9$, $P = 0.012$). Within transects, dropping densities were negatively related to distance from the seawall in 27% of the marshes (GLM interaction of distance and site significant), but had no relation in 67% of the cases. These proportions did not differ between grazing regimes (contingency test: $\chi 2 = 10.7$, n.s.). A visual inspection of dropping data in relation to this distance did not yield indications of a threshold level in any of the transects.

Sites without signs of geese

Of the 38 sites we visited, 11 sites (29%), had no goose droppings at all, with incidence not differing significantly between island and mainland (contingency test: $\chi 2 = 3.2$, n.s.) nor between marsh type (contingency test: $\chi^2 = 1.1$, n.s.). Twenty-three per cent of the transects were not visited by geese at all, and these were all positioned at the 11 sites mentioned above. The incidence of transects that were not visited by geese was independent of livestock grazing regime (contingency test: $\chi 2 = 0.033$, n.s.). The height of the canopy is 3.1 cm higher ($F_{1,57} = 5.1$, $P = 0.027$) and tiller density is 35% lower on average (Fig. 6, $F_{1,63} = 6.8$, $P = 0.01$) at these sites that are not visited by geese, after controlling for grazing regime (Fig. 6, $F_{3,63} = 6.5$, $P = 0.001$). Mean grass cover, mean cover of tall plants, community composition, transect length and our indices of disturbance and freshwater availability, were not significantly different between sites that were visited by geese and sites that were not. The latter finding also held when only the sites with the highest dropping densities (>10 droppings m^{-2}) were compared to sites that were not visited by geese.

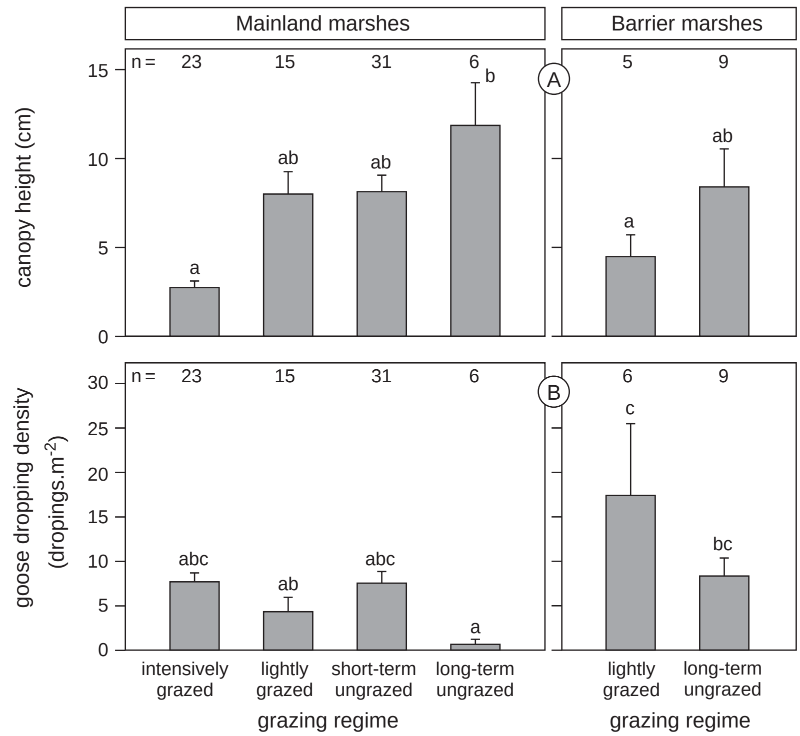

Figure 3. The relation of livestock grazing regime and marsh type with (A) canopy height and (B) grazing pressure by geese. Data represent the communities dominated by *Puccinellia maritima* and *Festuca rubra* for all sites that were visited by geese. Bars that do not share the same letter within a marsh type differ significantly ($P < 0.05$) from each other. Effects of marsh type were significant for both parameters.

