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Effects of vegetation patterns and grazers on tidal marshes

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Scale dependence of top-down vs. bottom-up control of plant composition and grazer abundance: a long-term case study on a tidal wetland ecosystem

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ABSTRACT

Herbivores can exert top-down control on the vegetation composition, whereas other studies showed herbivore presence is controlled bottom-up. We hypothesize that top-down control by the vertebrate species on the primary production and bottom-up control by the primary producers on the vertebrate species within an ecosystem often co-occur, but operate on different spatial and temporal scales. Ultimately, together they will determine vegetation type and vertebrate abundances in an ecosystem. We used a highly dynamic marsh system with a large population of greylag geese (*Anser anser*), to study the importance of spatial scale in top-down vs. bottom-up control on food supply and geese abundance. No predators are present within this marsh and hunting was abandoned in 1990. The greylag geese grub for below-ground storage organs of pre-dominantly *Bolboschoenus maritimus*, thereby creating bare patches of a few square metres within the marsh vegetation. On this local patch scale, greylag geese showed top-down control by setting-back plant succession. Typical early-successional marsh species took advantage of the bare patches created by the geese. This reduced the food supply shortly, but the patches regenerated back within 12 years to a *Bolboschoenus maritimus* dominated vegetation type. On a landscape scale of square kilometres, we found an increase in marsh surface elevation that outpaced the sea-level rise. This resulted in long-term succession with a decreased cover of *Bolboschoenus maritimus*, thus imposing a bottom-up control on the food supply. Ultimately, we conclude that bottom-up control is causing the greylag geese to get evicted from the ecosystem due to a reduction in food supply in the long term of decennia. This study shows the importance of covering temporal and multiple spatial scales when studying plant-animal interactions and highlights the necessity of long-term and landscape-scale studies when estimating determining factors for species abundances.

INTRODUCTION

Grazing pressure by large populations of herbivores is increasing in many ecosystems (Van Eerden et al. 2005, Myrnerud 2006, Kemp and Michalk 2007). Simultaneously, the carrying capacity of many ecosystems for herbivores is changing under the influence of global climate change (Zehnder and Hunter 2008, Madsen et al. 2011, Lohmann et al. 2012). Understanding which factors control herbivore abundances becomes increasingly important as environmental conditions will continue to change and grazing pressures could increase further (Madsen et al. 2011). Herbivore abundance is for a large part determined by the quantity and quality of the available food resources (Oene et al. 1999, White 2008). Presence of high quantity but low quality vegetation will limit the amount of herbivores able to feed successfully within an ecosystem.

The importance of top-down and bottom-up forces controlling population dynamics has been a long-standing debate in ecology (Hunter and Price 1992, Van De Koppel et al. 1996, Alberti et al. 2010). Sinclair and Krebs (2002) concluded that bottom-up control will primarily regulate population sizes of vertebrates, but this can be overruled by secondary processes such as top-down control by predators, social interactions within the species and disturbances. In this study, we will determine whether top-down control on the vegetation by the herbivores themselves, will be a key aspect that determines the food supply and grazer abundance in an ecosystem. We hypothesize that top-down control by the herbivores on the vegetation and bottom-up control through ecosystem properties, such as local productivity, often co-occur but operate on different spatial scales. Together, they will determine the food supply in an ecosystem. On the one hand, herbivores are known to affect the vegetation top-down (Olf and Ritchie 1998). They can change vegetation composition (e.g. Díaz et al. 2007), plant height (Andresen et al. 1990, Elschot et al. 2013), plant species richness (e.g. Bakker et al. 2006) as well as heterogeneity within an ecosystem (Oene et al. 1999, Adler et al. 2001). Such top-down control by grazing on the vegetation often occurs on a relatively small scale (few m²) by impacting the vegetation locally (Olf and Ritchie 1998). Therefore, by changing the vegetation, herbivores can indirectly exert top-down control on their food resources. On the other hand, it has been shown that vegetation is controlled bottom-up, which in turn will determine the grazer abundance (Kuijper and Bakker 2005, White 2008, Center and Dray 2010). Such bottom-up control generally occurs on a landscape-scale (km²) by large-scale external factors, e.g. natural succession (Van Der Wal et al. 2000b), available nutrients (Center and Dray 2010, Alberti et al. 2010) or other abiotic environmental factors such as weather conditions and tidal regime in wetland ecosystems (McKinney et al. 2001, White 2008, Davy et al. 2011). In these instances, large-scale bottom-up processes will primarily control grazer abundance through their food supply (Sinclair and Krebs 2002).

