

Spatiotemporal changes in vegetation
following range expansion in Svalbard
reindeer (*Rangifer tarandus platyrhynchus*)

Marit Hegseth Rønning

Biologi

Innlevert: mai 2014

Hovedveileder: Bernt-Erik Sæther, IBI

Medveileder: Brage Bremset Hansen, IBI
Åshild Ønik Pedersen, NPI

Norges teknisk-naturvitenskapelige universitet
Institutt for biologi

Abstract

Large herbivores have the ability to strongly modify vegetation composition and abundance when they occupy new areas and where predators are absent. Here, I examined changes in vegetation in three neighbouring areas that represent a gradient of accumulated grazing pressure following different time of re-establishment (1978, 1994, 1996) of the predator-free wild Svalbard reindeer (*Rangifer tarandus platyrhynchus*). To test for spatial and temporal changes in cover and composition as a result of changes in reindeer density, I repeated vegetation analyses from 2000 and 2005 in summer 2013. Lichens were largely depleted already in 2000 in the area with the longest grazing history and irruptive dynamics. This was also observed during 2000 – 2013, while there was a strong decline in the two other areas, showing evidence of a shift from lichen-rich to lichen-poor vegetation due to re-establishments of reindeer and an increase in accumulated grazing pressure. The cover of mosses also showed tendency of a decline but there was no clear lichen-moss transition. There was however an increase in graminoids in the more recently re-established areas during 2000 - 2013. This indicates a change from lichen-dominated to more graminoid-dominated vegetation and gives support for the “alternative stable states hypothesis”, predicting that changes in herbivore densities may cause vegetation state transitions in tundra ecosystems. The study thus supports the assumption that in the absence of predation, reindeer may have a strong impact on vegetation abundance through herbivory and trampling. This is in line with the “exploitation ecosystem hypothesis”, predicting a top-down control by herbivores on the vegetation.

Keywords: Accumulated grazing pressure – “Alternative stable states hypothesis” – Plant-herbivore interactions - “Exploitation ecosystem hypothesis” – Svalbard reindeer

Sammendrag

Store planteetere som introduseres til nye områder er i stand til å modifisere abundansen og sammensetting av vegetasjonen, spesielt i områder uten predatorer. I dette studiet undersøkte jeg endringer i vegetasjonen i tre nærliggende områder som representerer en gradient i akkumulert beitetrykk. Gradienten er en følge av forskjellige år med re-etableringer (1978, 1994, 1996) av den ville svalbardreinen (*Rangifer tarandus platyrhynchus*), som ikke har noen naturlige predatorer. For å undersøke forandringer i viktige arter og artsgrupper repeterte jeg vegetasjonsanalyser fra 2000 og 2005 sommeren 2013. I området med lengst beitehistorie og irrupsjonsdynamikk var lav generelt helt nedbeitet gjennom 2000 - 2013, mens det var en sterkt nedgang i denne plantegruppen i de to andre områdene. Dette viser en overgang fra lav-rik til lav-fattig vegetasjon som en følge av re-introduksjonen av reinsdyr og en økning i akkumulert beitetrykk. Mosedekket viste også en minking og det var ingen tydelig overgang fra lav-dominerende til mose-dominerende vegetasjon. Det var imidlertid en økning av graminoider i løpet av 2000 - 2013 i de senere etablerte områdene, som tyder på en overgang fra vegetasjon dominert av lav til en mer graminoid-dominerende vegetasjon. Dette stemmer overens med "alternative stable states - hypotesen" som sier at forandringer i tettheten av planteetere kan medføre vegetasjonsoverganger i økosystem på tundraen. Studiet støtter dermed antakelsen om at reinsdyr kan ha en betydelig innvirkning på vegetasjonen gjennom beiting og nedtråkking. Dette er også i samsvar med "exploitation ecosystem - hypotesen" som antar at planteetere styrer vegetasjon gjennom en "top - down"- kontroll.

Table of Contents

| | |
|--|------------|
| ABSTRACT | I |
| SAMMENDRAG | III |
| INTRODUCTION | 1 |
| METHODS | 5 |
| STUDY AREA AND SPECIES | 5 |
| DATA COLLECTION | 7 |
| ESTIMATING POPULATION SIZE OF REINDEER | 9 |
| EVALUATING VEGETATION TYPE | 9 |
| OBSERVER TEST | 10 |
| DATA ANALYSIS | 10 |
| RESULTS | 12 |
| LICHEN COVER | 12 |
| MOSS COVER | 15 |
| GRAMINOIDS | 18 |
| OTHER IMPORTANT REINDEER FOOD PLANTS | 23 |
| OBSERVER TEST | 26 |
| DISCUSSION | 27 |
| ACKNOWLEDGEMENTS | 33 |
| REFERENCES | 34 |
| APPENDIX | 39 |
| APPENDIX 1 | 39 |
| APPENDIX 2 | 40 |
| APPENDIX 3 | 41 |
| APPENDIX 4 | 42 |
| APPENDIX 5 | 43 |
| APPENDIX 6 | 44 |

Introduction

Large herbivores have the ability to strongly modify ecosystems at several temporal and spatial scales, influencing both the structure and diversity of plant communities (Hobbs, 1996, Augustine & McNaughton 1998, Van der Wal et al. 2004, Van der Wal, 2006). This is especially observed in grazing systems without predators (Oksanen et al., 1981). One important challenge in ecology is therefore to predict the development of the vegetation temporally and spatially in relation to the effect of grazing pressure (Van der Wal 2006), especially if the currently observed global climate change continues, which may cause changes in the distributions of herbivores (Klein, 1999).

