Effects of vegetation patterns and grazers on tidal marshes

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6 General synthesis: vegetation patterns and grazers on tidal marshes

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INTRODUCTION

Grassland ecosystems are used for livestock grazing on a global scale, resulting in very high grazing pressures (Kemp and Michalk 2007). Additionally, due to changing environmental conditions and human impact, populations of native grazers are reducing in some ecosystems (De Visser et al. 2011), while they are increasing in other ecosystems (e.g. Fox et al. 2005). With these global changes in grazing pressures, it is important to gain understanding on how they impact vegetation characteristics, the interactions between grazers and vegetation, and the effects on important ecosystem processes. In this thesis I studied this, using tidal marshes as a model ecosystem.

Many different grazers are present on tidal marshes. Migratory birds use marshes as stop-over sites along their migration route or as staging site during winter (Madsen 1991, Van Der Graaf et al. 2007). Small grazers, such as hare and rabbits, can graze on the marshes year-round (Van Der Wal et al. 2000c). Additionally, large grazers, such as cattle, sheep or horses, are kept on the marshes for nature management or agricultural purposes (Bakker 1989, Kiehl et al. 1996, Bouchard et al. 2003, Nolte et al. 2013a). Both small and large grazers can have a strong impact on the vegetation (e.g. Andresen et al. 1990, Silliman et al. 2005, Bertness et al. 2014), compact the soil (Schrama et al. 2013, Nolte et al. 2013b) and alter accretion rates (Suchrow et al. 2012, Nolte et al. 2015). Small grazers are known to retard succession (Van Der Wal et al. 2000, Kuijper and Bakker 2005, Gedan et al. 2009), while large grazers can set back the successional clock by bringing back young-successional plant species, thereby boosting plant diversity (Bos et al. 2002). In the past few decades, populations of geese have increased substantially and this resulted in increased grazing pressures on coastal wetlands as well as agricultural fields (Kerbes et al. 1990, Madsen 1991, Gauthier et al. 2005, Van Eerden et al. 2005, Wuczyński et al. 2012). For conservation purposes, we need to increase our understanding of how grazer presence impact important marsh characteristics, and how this in turn affects grazer abundance.

THESIS OVERVIEW

In this thesis, I used long-term field-based experiments together with long-term datasets, to study the role of grazers in tidal marshes and how grazer abundance is affected by small-scale topographic heterogeneity in the marsh platform. I included different spatial scales (few square metres vs. kilometres) as well as different grazer types (small grazers like hare and geese vs. large grazers like cattle and above-ground grazing by cattle, hare, Barnacle geese and Brent geese vs. below-ground grubbing by Greylag geese). Firstly, I determined how presence of small grazers and large grazers affect important marsh characteristics: vegetation height, the marsh accretion rates (**chapter 2**) and carbon sequestration (**chapter 3**). To unravel the formation of small-scale topographic heterogeneity in tidal marshes, I compared similar topographic patterns present in four different European marshes in **box 1**. In **chapter 4** I studied how the presence of the small grazers as well as the local plant diversity is affected when this topographic heterogeneity is present within the marsh. Finally, I included small-scale topographic heterogeneity that is created by grubbing Greylag goose, *Anser anser*, and studied their impact on plant diversity as well as the abundance of Greylag geese on the marsh (**chapter 5**).

I divided this study in three main questions:

1. What is the effect of long-term, above-ground grazing on the local marsh vegetation, salt-marsh accretion rates and carbon sequestration?
2. What is the effect of topographic heterogeneity on the local marsh vegetation and grazer presence?
3. What is the long-term effect of below-ground grubbing on the marsh vegetation and how this in turn affects grazer abundance?

These questions are discussed in detail in the following sections. The main findings are summarized in table 6.1.

MAIN FINDINGS

1. What is the effect of long-term, above-ground grazing on the local marsh vegetation, salt-marsh accretion rates and carbon sequestration?