To test whether top-down and bottom-up controls co-occur and operate on different spatial scales, we studied plant-animal interactions both on a local (a few m²) and on a landscape scale (a few km²) throughout long-term ecosystem development. We used tidal marshes with extensive goose grazing as a model. Tidal marshes are highly dynamic ecosystems, where the marsh vegetation slows down tidal current and thereby stimulates mineral sedimentation, resulting in accretion and hence an increasing surface elevation with marsh age (e.g. Oloff et al. 1997, Mudd et al. 2010, De Groot et al. 2011). If the marsh elevation rises faster than sea-level rise, this results in decreasing frequency, depth and duration of tidal inundations, and hence decreased accretion (Van Wijnen and Bakker 2001, Fagherazzi et al. 2012, Kirwan and Megonigal 2013). This dynamic character makes marshes very suitable to study ecosystem processes as strong successional differences can be shown in just a decade (Oloff et al. 1997). Global increase in migrating goose populations has resulted in increasing grazing pressures on many tidal marshes (Madsen et al. 1999, Gauthier et al. 2005, Van Eerden et al. 2005, Voslamber et al. 2010). We focus on a large brackish tidal marsh in the southwest of the Netherlands (Saeftinghe), which provides feeding habitats for a large proportion of the population of greylag geese (Castelijns and Jacobusse 2010). These geese grub below-ground for storage organs of *Bolboschoenus maritimus* that are mainly present in lower elevated depressions near the creeks. By grubbing belowground, the greylag geese create bare patches (a few m²) in the marsh surface (Esselink et al. 1997, McLaren and Jefferies 2004). Due to the abandonment of hunting, population size has strongly increased after 1990 (Castelijns et al. 1998), but reduced again in the past decade despite the absence of predators (Castelijns and Jacobusse 2010). Using the large marsh as a model, we aim at understanding the importance of top-down and bottom-up controls at various spatial scales on the long-term abundance of grubbing greylag geese in this marsh.

In this study, we specifically want to test two hypotheses that may explain the reduction in geese population size as observed in the study area: 1) local top-down control of grubbing greylag geese on the vegetation resulted in degradation of the marsh surface, a reduction in their preferred food source *Bolboschoenus maritimus*, and thus a reduction in geese abundance; 2) landscape-scale bottom-up control of sediment accretion on vegetation development resulted in a higher elevation, a reduction in the overall *Bolboschoenus maritimus* cover, and thus a reduction in geese abundance. Testing these two hypotheses will ultimately reveal to which extent herbivore abundance is controlled by local-scale (few m²) top-down control through grubbing greylag geese, or by landscape-scale (few km²) bottom-up control by sediment accretion. We tested both hypotheses by using long-term time series of goose counts (1987-2010), aerial photographs (1979-2008), vegetation maps (1979-2010) and elevation maps (1931-2010) to determine both local (m²) and landscape-scale (km²) ecosystem changes over time.

METHODS

Study site

The study area, Saeftinghe, is located in the Western Scheldt estuary in the Netherlands (Fig. 5.1, 51°21'N, 4°11'E). It is considered one of the largest brackish marshes in Western Europe, approximately 28 km² in size, and is an important feeding habitat for large populations of wintering greylag goose, *Anser anser* (Castelijns et al. 1998, Castelijns and Jacobusse 2010). A small part of the marsh is grazed by cattle. The largest part has been abandoned, but has been extensively sheep grazed up to 1993. Outside the cattle-grazed marsh the most important vegetation types are dominated by *Phragmites australis*, *Elytrigia atherica* and *Bolboschoenus maritimus*. *Phragmites australis* is mostly limited to the eastern part of Saeftinghe near the seawall, *Elytrigia atherica* is mainly dominating higher elevated creek bank levees and *Bolboschoenus maritimus* is mainly limited to the depressions between the creek bank levees. Only since the 1980s has this marsh become an important staging and wintering site for greylag geese. Till the 1990s, the greylag geese population size was limited by a high hunting pressure, but goose numbers increased rapidly when hunting was abandoned after 1990 (Fig. 5.3) (Castelijns et al. 1998). Greylag geese prefer to feed on the below-ground storage organs of *Bolboschoenus maritimus* for which they grub into the marsh soil (Amat 1986, Esselink et al. 1997). A study by Castelijns et al. (1998) showed that in the winters between 1994 and 1997, the main food sources of greylag geese in Saeftinghe consisted for 49% of tubers of *Bolboschoenus maritimus*, for 33% of above-ground plant parts of other marsh species such as *Aster tripolium* (personal observations), for 10% of agricultural plants (growing on



Figure 5.1. The study area located in the south of the Netherlands. It is a large brackish marsh 2800 ha in size. The greylag geese counts and vegetation covers were estimated on the entire marsh area. The black line indicates the area where we measured the marsh accretion rate (Approximately 2 km²), while, the dashed line indicates the area where we studied the regeneration of the depressions (approximately 7 km²).

arable fields adjacent to the marsh) and for 8% of seeds of *Elytrigia atherica*. They concluded this based on microscopic evidence found in fresh droppings that were collected in the field together with field observations (Castelijns et al. 1998).