Discussion

Livestock grazing and vegetation composition

Natural vegetation succession, i.e. at salt marshes that have never been grazed by livestock, and succession after cessation of livestock grazing on salt marshes often leads to the dominance of a few tall-growing species (Jensen, 1985; Andresen, Bakker, Brongers, Heydemann, & Irmler, 1990; Westhoff & van Oosten, 1991; Aerts et al., 1996; Olff et al., 1997; van Wijnen & Bakker, 1997; Bakker, Bos, & De Vries, 2003). Studies from barrier marshes show that succession will lead towards a vegetation dominated by *A. portulacoides* on the low marsh or *E. athericus* on the high salt marsh, while the latter may even invade the low marsh if sufficient nitrogen is available (van Wijnen & Bakker, 1997; Bakker et al., 2003). These changes take place over periods of decades. Based on comparisons of vegetation maps over time in long-term ungrazed mainland marshes, Bakker et al. (2003) conclude that on mainland marshes as well *E. athericus* can become dominant, though areas with low sedimentation rates, or under the influence of fresh water, are exceptions to that general pattern. Ungrazed transects in the present study had a higher incidence of communities dominated

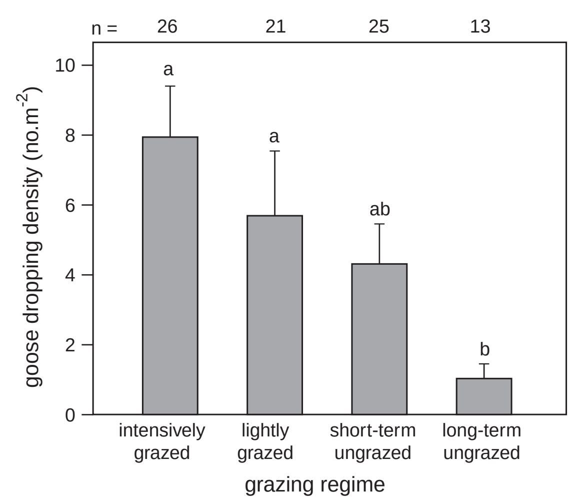

Figure 4. Average goose grazing pressure at the transect level in relation to livestock grazing regime for all transects that were paired within the same site. Bars that do not share the same letter differ significantly from each other ($P < 0.05$).

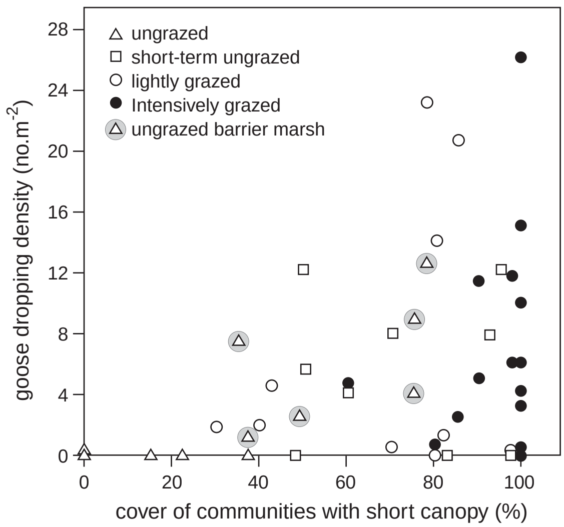

Figure 5. The relationship between average accumulated goose grazing pressure and the incidence of communities with a short canopy (the plant communities *Puccinellia maritima*, *Limonium vulgare*, *Juncus gerardi*, *Agrostis stolonifera* and *Festuca rubra*, see Appendix B).

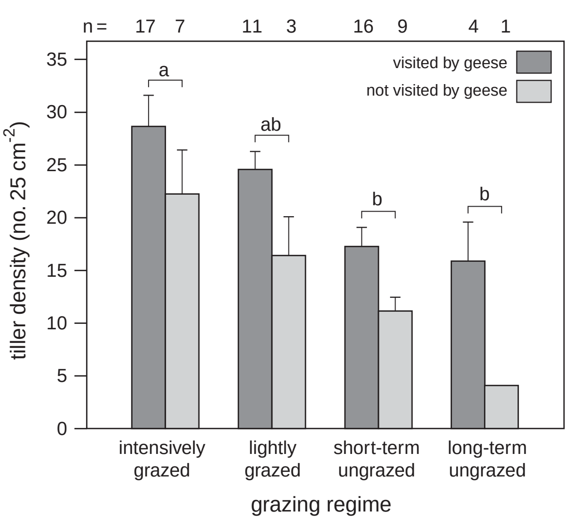

Figure 6. The relationship between tiller density and grazing regime in the communities of *Festuca rubra* and *Puccinellia maritima* on the mainland marsh. Averages for sites that were visited by geese are given separately from those that did not receive any grazing pressure in our sample.