Effects of grazing on vegetation height and marsh accretion rates

Marshes need to accumulate enough sediment from the inundating water, to keep up with the accelerating sea level (FitzGerald et al. 2008, Church and White 2011). Many studies already have tried to predict this by estimating the marsh accretion rates (Van Wijnen and Bakker 2001, Kirwan and Megonigal 2013). However, the number of studies focusing on the long-term effects of herbivores on vegetation structure and subsequent effects on marsh accretion has been limited (but with exception of: e.g. Neuhaus et al. 1999, Suchrow et al. 2012, Nolte et al. 2013b, 2015). In **chapter 2**, we showed that both small grazers (hare, Barnacle goose and Brent goose) and large grazers (cattle) reduced vegetation height. However, they did not affect sediment deposition. An important result we found was that trampling by large grazers negatively affected marsh accretion rates by compacting the soil, whereas small grazers had no effect on the marsh accretion rates. Grazing by livestock is used as a tool in nature management to maintain plant diversity in many European marshes (Bakker 1989, Kiehl et al. 1996). Although we did not find that grazers significantly reduced the amount of sediment deposited on the marsh platform, we found a reduced marsh accretion rate and proposed that soil compaction by large grazers needs be taken into account when estimating the ability of coastal systems to cope with an accelerating sea-level rise.

EFFECTS OF GRAZING ON CARBON SEQUESTRATION

Another effect of grazers on marshes that has received limited attention is the impact of grazers on carbon sequestration. Tidal marshes can trap large amounts of carbon in the marsh soil (e.g., see Laffoley and Grimsditch 2009, Mcleod et al. 2011). However, knowledge of how presence of grazers affects soil carbon sequestration is limited. In **chapter 3** we estimated total accumulated organic carbon in soils of a back-barrier salt marsh, and determined how this is affected by long-term grazing by both small and large grazers. Small grazers (hare, Barnacle goose and Brent goose) had a limited effect on total accumulated organic carbon, whereas large grazers (cattle) enhanced carbon content in the marsh soil substantially, due to soil compaction and a shift in biomass distribution in the

Table 6.1. A summary of the main findings presented in this thesis. Each column represents one type of grazer included in this thesis, as well as presence of topographic heterogeneity. Each row shows a marsh characteristic that was either positively (+), negatively (–) or unaffected (0) by the grazing type or topographic heterogeneity present. Empty cells indicate that it was not estimated in this study. The corresponding chapter is given in brackets behind each effect.

Marsh characteristic	**Small above-ground grazers** (hare, Barnacle goose and Brent goose)	**Large above-ground grazers** (cattle)	**Topographic heterogeneity**	**Small below-ground grubbers** (Greylag geese)
Vegetation height	– (Ch. 2)	– (Ch. 2)		– (Ch. 5)
Sediment deposition	0 (Ch. 2)	0 (Ch. 2)		
Bulk density	0 (Ch. 2)	+ (Ch. 2)		
Salt–marsh accretion rate	0 (Ch. 2)	– (Ch. 2)	0 (Ch. 4)	
Redox potential	– (Ch. 3)	– (Ch. 3)		
Shoot biomass	0/– (Ch. 3/Ch. 4)	– (Ch. 3)	+ (Ch. 4)	– (Ch. 5)
Root biomass	0 (Ch. 3)	+ (Ch. 3)		– (Ch. 5)
Litter biomass	– (Ch. 3)	– (Ch. 3)		
Carbon sequestration	0 (Ch. 3)	+ (Ch. 3)		
Veg. succession			+ (Ch. 4)	– (Ch. 5)
Plant diversity			+ (Ch. 4)	+ (Ch. 5)
Small grazer abundance			+/0 (Ch. 5/6)*	– (Ch. 5)***

+ = positive effect, – = negative effect, 0 = no effect. * Positive effect on Hare, Brent geese and Barnacle geese; no effect on Greylag geese, ** Positive effect on hare abundance; no significant effect on abundances of Barnacle geese and Brent geese, ***Greylag geese had a short–term negative effect on their own food supply.