Estimating the population dynamics of greylag geese

Between 1987 and 2011, numbers of greylag geese in Saeftinghe were estimated on a monthly interval from July until March the consecutive year. The majority of the geese arrive in October and all have left again by the end of February, except for a small breeding population that will remain present year round. Goose numbers were estimated on the entire marsh area (28 km²) (data provided by Natuurbeschermingsvereniging De Steltkluut). To include estimates of the population before 1987, we included the population size estimated in literature (Castelijns and Jacobusse 2010). Between 1980 and 2011, the numbers of geese in the Netherlands were estimated based on local goose counts performed in ecosystems throughout the Netherlands in a similar manner as in Saeftinghe (data provided by Sovon).

Top-down control of grubbing geese on vegetation on a local scale

To determine the strength of the top-down control of greylag geese on the local vegetation, we studied the formation of bare patches within the vegetation by grubbing greylag geese and the subsequent re-generation of these bare patches by vegetation re-establishment. We used false-colour aerial photographs from 1979, 1990, 1998, 2004 and 2008 and analysed them in ArcGIS. We identified all bare patches in the eastern region of Saeftinghe, an area approximately 7 km² in size (most central point: 51°21'45N, 4°11'46E, Fig. 5.1). For each bare patch, we determined year of presence as well as absence. Once the bare patch was not visible on the aerial photograph anymore, we assumed vegetation had re-established in these bare patches (Fig. 5.2). This way, we could determine for each bare patch the minimum number of years that the vegetation had re-established in the bare patch (i.e., the minimum re-generation time). For example: when a bare patch present in the photo of 1990 had disappeared from the photo of 2004 (Fig. 5.2), we assumed this bare patch had re-generated for at least six years when we measured the vegetation composition in 2010. As we did not have aerial photographs for every year, we have five classes of 0, 2, 6 and 12 years of minimum re-generation time. After determining the coordinates from the photographs, we visited all the regenerated bare patches in the field in July and August of 2010. For each regenerated patch, we performed vegetation composition measurements in 2 m × 2 m plots using the decimal scale (Londo 1976). In order to assess the impact of greylag geese on the vegetation composition, we compared the vegetation composition in re-generated patches with the vegetation composition in depressions unaffected by the geese. As geese prefer to feed on the below-ground tubers of *Bolboschoenus maritimus*, we considered the *Bolboschoenus maritimus* dominated

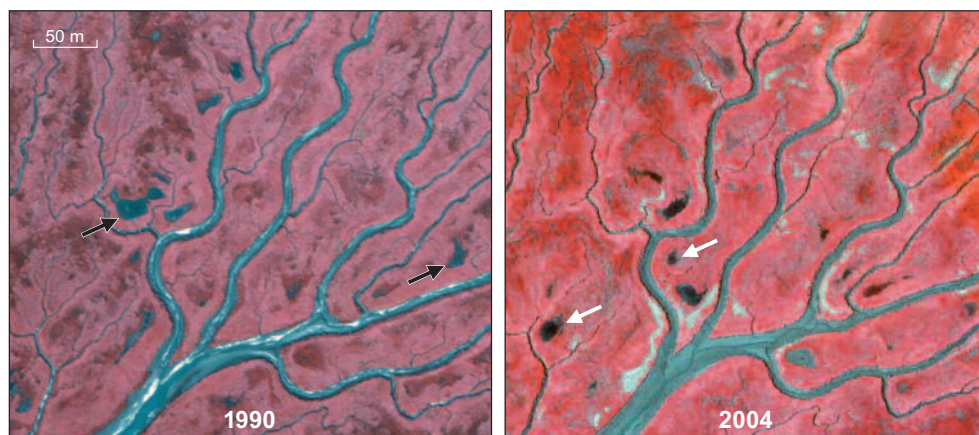


Figure 5.2. Depressions present and absent on two aerial pictures comparing 1990 with 2004. The black arrows indicate depressions present in 1990 that had disappeared in 2004 and the white arrows point to depressions present in 2004 that were not present yet in 1990.

vegetation type as the original vegetation type before geese started grubbing and created the bare patches. Hence, as a control, we measured vegetation composition in 13 plots located in *Bolboschoenus maritimus* dominated vegetation, where no visible signs of geese grubbing were present. As only three bare patches were recorded in the aerial photograph of 1979, we excluded this year from further analyses.