by *A. portulacoides*, *A. maritima* or *E. athericus* (Fig. 1) than grazed transects, but were nevertheless not entirely dominated by them. The six long-term ungrazed transects on the mainland had higher coverage by tall communities (on average 75%) as against the barrier marshes (28% on average). For some of these transects on barrier marshes (Griend, Rottumeroog, Schiermonnikoog, Terschelling), this may be due to the fact that the sampled marsh was young and hence the productivity low (Westhoff & van Oosten, 1991; van der Wal, van Lieshout, Bos, & Drent, 2000a).

The effects of livestock grazing regime were also detectable in terms of significant differences in average canopy height, cover of preferred grasses and cover of structure plants on the transects. Even within the communities of *Puccinellia maritima* and *F. rubra*, we observed differences between grazing regimes (Fig. 3A), with stands of the same community having a taller canopy on ungrazed marshes. The short-term ungrazed marshes in our study differ from their grazed counterparts in most of the vegetation parameters we studied (e.g. Fig. 3A), although the plant communities were the same. This is in agreement with data for the *Puccinellia maritima* community at the mainland marsh of the Hamburger Hallig (Kiehl, Schröder, Bredemeier, & Wiggershaus, 2000b).

Kiehl (1997) and Kiehl, Gettner, Heinze, and Stock (2000a), argue that heterogeneity in abiotic conditions in space and time will prevent absolute dominance of a single community in the absence of livestock grazing and caution against applying studies on well-drained sandy barrier marshes to mainland marshes. Waterlogging in undrained mainland marshes, for example, may render parts of the marsh unsuitable for *E. athericus* and *A. portulacoides*. Results of Esselink (2000) indeed indicate that a lack of drainage, although in interaction with goose and cattle grazing, affects vegetation composition substantially at the brackish marshes of the Dollard (NL). Some of the short-term ungrazed marshes along the coast of Schleswig–Holstein are subject to neglect of the drainage system in the past decade yet have high goose grazing pressure. For the present, it remains an open question to what extent the geese may be able to maintain suitable habitat within these areas, in the absence of livestock.

Goose grazing pressure

Canopy height was found to be closely correlated to goose grazing pressure. This is consistent with observations by several authors (Summers & Critchley, 1990; van de Koppel et al., 1996; van der Wal, van de Koppel, & Sagel, 1998). Short canopies tend to be homogeneous swards with grazed tillers, a favourable leaf/stem ratio and, in spring, characterised by high food quality. Low canopy height also coincided with the plant communities characterised by the forage species of geese, and we found a positive relation between the cover of communities with a short canopy and the dropping density at the transect level (Fig. 5). Decreased intensity of livestock grazing leads to a decrease in the cover of communities with a short canopy (Fig. 1) and lower grazing pressure by geese (Figs. 4 and 5). The magnitude of this effect is considerable, as ungrazed marshes only account for 12% of the droppings found at intensively grazed marshes. However, this effect is not absolute, as the ungrazed marshes at Griend, Rottumeroog, Schiermonnikoog and Terschelling stand out with high goose-dropping densities. The results for these barrier marshes are consistent with the course of vegetation succession at these young marshes with low productivity (van de Koppel et al. 1996). van der Wal et al. (2000a) in fact showed that the ungrazed barrier marsh of Schiermonnikoog had an optimal vegetation composition for small vertebrate herbivores at an age between 20 and 50 years, and a decrease in goose numbers after succession had proceeded for longer periods of time. Goose-dropping densities at the short-term ungrazed marshes on the mainland are intermediate to those on intensively grazed and ungrazed marshes.