local vegetation towards the roots. By compacting the soil, large grazers enhanced anoxic conditions, thereby reducing the oxygen availability for organic carbon decomposition by the local microbial community. Effects of large grazers on carbon stocks likely differ between ecosystems with soils consisting of fine-grained or large- grained sediment. Independent of grain size, in many different ecosystems grazing has been shown to enhance the below-ground biomass of the local vegetation (see for example McNaughton et al. 1998, Yu and Chmura 2010, Olsen et al. 2011, Sjögersten et al. 2012). However, when the soils consist of coarse-grained sediment, trampling by large grazers will likely have a limited effect on the anoxicity of the soil (Schrama et al. 2013a). In these instances, the most dominant effect of large grazers will be above-ground biomass removal and grazing will negatively affect carbon sequestration (McNaughton et al. 1998, Sjögersten et al. 2012). When the soil consists of fine-grained sediment, then large grazers can compact the soil, reduce oxygen availability for the decomposers and thus positively affect carbon sequestration. Ultimately, we hypothesized that large grazers can increase carbon sequestration in ecosystems, when the soil consists of fine-grained sediment and soil compaction by trampling results in anoxic conditions in the soil.

2. **What is the effect of topographic heterogeneity on the local vegetation and grazer presence?**

At several tidal marshes we observed small-scale (i.e., a few square metres) heterogeneity in marsh morphology that consisted of higher elevated hummocks alternating with lower elevated depressions. These heterogeneities have been mentioned in literature before (e.g. Gray and Bunce 1972, Allen 2000), but it remained relatively unknown how they are formed or how they impact important marsh dynamics. In **box 1**, we determined that the largest part of the heterogeneity was explained by heterogeneity in the underlying coarse-grained sediment. Additionally, a smaller part was explained by a thicker fine-grained sediment layer on top of the hummocks compared to the depressions. Based on these results we concluded that the patterns are formed in pioneer stage before fine-grained sediment is accumulating on the vegetated marsh platform. Several studies showed that vegetation will increase sediment deposition locally and/or reduce erosions rates (e.g. Peralta et al. 2008, Mudd et al. 2010). As vegetation establishes on the hummocks first (**box 1**), they will have a higher fine-grained sediment deposition and hence accretion compared to the neighbouring depressions. When the marsh develops further and vegetation has established successfully in the depressions, marsh accretion rates become equal between hummocks and depressions (**box 1**). This resulted in the patterns to get maintained throughout ecosystem development and we found that they were still present at 120 years old marsh (**box 1**).

In **chapter 4** we studied how presence of this topographic heterogeneity altered plant diversity and grazer presence (hare, Barnacle goose and Brent goose). A general theory in ecology is that young ecosystems are unsuitable for grazers due to low primary production (Oksanen et al. 1981, Van De Koppel et al. 1996). Plant diversity is still low as well. With increasing marsh age: 1) an increase in primary production, 2) an increase in plant diversity and 3) a larger population of grazers is found (Van De Koppel et al. 1996, Olff et al. 1997). Studies on tidal marshes have shown that when succession continues even further, the palatable plant species get replaced with unpalatable ones. This results in grazers to get evicted from the ecosystem and populations of small grazers (Van Der Wal et al. 2000b) and plant diversity (Gray and Bunce 1972, Veeneklaas et al. 2013) reduce again. This thesis now showed that throughout ecosystem development (from 15 to 120 yrs-old marsh), plant diversity increased and this was maintained in time when topographic heterogeneity was present (compared with a homogeneous marsh) (**chapter 4**). Additionally, we found a high grazing pressure on top of hummocks at very young successional stage. Elevation determines for a large part the plant community in tidal marshes (Davy et al. 2011) and presence of higher elevated hummocks allowed later successional plant species to establish earlier in succession. Ultimately, we concluded that topographic heterogeneity: 1) increased plant diversity throughout ecosystem development, and 2) increased the abundance of small grazers, such as hares and geese, in young marshes.