Bottom-up control by system development on a landscape scale

To determine the strength of bottom-up control on the marsh vegetation, i.e. the control of vertical sediment accretion on increase of marsh elevation relative to sea level and hence on succession of *Bolboschoenus maritimus* vegetation towards other vegetation types, we determined both changes in vegetation type as well as long-term surface elevation changes. To determine cover of different vegetation types we analysed aerial photographs of Saeftinghe from 1979, 1998, 2004 and 2010. Based on the false colour ranges, different vegetation types could be identified by Rijkswaterstaat. For each type, multiple vegetation composition measurements were performed in the field. Ultimately, specific vegetation types were linked with specific colour ranges in the aerial photographs, and this resulted in vegetation maps (maps and data provided by Rijkswaterstaat). This method has been intensively used and validated before, for more information see Reitsma (2006). Generally, pioneer marsh harbours a combination of *Salicornia europaea* and *Spartina anglica*, which will be replaced by secondary species such as *Puccinellia maritima*, *Aster tripolium* and *Glaux maritima* (for further details see e.g. (Olf et al. 1997). Ultimately, the lower marsh becomes dominated by a cover of *Bolboschoenus maritimus* and the higher marsh by *Elytrigia atherica* and *Phragmites australis*. In this

study we focused on the total cover of three dominant vegetation types dominated by *Bolboschoenus maritimus*, *Elytrigia atherica* or *Phragmites australis*. When one of these three species was either dominant (at least 50% cover) or indicated as co-dominant, that specific vegetation type was included in the analysis. All other vegetation types were excluded from the analysis.

The distribution of marsh plant species is determined for a large part by the local marsh surface elevation (Davy et al. 2011). As marshes accumulate tidally introduced mineral sediment, the marsh surface increases in elevation as marshes become older (Lovelock et al. 2011, Suchrow et al. 2012). With ecosystem development and an increase in surface elevation, a change in vegetation composition is expected (Oloff et al. 1997). An area of approximately 2 km² was used to estimate long-term marsh surface elevation change (51°21'48N, 4°11'15E). Data were available for the years 1931, 1951, 1963, 1992, 2004 and 2010. For the years 1931, 1951, 1963 and 1992 data were provided as Digital Terrain Models (DTMs) with a resolution of 20 m x 20 m. These are based on topographic and bathymetric surveys performed by the Dutch and Belgian waterway management authorities (see also Wang and Temmerman 2013; Vandenbruwaene et al. 2013). Topographic surveys were performed that resulted in elevation data points with a density of 1 point/7500 m². The elevations were mapped to 0.1 m relative to the Dutch Ordnance Level (NAP, which is close to mean sea level at the Dutch coast), resulting in a maximum vertical error of ± 0.05 m. For the more recent time steps (2004 and 2010), DTMs with a 2 m x 2 m resolution were available based on LIDAR data. These LIDAR surveys were carried out during low tide with a density ranging from 1 point/16 m² to several points/m² and a vertical accuracy of 0.2 m. The channel networks for 1931 and 2010 were merged and used as a mask to exclude grid cells located within the tidal channel network. The changes in the creek edges between the tidal channel networks of 1931 and 2010 were fairly limited (slow migration rate of the channels). We used this mask for all time steps, as the creek edges in the intervening time steps between 1931 and 2010 will be located within this mask. Besides the mean platform elevation of the selected site, additionally the standard deviation was calculated representing the spatial variation in marsh platform elevation. Historical data on mean high water level (MHWL) and mean high water level at spring tide (MHWLS) were derived from the nearby tidal gauge station at Bath. The marsh surface elevation and the levels of MHWL and MHWLS are expressed in metres above the Dutch ordnance level (NAP).

Data analyses

To link the number of bare patches to the number of geese we calculated the number of bare patches as well as number of geese per unit marsh surface area (ha). We first determined the maximum number of geese for the wintering season of each year, i.e. starting from October up until March the next year. As geese grub during winter and the number

of bare patches is based on aerial photographs taken in summer, we averaged the maximum number of geese in the two years prior to the year the number of bare patches was identified. Cover of each plant species in the re-generating bare patches was tested against the cover of that same species in the control plot using two-tailed t-tests. A p -value < 0.05 was considered to indicate significant differences.

RESULTS

Estimating the population dynamics of greylag geese

After hunting was abandoned in 1990, population size of wintering greylag geese in Saeftinghe increased substantially, from approximately 5,000 in 1985 to over 50,000 geese in 1998-1999 (Fig. 5.3). Thereafter, the number of geese showed a strong decrease again. Meanwhile, the number of geese in the Netherlands was still increasing (Fig. 5.3). This implies that the decrease in Saeftinghe is only a local effect that is likely due to a decrease in food supply, given that there is a lack of predators in this ecosystem.