Apart from canopy height, goose grazing pressure was also related to our index of combined abundance of *Plantago maritima* or *Triglochin maritima*. This relationship may be interpreted as a direct causal link, as Prop & Deerenberg (1991) have shown that the rate of accumulation of fat in spring staging Brent Geese is contingent upon the amount of these plant species in the diet. It might, however, also be interpreted as a pseudo-correlation, since *Plantago maritima* and *T. maritima* were found to be associated with barrier marshes where the sandy soils form a suitable habitat for these species (Schaminée, Weeda, & Westhoff, 1998). Barrier marshes may have more benefits to Brent Geese such as lower levels of predation and disturbance. Barnacle Geese do not occur in reasonable numbers on the barrier marshes that were included in this study, except for Schiermonnikoog. No relation was observed between dropping densities of geese and hare at the scales that we sampled. This suggests that the facilitative effect of hare grazing on geese, that was observed at the barrier marsh of Schiermonnikoog (van der Wal et al., 2000b), is not of overriding importance in the Wadden Sea as a whole, under current conditions.

In April the differences in dropping densities between livestock grazing regimes were not statistically significant, while they were apparent in the combined data set and the data for May, when the majority ($>75\%$) of the Barnacle Geese had departed. In April three out of 11 of the short-term ungrazed transects had higher droppings than their grazed counterpart, while in May all short-term ungrazed transects had lower dropping densities than grazed transect at the same site. This may be related to a difference in the presence of the two goose species, as in April the Barnacle Geese are still present together with the Brent Geese, and the two species differ in the selection of habitat to some extent (Bos, 2002). In addition to that, the differences between salt marshes with different livestock grazing regimes become more pronounced during the growing season, and higher primary production in combination with lower numbers of geese allows the geese to be more selective in their choice of habitat.

We are aware of only a few published studies that have explicitly considered the effects of livestock grazing on salt marshes for feeding conditions of waterfowl. Detailed studies at the Hamburger Hallig and Westerhever give results that differ somewhat from ours. Cessation of grazing at these sites led to only minor effects on goose-dropping densities in spring, even after 9 years without grazing. Over this period, the prevailing *Puccinellia maritima* community did not shift into another community, but the canopy did become taller. In autumn, the differences in goose-dropping densities between grazed and short-term ungrazed parts of the marsh were however very pronounced (Stock & Hofeditz, 2000). Work at the mainland marshes of the Leybucht and the Dollard, revealed a quick change in the vegetation composition after cessation of grazing, followed by an almost immediate strong reduction in grazing pressure by geese in autumn and spring (Aerts et al., 1996; Bergmann & Borbach-Jaene, 2001). Cadwalladr, Owen, Morley, and Cook (1972) demonstrated that grazing pressure by wigeon *Anas Penelope* (L.) was higher in sheep grazed swards, compared to swards that were left ungrazed. Results presented by Boudewijn and Ebbinge (1994) indicate that the ungrazed barrier marsh at Terschelling, although of relatively young age, had somewhat lower goose grazing pressure at the end of the 1970s than the grazed marsh. The positive effects of livestock on goose grazing conditions result from their long-term effect on the vegetation composition, as livestock is not yet present on the marshes in spring. Within a season, grazing by livestock may also affect goose-feeding conditions positively by maintaining a short sward, thus preventing a decrease in forage quality due to ageing of leaves (Holmes, 1989; Riddington, Hassall, & Lane, 1997) and/or intake rate (van der Graaf, Bos, Loonen, Engelmoer, & Drent, 2002; Bos, 2002). Vickery, Sutherland, O'Brien, Watkinson, and Yallop (1997) found a positive correlation between livestock grazing intensity and Brent Goose grazing pressure within a series of coastal swards that were all livestock grazed, but had very similar vegetation composition.