3. **What is the long-term effect of below-ground grubbing on the vegetation and how this in turn affects grazer abundance?**

So far, we have focused on the effects of grazers that feed on above-ground plant parts. This type of grazing is much less detrimental for the marsh vegetation, compared to grazers that grub below ground for storage organs of the vegetation. Several migrating bird species, such as Greylag goose (Esselink et al. 1997) and Lesser Snow goose (Mclaren and Jefferies 2004), are known to create large bare patches in the marsh vegetation (Esselink et al. 1997, Mclaren and Jefferies 2004). In extreme cases, they can even degrade large marsh areas (Kerbes et al. 1990, Jefferies et al. 2006, Peterson et al. 2013). In **chapter 5**, we studied a large population of grubbing Greylag goose and estimated their top-down effect on the marsh vegetation. Additionally, we estimated large-scale bottom-up effects of marsh accretion on the cover of their preferred food source: Sea club-rush, *Bolboschoenus maritimus*.

Greylag geese grub for the below-ground storage organs, thereby creating bare patches (of a few square metres) within the marsh vegetation. We determined how these patches regenerated in time. In our study site, a reduction in population size of the Greylag goose has been observed in the past decade, despite the absence of predators (Castelijns and Jacobusse 2010). We hypothesized that this is the result of a reduction in their food source. We found that on a local patch scale, Greylag geese set back plant succession. Typical early-successional plant species established in the bare patches created by the geese. In contrast to other studies that observed negative effects of grubbing geese (e.g. Kerbes et al. 1990), we found a positive effect on plant diversity. Grubbing reduced the food resources of the marsh for Greylag geese 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 current sea-level rise. This resulted in a strong decrease in cover of *Bolboschoenus maritimus* as part of the natural succession, which could explain the reduction in Greylag geese abundance. Ultimately, we conclude that although Greylag geese can exert a top-down control on plant diversity, on the long-term bottom-up control by marsh accretion is causing the Greylag geese to get evicted from the ecosystem and thereby plant diversity to decline.

THE IMPACT OF GRAZERS ON IMPORTANT ECOSYSTEM DYNAMICS

The results in this thesis showed that the impact of grazers on marshes depends largely on body size as well as forage mechanism. Larger-bodied grazers have been shown to have a larger impact on plant diversity (Bakker et al. 2006). Additionally, they are also more likely to change processes in an ecosystem by changing local soil properties due to their increased body weight (Olff and Ritchie 1998, Schrama et al. 2013a). We found a very limited effect by small above-ground grazers, whereas large above-ground grazers had a large impact on marsh dynamics through trampling of the soil (**chapter 2 & 3**). The largest effect is likely to occur in grasslands with fine-grained or peat-based soils (Schrama et al. 2013b). Soil compaction might not only alter the soil properties, such as aeration and water content, but will also change the vegetation composition (Van Klink et al. 2015). When we want to introduce livestock to ecosystems that have never been grazed by livestock before, we need to take into account the potential indirect effect on an ecosystem through changing soil properties.

Next to body size, we also found that the forage mechanism will determine for a large part the impact of a grazer. Grazers that remove only the above-ground plant parts of the vegetation will allow the vegetation to recover fairly quickly. However, when grazers remove both the above- and below-ground plant parts, then it will become much more difficult for the vegetation to regenerate (Peterson et al. 2013), and may even cause ecosystem collapse (Kerbes et al. 1990, Jefferies et al. 2006, Christianen et al. 2014). In marshes, grubbing geese feed on below-ground storage organs of the local vegetation. This foraging behaviour results in bare patches to occur within the marsh vegetation (Esselink et al. 1997, Mclaren and Jefferies 2004). These bare patches can have large impacts on the functioning of marshes, both negatively; by enhancing erosion of the marsh surface and deteriorating soil conditions (Mclaren and Jefferies 2004, Jefferies et al. 2006, Peterson et al. 2013), but also positively; by providing a habitat for other marsh species, such as crabs (Daleo et al. 2011), and an increase in plant diversity (**chapter 5**).