According to the “exploitation ecosystem hypothesis” (Fretwell, 1977, Oksanen et al., 1981), the number of trophic levels in an area is strongly related to the environment’s productivity. The hypothesis assumes that the impact of herbivory is most prevalent in moderately unproductive environments, which only provide enough forage to hold herbivore densities that are too low to support the addition of a predator. Thus, this type of environment is a two trophic system where herbivores may suppress the vegetation by a top-down control and cause a decrease in plant phytomass. Many of the unproductive ecosystems, e.g. some tundra regions, are characterized by such intense herbivory (Oksanen and Oksanen, 2000) and it is thus of importance to understand the potential impact these herbivores have on tundra ecosystems.

Herbivores` effect on plant cover and abundance through grazing and trampling may be especially pronounced in areas with new establishments of herbivore populations, where an irruption of the population may occur (Leopold, 1943, Riney, 1964, Caughley, 1970). An irruption is described as a rapid increase in population size above the threshold of what the area with its resources can hold. Due to lack of resources at the peak abundance, the population subsequently crashes to lower abundances (Leopold, 1943). Irruption can potentially cause

changes in vegetation composition and abundance, and cause depletion of highly preferred species (Mysterud, 2006).

The impact of herbivores on the vegetation may be described through the “alternative stable states” concept (Noy-Meir, 1975, May, 1977, Beisner et al., 2003), predicting that the vegetation in ecosystems can occur in two or more alternative stable states, with relatively sudden and predictable stepwise transitions between each state. Large herbivores and changes in herbivore densities may be responsible for the vegetation transitions, where net primary productivity and carrying capacity are expected to increase with grazing pressure (Noy-Meir, 1975, May, 1977, Beisner et al. , 2003, Van der Wal 2006). This is especially important in tundra ecosystems, which are often highly resource-limited (Van der Wal 2006). According to Van der Wal (2006), the Arctic tundra can occur in three different vegetation states, with transitions between states caused by reindeer/caribou herbivory. At low grazing pressure, lichens may dominate the tundra ecosystem (Van der Wal et al., 2001). However, an increase in density may induce a transition from lichen dominance to a state dominated by mosses due to lichens’ slow growth rate, their sensitivity to grazing and trampling (Van der Wal 2006), and because the plant group is more preferred as a food source than mosses by the reindeer in the tundra ecosystem (Cooper & Wookey 2001). In the moss-dominated state, graminoid growth is prevented through cold and wet soil (Van der Wal and Brooker, 2004, Van der Wal 2006). An increase in herbivore density may, however, promote a further transition to a graminoid-dominated state through nutrient admission and soil temperature manipulation from foraging and trampling (Van der Wal and Brooker, 2004). Graminoids benefit from increased grazing pressure due to increased soil nutrient availability from faeces depositions and their ability to tolerate repeated defoliation (Van der Wal and Brooker, 2004), thus keeping the tundra in a graminoid-dominated state at high herbivore densities (Van der Wal, 2006). The vegetation states may also be reversed when grazing pressure is reduced. With a decrease in grazing pressure, moss has an advantage over graminoids due to reductions in soil temperature and nutrient availability. In areas with further declines, lichens are seen to suppress mosses, possibly due to

the release of toxins (Van der Wal et al., 2001, Van der Wal, 2006). However, this is likely to occur in a slower speed than transformation in the opposite direction due to the slow growth rate of moss and lichen compared to graminoids (Cooper and Wookey, 2001, Van der Wal 2006).

Despite herbivores' strong ability to change vegetation composition, e.g. when they occupy new areas or are released from predators (Myserud, 2006), there are few studies from the Arctic examining the long-term impact of changes in herbivore densities on vegetation (but see Klein 1987, Manseau et al., 1996, Olofsson et al., 2001). One explanation may be the lack of data with long-term monitoring of both the vegetation and herbivore densities (Forsyth & Caley 2006). Further, interactions between herbivores and their food supply are often affected by other trophic levels (Hairston et al., 1960) and migration (Fryxell and Sinclair, 1988), thus making it difficult to evaluate vegetation changes due to changes in herbivore population density while excluding other interactions and the possibility of an altered space utilization.