About 20% of the sites sampled did not show signs of goose grazing. These sites differed from those that were visited by geese in taller canopy height (by 3 cm) and in higher tiller density (35% on average). The small difference in canopy height is likely a result of the geese grazing themselves. The same may apply for the observed differences in tiller density (Bazely & Jefferies, 1989), but the differences may also be inherent to the sites themselves. The importance of this finding remains obscure, since within the selection of transects that were visited by geese tiller density was not found to be related to dropping density. Madsen, Frikke, and Laursen (1990) mention that the narrow Danish mainland marshes are less suitable for the Brent Geese than the wide mainland marshes along the coast of Schleswig–Holstein due to their dimensions (lateral extent), but we did not find evidence for such a relationship in our sample. So, apart from the unexplained difference in tiller density between sites that were visited by geese and sites that were not, it appears that there was no shortage of available habitat for spring staging geese in the Wadden Sea, during our study period, conforming to the view of Madsen et al. (1990) and Rösner and Stock (1994).

Implications for management

Arctic breeding geese are dependent on the Wadden Sea for fattening during spring staging (Madsen, Cracknell, & Fox, 1999). Natural succession, i.e. in the absence of livestock grazing, on salt marshes leads to a declining suitability of the marsh as a feeding habitat for geese. To a certain extent the geese may be able to feed on alternative habitat, such as agricultural grassland, but this has economic implications and may not provide an adequate alternative. Salt-marsh habitat appears to be preferred by the geese over agricultural grassland (Ebbinge, 1992, Vickery, Sutherland, Watkinson, Lane, & Rowcliffe, 1995). A comparative study by Prop and Black (1997) furthermore suggests that staging in agricultural habitat may have negative consequences for the reproductive performance of the birds. Long-term data on individual reproductive success of Brent Geese presented by Spaans and Postma (2001) do not support the latter suggestion, however. Seagrass (*Zostera* sp. (L., Hornemann)) is no longer an important food source in spring for Brent Geese (Ebbinge et al., 1999), as its occurrence in the Wadden Sea is low since the 1930s (den Hartog, 1987; Reise, Herre, & Sturm, 1989; Landesamt für den Nationalpark Schleswig-Holsteinisches Wattenmeer, 1998).

Coastal protection works along the Wadden Sea shore, reduce the natural dynamics within the marshes and prevent a landward expansion of the marsh area. However, as a result of enhanced sedimentation within brushwood groynes, the coastal protection measures contribute to the creation of new and young salt marsh that is not dominated by unpreferred plants. New and young salt marsh also emerges on barrier islands as part of the natural cycle of accretion and breakdown (de Jong et al., 1999). Since the cessation of livestock grazing in large areas leads to an ageing of the vegetation, Esselink (2000) proposed that sufficient areas must be kept under livestock grazing, so that the grazing by large herbivores maintains the marsh vegetation at a younger successional stage. So far we do not have indications that the species of livestock used is of crucial importance for goose usage in spring.

Livestock grazing on salt marshes has been demonstrated to affect more than merely the vegetation and the feeding conditions of waterfowl, but also the relative abundance of entomofauna (Andresen et al., 1990; Meyer, Fock, Haase, Reinke, & Tulowitzki, 1995) and breeding birds (Norris, Cook, O' Dowd, & Durdin, 1997; Esselink, 2000; Eskildsen, Fiedler, & Hälterlein, 2000). We support the view that nature management of salt marshes should not be guided by the needs of a single species, but rather aim at maintaining the characteristic communities of salt marshes. Establishing variation in the grazing intensity over large areas will lead to this objective. It is recommended to specify the ecological targets, to consider to what extent livestock grazing is a suitable tool for reaching these targets, and to monitor the developments in the field.

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Appendix A

An overview of the selected sites. I = intensive, SU = short-term ungrazed, E = extensive and LU = long-term ungrazed.