THE IMPACT OF LARGE GRAZERS AND HETEROGENEITY ON SMALL-GRAZER ABUNDANCE

The abundance of a species within an ecosystem is largely determined by the available food resources (White 2008). This in turn is largely determined by large-scale abiotic factors, such as weather conditions and available nutrients. However, interactions between grazers (both negative through competition and positive through facilitation) can also have a large impact on the abundance of a grazer (Arsenault and Owen-Smith 2002, Farnsworth et al. 2002). For example, many grassland ecosystems are grazed by multiple grazer species and may also be used for livestock grazing (Kemp and Michalk 2007). They will have to compete for the available food resources, which could lead to a reduction in grazer abundance (Farnsworth et al. 2002, Augustine and Springer 2013). In contrast, in several grassland ecosystems different grazer species were found to facilitate for each other (McNaughton 1976, Augustine and Springer 2013).

In tidal marshes, grazers have been shown that they can facilitate for each other, namely, hare facilitating for geese (Van Der Wal et al. 2000c) and cattle facilitating for geese (Bos et al. 2002, Kuijper et al. 2008). In this study, we estimated the effects of cattle grazing on 1) small grazers that graze above ground and 2) geese that grub for below-ground storage organs (Fig. 6.1 and 6.2). In line with previous studies, we found highest above-ground grazer abundance of Barnacle geese, Brent geese and hare at marshes of intermediate age, after which they reduced in abundance again (Fig. 6.1.A, chapter 2, Van De Koppel et al. 1996). The number of the small grazers increased again when cattle were introduced (Fig. 6.1A, Bos et al. 2002, Kuijper et al. 2008). Meanwhile, dropping counts estimated in Saeftinghe showed that the below-ground grubbing Greylag geese highly preferred to feed in *Bolboschoenus maritmus* vegetation and in the bare patches surrounded by *Bolboschoenus maritmus* (Fig. 6.2), whereas we found almost no droppings in the drier cattle-grazed parts. Presence of livestock can facilitate for the small above-ground grazers, but we found no facilitation for the below-ground grubbers. When grazers facilitate for each other, they generally enhance the available food resources (McNaughton 1976, Arsenault and Owen-Smith 2002). Greylag geese prefer to feed on *Bolboschoenus maritimus* (Amat 1995) that dominates in the lower elevated depressions, whereas cattle were present on the drier parts of the marsh. Similarly as in other marshes, we observed short grazing lawns with high plant species diversity in the cattle-grazed marsh (Bos et al. 2002, Wanner et al. 2014) and not an increase in *Bolboschoenus maritimus* cover (personal observations).