Top-down control of grubbing geese on a local scale

The total number of bare patches and the population size of the greylag goose showed similar trends (Fig. 5.4). That is, both increased up to 2004 and showed a similar decrease after 2004. They were strongly positively linearly related (number of bare patches = $3.3 \times$ number of greylag geese - 7.3, $R^2 = 0.93$). On a marsh area of approximately 7 km² we identified in total 107 bare patches. Of these patches 9, 7, 25 and 66

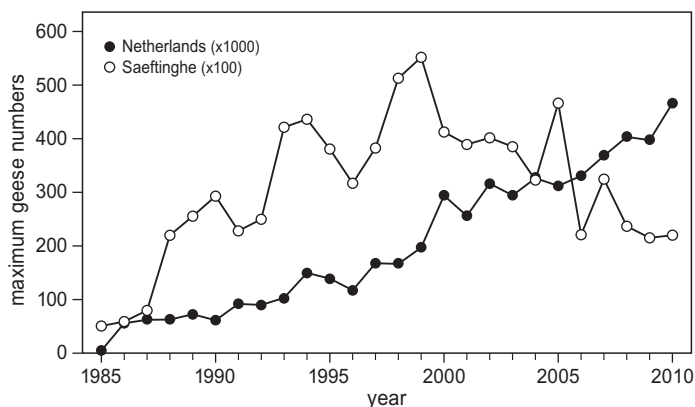


Figure 5.3. Maximum number of wintering greylag geese, estimated annually in the Netherlands (± 41.500 km²) and Saeftinghe (± 28 km²). Maximum numbers are estimated on a monthly interval between fall and spring of the consecutive year. Goose numbers are shown $\times 1000$ for the Netherlands and $\times 100$ for Saeftinghe (data from Sovon Vogelonderzoek Nederland and Natuurbeschermingsvereniging De Steltkluut). Data between 1985 and 1987 were obtained from literature (Castelijns and Jacobusse 2010).

became re-vegetated in 1990, 1998, 2004 and 2008 respectively (Table 5.1). Most of them were between 4 and 10 m in diameter, with some exceptions ranging up to 25 m in diameter. As a control, we studied 13 plots in non-disturbed *Bolboschoenus maritimus* dominated vegetation.

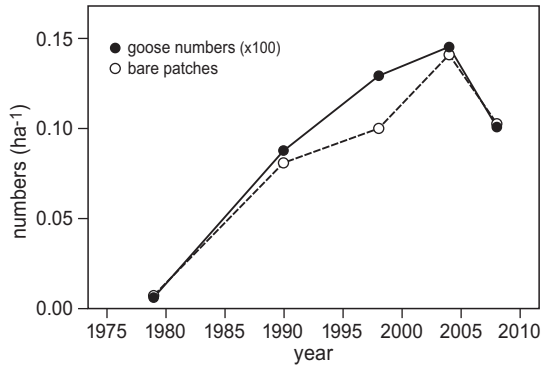


Figure 5.4. The temporal evolution of the number of bare patches and the number of greylag geese. Numbers of geese were determined by the maximum number of geese counted for the entire marsh area (28 km²) and these were averaged over the two years prior to the year the number of bare patches was determined. Number of bare patches was determined for the eastern part of the marsh (approximately 7 km²).

Table 5.1. Vegetation cover (%) estimated per 2 m x 2 m in bare patches after 0, 2, 6 and 12 years of vegetation re-establishment (average ± SE). Plots estimated in *Bolboschoenus maritimus* dominated vegetation are shown as control plots indicating the vegetation composition before greylag geese grub for below-ground tubers and hence remove the vegetation to form bare patches.

	Years after vegetation re-established				Control plot
	0	2	6	12	
Sample size (n)	66	25	7	9	13
Bare	79 ± 3	43 ± 6	21 ± 8	19 ± 7	12 ± 4
Litter	1 ± 1	6 ± 5	3 ± 5	17 ± 5	12 ± 4
<i>Agrostis stolonifera</i>	1 ± 1	4 ± 2	18 ± 10	6 ± 3	10 ± 5
<i>Aster tripolium</i>	8 ± 2	28 ± 5	13 ± 8	8 ± 5	0
<i>Atriplex prostrata</i>	1 ± 1	5 ± 2	3 ± 2	4 ± 2	9 ± 3
<i>Elytrigia atherica</i>	0	4 ± 3	13 ± 8	15 ± 6	11 ± 4
<i>Glaux maritima</i>	2 ± 1	0	6 ± 4	0	0
<i>Juncus Gerardii</i>	0	0	0	0	1 ± 1
<i>Puccinellia maritima</i>	1 ± 1	5 ± 2	5 ± 3	2 ± 2	0
<i>Salicornia europaea</i>	6 ± 2	3 ± 2	7 ± 6	0	0
<i>Bolboschoenus maritimus</i>	2 ± 1	2 ± 1	17 ± 8	38 ± 4	46 ± 4
<i>Spartina anglica</i>	0	0	0	0	3 ± 3
Total cover	20 ± 3	53 ± 6	79 ± 8	64 ± 8	76 ± 4

Several early-successional species were found in the bare patches which were not present in the control plots, implying greylag geese facilitate for these early-successional species (Table 5.1, Fig. 5.5). *Salicornia europaea* was observed as one of the first species re-establishing in the bare patches. However, cover was generally limited and therefore, it was not significantly different from the control plots where the species was never present (Fig. 5.5A). We found significantly higher cover of both *Aster tripolium* and *Puccinellia maritima* in the bare patches compared to the control plots (Fig. 5.5B and C). Both species, *Elytrigia atherica* and *Bolboschoenus maritimus*, gradually re-colonized