No	Location	Marshtype	Grazing regime	Species of livestock	dropping density (no.m^{-2}) Goose April	Goose May	Hare	Cover of communities with short canopy (%)	Disturbance class
1	Skallingen	Barrier	E	Cattle	0.0	.	0.0	50	Undisturbed
1	Skallingen	Barrier	LU	—	0.0		0.0	17	Undisturbed
2	Langli	Barrier	LU	—	12.7		1.5	78	Undisturbed
3	Vilslev	Mainland	I	Sheep	0.0		0.0	100	Undisturbed
4	Kammerslusen	Mainland	I	Sheep	0.8		0.0	80	Undisturbed
5	Mandø	Barrier	E	Cattle	0.0	0.0	0.3	80	Undisturbed
5	Mandø	Mainland	E	Sheep	1.9	2.0	0.1	40	Undisturbed
5	Mandø	Mainland	LU	—	0.3	0.0	0.3	23	Undisturbed
6	Råhede	Mainland	E	Sheep	0.0	0.0	0.0	63	Undisturbed
7	Rejsby	Mainland	I	Sheep	0.0		0.0	100	Undisturbed
8	Brøns	Mainland	I	Sheep	0.0		0.0	100	Undisturbed
9	Astrup	Mainland	I	Sheep	2.6		0.0	85	Moderate
10	Rømø	Mainland	E	?	1.0		0.0	100	Moderate
11	Ballum Enge	Mainland	I	Sheep	2.5	9.8	0.0	98	Undisturbed
12	Marienkoog	Mainland	I	Sheep	0.0	0.0	0.0	93	Undisturbed
12	Marienkoog	Mainland	SU	—	0.0	0.0	0.0	100	Undisturbed
13	Gröde	Mainland	E	Cattle/sheep	16.0	30.6	0.0	78	Undisturbed
13	Gröde	Mainland	SU	—	6.1	18.5	0.0	40	Undisturbed
14	Sönke Nissenkoog	Mainland	I	Sheep	11.7	8.5	0.0	100	Undisturbed
14	Sönke Nissenkoog	Mainland	SU	—	0.0	0.0	0.0	98	Undisturbed
15	Hamburger Hallig	Mainland	I	Sheep	9.8	14.0	0.0	98	Moderate
15	Hamburger Hallig	Mainland	E	Sheep	1.4	0.0	0.0	70	Undisturbed
15	Hamburger Hallig	Mainland	SU	—	5.0	6.5	0.0	50	Undisturbed
16	Nordstrand	Mainland	I	Sheep	0.1	0.0	0.0	100	Undisturbed
16	Nordstrand	Mainland	SU	—	0.0	0.0	0.0	83	Undisturbed
17	Norderheverkoog	Mainland	SU	Sheep	0.0	.	0.1	90	Undisturbed
18	Westerhever	Mainland	I	Sheep	3.8	8.7	0.0	100	Undisturbed
18	Westerhever	Mainland	SU	—	9.7	6.6	0.0	70	Undisturbed
19	Friedrichskoog	Mainland	I	Sheep	5.6	3.1	0.0	100	Undisturbed
19	Friedrichskoog	Mainland	SU	—	0.1	0.0	0.0	98	Undisturbed
20	Dieksanderkoog Nord	Mainland	I	Sheep	2.1	4.5	0.0	100	Moderate
20	Dieksanderkoog Nord	Mainland	SU	—	13.7	2.4	0.1	93	Moderate
21	Dieksanderk Sud	Mainland	I	Sheep	16.6	13.9	0.0	100	Moderate
21	Dieksanderk Sud	Mainland	SU	—	19.2	5.4	0.0	95	Undisturbed
22	Berensch	Mainland	I	Sheep	0.0	.	0.0	100	Undisturbed
22	Berensch	Mainland	SU	—	0.0	.	0.0	95	Undisturbed
23	Wremen	Mainland	I	Cattle	0.0	.	0.0	100	Undisturbed
24	Langwarder Außengroden	Mainland	SU	—	0.0	.	0.0	55	Undisturbed
25	Elisabeth Außengroden	Mainland	LU	—	0.0	.	0.0	30	Moderate
26	Harlesiel	Mainland	E	Cattle	0.6	0.0	0.2	98	Undisturbed
26	Harlesiel	Mainland	SU	—	0.0	0.0	0.6	48	Undisturbed
27	Neßmersiel	Mainland	E	Cattle	0.0	.	0.0	90	Undisturbed
27	Neßmersiel	Mainland	SU	—	0.0	.	0.0	30	Undisturbed
28	Leybucht	Mainland	I	Cattle	20.3	32.3	0.0	100	Undisturbed