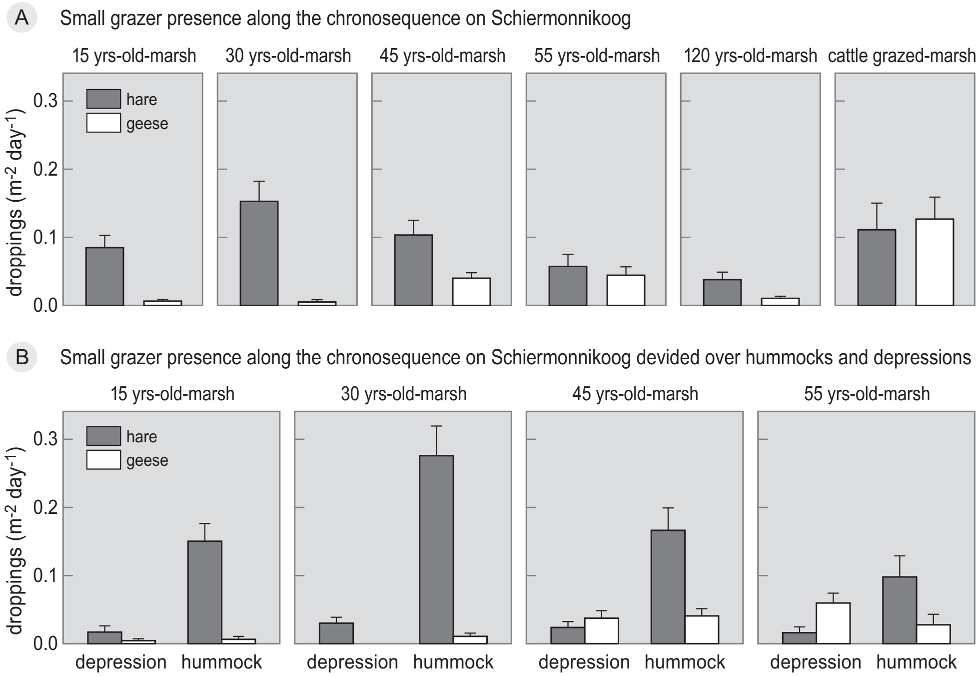

Figure 6.1. Dropping counts estimated for Barnacle geese, Brent geese and hares together, along the natural chronosequence on Schiermonnikoog in November 2010. First we show the dropping counts estimated in 15 yrs-old marsh up to 120 yrs-old marsh, and we compared them with the cattle-grazed marsh (A). Secondly, we zoom in on the young marshes (15 yrs-old marsh up to 55 yrs-old marsh) to show the effect of small-scale patterns present in marsh morphology (B).

Next to grazer presence we found that topographic heterogeneity also affected the abundance of grazers in tidal marshes (**chapter 4** and Fig. 6.1.B). Many studies estimating the impact of spatial heterogeneity in ecosystems found an increase in plant diversity (Costanza et al. 2011, Ruifrok et al. 2014, Stein et al. 2014). However, the impact of topographic heterogeneity on the presence of grazers had not received a lot of attention. Red fescue, *Festuca rubra*, is a preferred food choice of the small grazers in tidal marshes (Van Der Wal et al. 2000c, Van Der Graaf et al. 2005) and we found a very high cover on top of higher elevated hummocks, while cover was still very low when the heterogeneity was not present (**chapter 4**). In young low productive marshes, where limited biomass production limits the number of grazers, the presence of such higher elevated hummocks increased the number of grazers able to forage efficiently within the ecosystem (**chapter 4**, Fig. 6.1.B). Whether heterogeneity will increase grazer abundance in other ecosystems will likely depend on the overall level of stress. Low productivity or high stress environmental conditions, such as high temperature, drought or high salinity, that gets alleviated when heterogeneity is present, could increase the food supply and thereby grazer abundance in other ecosystems as well.