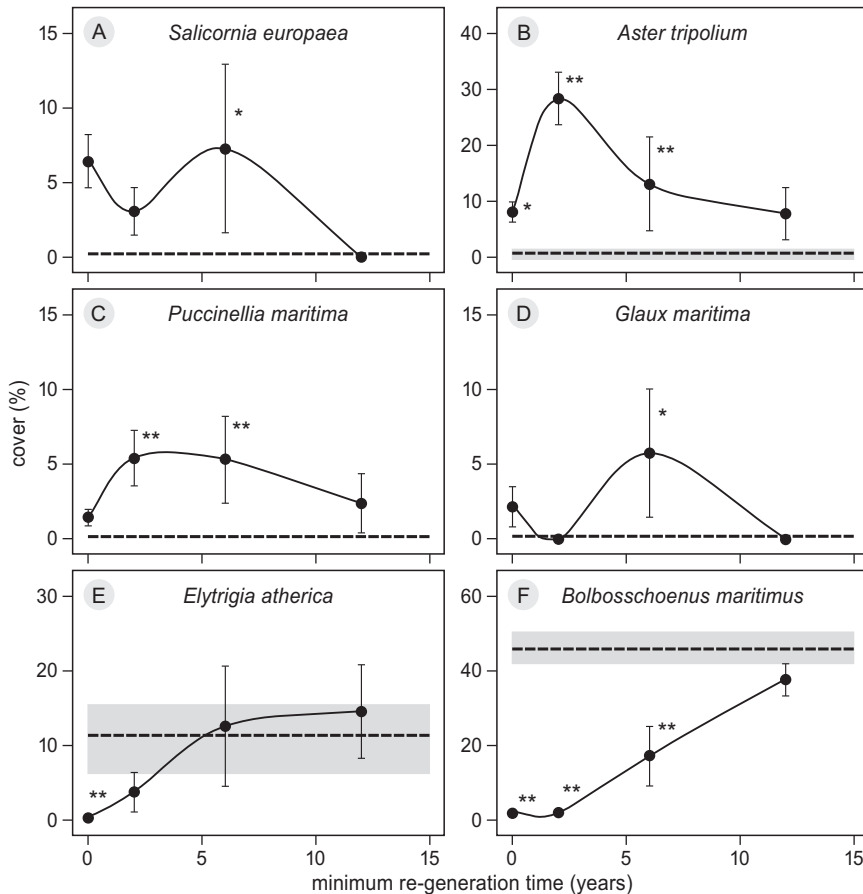


Figure 5.5. The cover of six plant species that established in the bare patches (average \pm SE) showed in relation to the minimum number of years of re-generation (note: different y-axes for different species). Data are shown for different times of re-generation, after 0, 2, 6 and 12 years (with $n = 66, 25, 7$ and 9 , respectively). Average cover of each species in control plots (in *Bolboschoenus maritimus* dominated vegetation, $n = 13$) is indicated with a black broken line surrounded by the standard error (grey area). For each point the significant difference between bare patch and control plot were indicated (** = $p < 0.05$, * = $p < 0.10$).

the bare patches and re-generated back to similar cover percentages as the control plots (Fig. 5.5E and F). *Elytrigia atherica* reached a similar cover of approximately 11% after six years of re-generation, and *Bolboschoenus maritimus* reached a similar cover of approximately 50% after 12 years of re-generation. Even though greylag geese did degrade the marsh locally thereby reducing their food supply, the bare patches re-generated back to a similar vegetation type as the control plots after about a decade.

Bottom-up control by system development on a landscape scale

Total cover of the three potential late successional vegetation types all clearly showed an increase from 1979 up to 2004 (Fig. 5.4). However, between 2004 and 2010 both *Phragmites australis* and *Elytrigia atherica* types continued to increase, whereas the *Bolboschoenus maritimus* vegetation type showed a decrease in cover from 8.8 km² in 2004 to 4.6 km² in 2010. Thus, the evolution of the *Bolboschoenus maritimus* vegetation cover (Fig. 5.6), the number of geese and the number of bare patches (Fig. 5.4) followed a similar temporal evolution. They increased to a maximum in 2004 and after that decreased again.

The surface elevation of the marsh platform strongly increased with time at a rate which was faster than the rise of mean high water level (MHWL) (Fig. 5.7). The rate of surface elevation change reduced from 2 cm year⁻¹ towards 1 cm year⁻¹ in the past few decades, but this was still higher than the average 0.4 cm year⁻¹ increase in MHWL between 1930 and 2010. Hence, from 1931 to 2010 the marsh evolved from a low elevated tidal marsh (mean platform elevation 0.47 m below MHWL) towards a more high elevated tidal marsh (mean platform 0.31 m above MHWL) and through natural succession the vegetation composition is changing accordingly (increase in cover of *Elytrigia atherica* and *Phragmites australis*, whereas *Bolboschoenus maritimus* vegetation type decreased in cover).