28	Leybucht	Mainland	SU	–	4.0	4.9	0.0	60	Undisturbed
29	Rottumeroog	Barrier	LU	–	6.1	9.0	0.0	35	Undisturbed
30	Noordpolderzijl	Mainland	I	Sheep	.	4.8	0.1	60	Moderate
30	Noordpolderzijl	Mainland	LU	–	.	0.0	0.0	0	Undisturbed
31	Groningen coast	Mainland	I	Sheep	15.5	7.5	0.0	90	Moderate
31	Groningen coast	Mainland	E	Sheep	7.5	1.8	0.0	43	Moderate
32	Groningen coast	Mainland	I	Sheep	3.0	7.3	0.0	90	Moderate
32	Groningen coast	Mainland	LU	–	2.4	0.2	0.1	38	Moderate
33	Groningen coast	Mainland	E	Sheep	3.8	0.1	0.1	30	Undisturbed
33	Groningen coast	Mainland	LU	–	0.0	0.0	0.0	38	Undisturbed
34	Schiermonnikoog	Barrier	E	Cattle	16.1	12.4	1.4	80	Moderate
34	Schiermonnikoog	Barrier	LU	–	3.7	1.6	1.5	49	Undisturbed
35	Noord Friesland Buitendijks	Mainland	I	Cattle	5.7	6.8	0.0	100	Undisturbed
35	Noord Friesland Buitendijks	Mainland	E	Cattle	1.5	1.3	0.0	82	Undisturbed
35	Noord Friesland Buitendijks	Mainland	LU	–	0.1	0.2	0.0	15	Undisturbed
36	Terschelling	Barrier	E	Cattle/horses	.	20.8	0.1	85	Undisturbed
36	Terschelling	Barrier	LU	–	.	4.2	1.6	75	Undisturbed
37	Texel	Barrier	LU	–	0.3	.	0.0	0	Undisturbed
38	Griend	Barrier	LU	–	9.0	.	0.0	75	Undisturbed

Appendix B

Key to the classification of plant communities on saltmarshes. A globalisation of the classification by de Jong et al. (1998). Follow the key from above to below.

There are four salt-marsh zones: the pioneer zone, the low marsh, and the middle to high marsh. First decide on the zone, based on the underlined decision rules. Then choose the first option that fits the plot.

If total cover > 1% and pioneer species > species of low marsh

Spartina	*Spartina anglica* > *Salicornia* and *Suaeda maritima*
Salicornia	*Salicornia* and/or *Suaeda maritima* > *Spartina anglica*

If Pioneer species < species of low marsh > species of high and middle marsh:

Atriplex	*Atriplex portulacoides* > 25% cover or (*Atriplex portulacoides* > 15% and *Limonium vulgare* < 15% cover)
Puccinellia	Other low marsh

If (Pioneer species+species of low marsh) < species of high and middle marsh:

Artemisia	*Artemisia maritima* > 15% cover and *Artemisia Maritima* > *Festuca rubra*
Atriplex	*Atriplex portulacoides* > 15% cover
Limonium	*Limonium vulgare* > 15% cover
Juncus gerardi	*Juncus gerardi* > *Festuca rubra*
Juncus maritimus	*Juncus maritimus* > 10% cover
Glaux	*Glaux maritima* dominant
Elymus	*Elymus* sp.+*Atriplex prostrata*+*Atriplex lanceolata* > 25% cover
Agrostis	*Agrostis stolonifera* dominant
Festuca	Other middle high marsh
No vegetation/other	

Pioneer species: *Spartina anglica, Salicornia sp. and Suaeda maritima.*

Species of the low marsh: *Puccinellia maritima, Atriplex portulacoides, Cochlearea anglica, Aster tripolium, Spergularia* sp., *Triglochin maritima, Limonium vulgare, Plantago maritima, Parapholis* sp., *Atriplex pedunculata.*

Species of the middle marsh: *Artemisia maritima, Armeria maritima, Juncus gerardi, Glaux maritima, Festuca rubra.*

Species of the high marsh: *Potentilla anserina*, *Trifolium* sp., *Poa* sp., *Lolium* sp., *Elymus* sp., *Lotus corniculatus*, *Plantago coronopus*

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