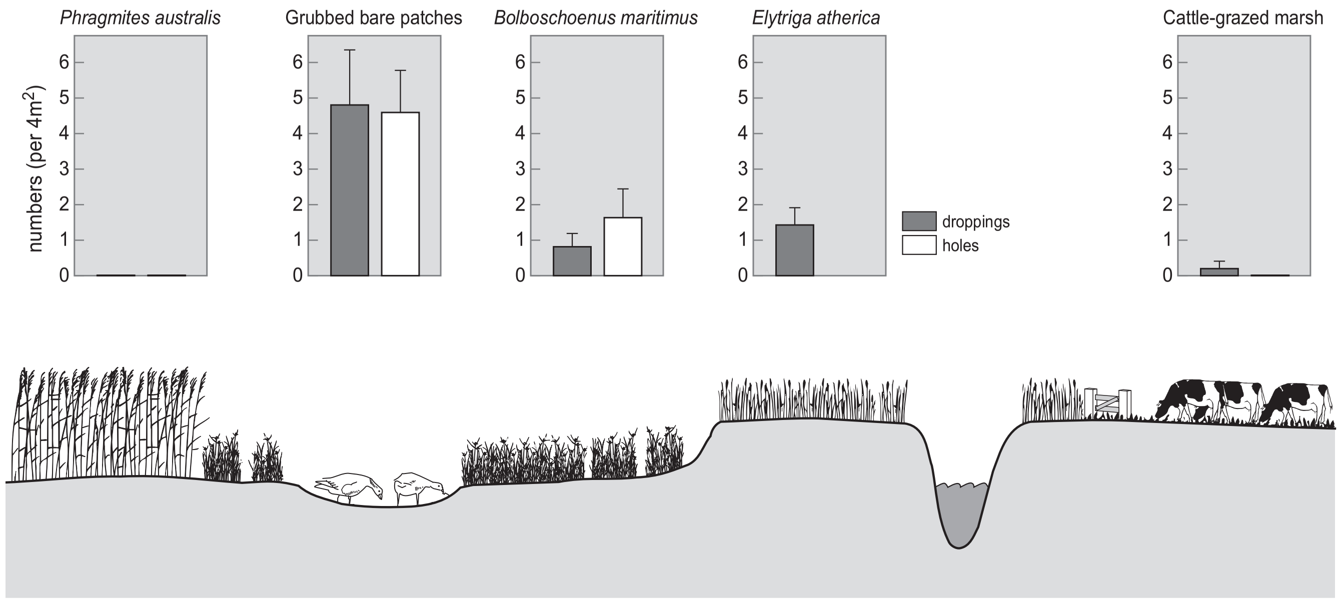

Figure 6.2. Number of droppings and grubbed holes (of a few cm wide and a few cm in depth) by Greylag geese comparing several plant communities and the cattle-grazed marsh. Droppings were estimated in February 2009 on Saeftinghe.

MANAGEMENT IMPLICATIONS

Marshes get frequently inundated and harbour many specialized plant species which can cope with these stressful environmental conditions (Więski et al. 2009). Therefore, the protection of marshes has become important in the conservation of biodiversity in Europe. Many European marshes are used for livestock grazing, which is generally used as a nature management tool (Kiehl et al. 1996, Bakker et al. 2003, Bouchard et al. 2003). Cattle grazing can bring back young-successional plant species and thus increase or maintain local plant diversity in these coastal habitats (Bos et al. 2002, Bakker et al. 2003). Next to numerous plant species, also many vertebrate species benefit from grazing (Van Wieren and Bakker 2008). For example, breeding birds prefer low to moderate grazing pressure with a high patchiness in the vegetation structure (Mandema et al. 2014b), while geese prefer marshes with high stocking densities (Mandema et al. 2014a). Many invertebrate species prefer tall vegetation, which can be found in moderately grazed or ungrazed salt marshes (Van Klink et al. 2013).

In this study, I focused on the impact of the different types of grazers on the vegetation and how this affects important marsh dynamics. Effects of small above-ground grazers were very limited. Below-ground grubbers had a large impact on the vegetation composition, but only for a limited period of time as the bare patches regenerated back in approximately 12 years. With respect to cattle, I found that these large animals had a very large effect through trampling of the soil. Trampling by livestock has been largely neglected in ecology so far (but with exceptions of e.g. (Schrama et al. 2013a, Nolte et al. 2013c, Veldhuis et al. 2014). Trampling by cattle reduced the marsh accretion rates (**chapter 2**) while, it enhanced the carbon sequestration rate in the marsh soil (**chapter 3**). Whether the positive impact of large grazers on biodiversity and carbon sequestration, outweighs the negative impact on marsh accretion rate will be very site specific, depending on the problems the marsh are facing. Marshes with high sedimentation rates will be less affected by a reduced accretion rate following cattle grazing. Hence, livestock grazing on these sites could be used to provide increased carbon sequestration rates as well as increased biodiversity. The impact of grazers on both vegetation and soil characteristics should be taken into account in future studies that use models to estimate whether coastal habitats can cope with an accelerated sea-level rise.