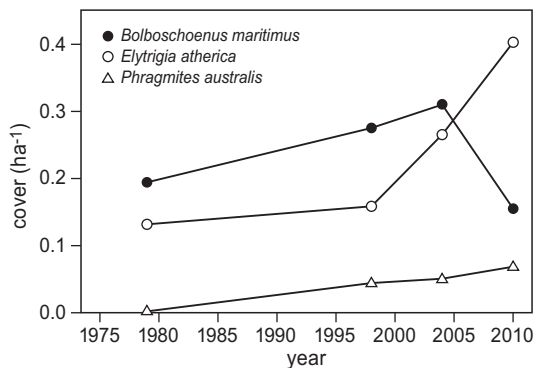


Figure 5.6. The temporal evolution of the total cover of the three dominant vegetation types (*Bolboschoenus maritimus*, *Elytrigia atherica* and *Phragmites australis*) estimated on the entire marsh area (cover of the plant species is given in ha per ha of marsh surface area).

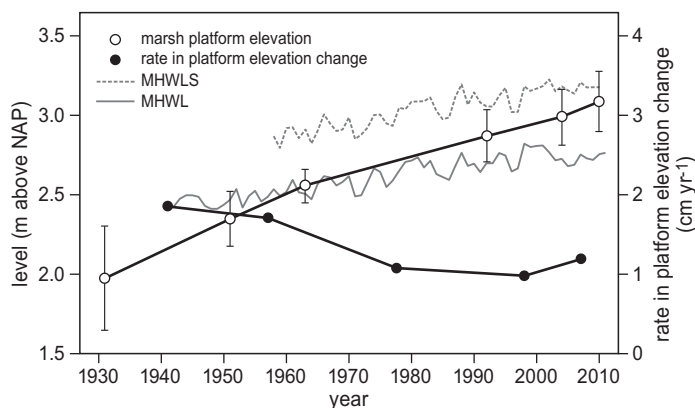


Figure 5.7. Marsh platform elevation change (m) and rate of elevation change (cm yr⁻¹) in relation to Mean High Water Level (MHWL) and Mean High Water Level during Spring tides (MHWLS). All levels are shown relative to the Dutch ordnance level (NAP).

DISCUSSION

Our results are partially in line with our first hypothesis that top-down control of grubbing geese on the vegetation resulted in local degradation of the marsh surface, a reduction in their preferred food source *Bolboschoenus maritimus*, and this would reduce the food supply for the geese. However, these effects were limited in time, as in 12 years the patches regenerated back to a *Bolboschoenus maritimus* vegetation type. This is also in contrast to previous studies, where grubbing geese caused large-scale marsh degradation that continued even after the geese had disappeared (Jefferies et al. 2006, Peterson et al. 2013). Our results were in line with our second hypothesis that landscape-scale bottom-up control of sediment accretion on vegetation development resulted in a higher elevation, a reduction in the overall *Bolboschoenus maritimus* cover (through vegetation succession during 30 years), and thus would result in a reduction of the food supply for geese. Present results showed that bottom-up and top-down controls can co-occur, be it on different spatial as well as temporal scales. Overall, we found that in the long-term (decades) the food supply for greylag geese is controlled bottom-up by landscape-scale ecosystem development driven by sediment accretion, rather than by top-down control of the geese on the vegetation development.

Local-scale top-down control of grubbing geese

On a local patch scale of a few square metres, grubbing greylag geese showed to exert top-down control on the vegetation by creating bare patches thereby reducing their food source. This is in line with previous studies showing that grubbing geese can have strong

negative effects on coastal habitats (Kerbes et al. 1990, Srivastava and Jefferies 1996, Esselink et al. 1997, McLaren and Jefferies 2004). However, in contrast to these studies, we found regeneration of the patches to a similar vegetation type, whereas some conclude regeneration might not even be possible (Peterson et al. 2013). In the present study, we could not determine when the first pioneer species successfully established in the bare patches. However, we did find recovery of the patches towards a similar vegetation type dominated by *Bolboschoenus maritimus* (Fig. 5.5). During recovery several early successional species established in the bare patches. Therefore, presence of grubbing geese resulted in our study in a local set-back of the vegetation succession and not in the more permanent and large scale degradation as observed in previous studies (Jefferies et al. 2006, Peterson et al. 2013). It has been shown that small grazers, such as hare, can retard succession (Kuijper and Bakker 2005, Gedan et al. 2009), whereas large grazers, such as livestock, can bring back earlier-successional plant species in older marsh systems (Bos et al. 2002). Our results showed that greylag geese can temporarily bring back younger-successional plant species, be it on a much smaller scale of a few m² instead of the potential km² wide impact of cattle (Bos et al. 2002).

Landscape scale bottom-up control through marsh accretion

The marsh surface increased rapidly due to high accretion rates that outpaced local sea-level rise (Fig. 5.7). Marsh surface elevation and inundation frequency are important determinants for the distribution of plant species in marshes (Olf et al. 1997, Davy et al. 2011). *Bolboschoenus maritimus* is the preferred food choice for greylag geese (Amat 1995, Castelijnns et al. 1998) and this plant species generally dominates the lower elevated depressions in between creek bank levees with high soil water availability (Dijkema 1990, Piernik 2005). *Elytrigia atherica* is generally limited to higher elevated creek bank levees without water logging conditions (Davy et al. 2011, Veeneklaas et al. 2013). An increase in marsh elevation and a reduction in water logging conditions enable *Elytrigia atherica* expansion from the higher elevated levees towards the lower elevated depressions, thereby outcompeting *Bolboschoenus maritimus* and reducing it in cover.

Herbivore presence in time

A bottom-up induced landscape-scale decrease in the main food source will reduce the food supply for the greylag geese and reduce their abundance. This is especially the case when not all *Bolboschoenus maritimus* present in the system will be accessible for the geese, as is highly likely given earlier studies. These previous studies showed that greylag geese need a local disturbance of otherwise tall and dense *Bolboschoenus maritimus* vegetation, so that they can land in the disturbed area and use such spots to get access to the *Bolboschoenus maritimus* food source (Esselink et al. 1997). Furthermore, greylag geese can only forage on small, newly developed tubers of limited sizes (Amat and Varo

2008). Moreover, greylag geese might be limited to *Bolboschoenus maritimus* in lower elevated depressions with water-logging conditions. This will soften the soil and allow the geese to easier grub into the soil (Esselink et al. 1997). A landscape-scale increase in the marsh platform elevation, as observed in Saefthinghe, generally decreases tidal inundation and increases soil drainage and soil compaction (He et al. 2011). This will reduce the number of *Bolboschoenus maritimus* patches that are accessible for the geese even further. Ultimately, we showed both top-down and bottom-up control on the vegetation occurred simultaneously but on different spatial scales and the effect changed along a temporal scale. Based on the increase in marsh surface elevation and the natural succession towards *Elytrigia atherica* on a landscape scale, we conclude that grazer abundance is pre-dominantly controlled bottom-up on a landscape-scale (km²).

Conservation implications

Global increase in migrating goose populations has resulted in increasing grazing pressures on many tidal marshes (Gauthier et al. 2005, Van Eerden et al. 2005, Jefferies et al. 2006, Voslamber et al. 2010). The impact of such high grazing pressures differs between marshes and could depend on local abiotic stress as well as heterogeneity present within the system. Firstly, extreme abiotic conditions (Shumway and Bertness 1994, McLaren and Jefferies 2004, Davy et al. 2011, Peterson et al. 2013) or low tidal regime (Kirwan and Guntenspergen 2010) can limit successful (re-) establishment and development of many marsh species. Our study site is a relatively high productive, brackish marsh with a high tidal regime. Re-colonization by early successional species in the bare patches will be less limited in this marsh, compared to less productive, more saline marshes with low tidal regimes. Secondly, Saefthinghe is a very heterogeneous marsh. Creeks are bordered by higher elevated levees dominated by *Elytrigia atherica*, alternating with small depressions covered by *Bolboschoenus maritimus*. When grubbing geese start feeding on below-ground tubers, they generally continue until all their preferred food choice is removed (Esselink et al. 1997, Jefferies et al. 2006). According to many studies, this foraging behaviour results in degradation of large marsh areas (Kerbes et al. 1990, Jefferies et al. 2006, Peterson et al. 2013). Due to the patchy and heterogeneous structure of Saefthinghe, *Bolboschoenus maritimus* is present in smaller patches forcing the geese to continuously move on to new unexplored patches and thereby limiting their potential detrimental impact on the marsh' vegetation. Thus, the impact of grubbing geese could be very marsh specific and may depend on many different environmental conditions such as present heterogeneity and local abiotic conditions.

This study showed the complexity of determining the factors that control grazer abundance within an ecosystem. Many studies try to determine sustainable population densities for grazers in ecosystems by monitoring the food supply, but often they focus on the top-down control by the grazers and do not include large- scale, bottom-up con-

trols on the food supply (e.g. (Hansen et al. 2006, Perea et al. 2015), but see also (Madsen et al. 2011). Marino et al. (2014) found that the number of grazers sustainable within an ecosystem is not static but fluctuates with annual precipitation. Additionally, we showed that next to environmental conditions, such as weather, and the impact of the grazers themselves, also the natural development of an ecosystem needs to be taken in account when we want to estimate the number of grazers that can be maintained sustainable within an ecosystem.

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