The Arctic tundra on Svalbard is well suited for studying herbivore-vegetation interactions in a predator-free environment, with the non-migratory wild Svalbard reindeer as the only large herbivore living in the area. The Svalbard reindeer is relatively unaffected by interactions with other large herbivores and predators, however, some killings by polar bear (*Ursus maritimus*) have been reported (see Derocher et al. (2000)). A unique opportunity to study how herbivory causes spatiotemporal changes in vegetation was given by the re-introduction of reindeer to Brøggerhalvøya in 1978 and their later re-occupation of neighbouring areas (Aanes et al., 2002). Due to approximately a century of reindeer absence before the re-introduction, the vegetation was at a climax with high abundances of lichens, which subsequently changed with changes in reindeer density (Øritsland and Alendal, 1986).

In this study, I repeated vegetation measurements (in summer 2013) that were previously done on Brøggerhalvøya in 2000 and 2004-2005, as well as on Sarsøyra in 2000 and 2004-2005 and on Kaffiøyra in 2005, to investigate how

vegetation varies spatially and temporally with variation in herbivore grazing pressure. Due to different time of re-establishments (Aanes et al., 2002), the three areas represent a gradient of accumulated grazing pressure. Based on Van der Wal (2006) predictions on plant-herbivore interactions, I expected to see changes in cover and composition of the plant community with changes in reindeer density. In particular, I expected a change from lichen-dominated to more moss-dominated vegetation with increasing reindeer densities (Van der Wal, 2006), and that this vegetation followed a “wave-like” spatial pattern according to the step-wise re-colonisation of new areas (Hansen et al., 2009). A further increase in reindeer density could also result in a more graminoid dominated state (Van der Wal, 2006).

Methods

Study area and species

Data were collected on the three neighbouring and semi-isolated areas Brøggerhalvøya, Sarsøyra and Kaffiøyra situated northwest on Spitsbergen, at the high-Arctic archipelago of Svalbard (Figure 1). Despite the northern location, the study area has a relatively mild and oceanic climate caused by the Gulf Stream, bringing warm Atlantic currents to the northwest area of Spitsbergen (Hanssen-Bauer et al., 1990). The growth season typically lasts from June until late August (Van der Wal et al., 2004), with summer average air temperature during July - August of approximately 4.4 °C (SD = 0.7), and average total precipitation in the area of 31.9 mm (SD = 19.4) (during 1976 – 2000, Norwegian Meteorological Institute).

On the peninsula Brøggerhalvøya, the areas below 200 m a.s.l cover approximately 88 km² with a total vegetated area of 35 km² (Le Moullec, 2014, based on Johansen et al., 2009). Here, areas utilised by reindeer are mainly found in relatively productive coastal areas and flat lowland plains dominated by heath vegetation, surrounding the scarcely vegetated middle parts, which consist of glaciers and mountains. Sarsøyra and Kaffiøyra are located south of Brøggerhalvøya and constitute an area below 200 m a.s.l of about 40 km² (with a vegetated area of 27 km²) and 35 km² (with a vegetated area of 18 km²), respectively (Le Moullec, 2014, based on Johansen et al., 2009). Both areas have large lowland plains and are mainly dominated by heath vegetation, which constitute the main habitat utilised by reindeer. Glaciers, mountains and moraines surround and separate the areas, in addition to the sea (see Fig. 1), which thus limit long-distance migration between the three areas. However, spatiotemporal variation in forage availability may induce some reindeer movement between the study populations (Hansen et al., 2010b, Stien et al., 2010).



Figure 1: The study areas Brøggerhalvøya, Sarsøyra and Kaffiøyra on the northwest coast of Spitsbergen, Svalbard (insert). On the northern part of Brøggerhalvøya, there is a small research settlement, Ny-Ålesund (red dot). In the study area, vegetation was analysed in 80 plots at Brøggerhalvøya, 92 plots at Sarsøyra and 100 plots at Kaffiøyra. Source: Norwegian Polar Institute.

Brøggerhalvøya, Sarsøyra and Kaffiøyra represent a gradient of accumulated grazing pressure due to different time of establishments of reindeer populations in the three areas. First, a population was re-introduced at Brøggerhalvøya when 12 animals were successfully transferred from Adventdalen to the area in 1978 after approximately a century of absence due to hunting (Aanes et al., 2000). The population irrupted, and in the winter 1993-1994, the effects of overgrazing (Hansen et al., 2007), reduced foraging access from heavy ground icing, and high animal densities (Aanes et al., 2000, 2002, Kohler & Aanes 2004) became prominent and the population declined sharply from ca. 360 to ca. 80 individuals. A new population was established at the neighbouring area Sarsøyra during this decline and around 1996-1997, animals migrated further south and established a new population at Kaffiøyra (Hansen and Aanes, 2012).

The plant cover in the study area is scarce and is mainly dominated by mosses, vascular plants or, in some habitats on Sarsøyra and Kaffiøyra, lichens. The vegetation rarely exceeds a length of 5 cm, except for some graminoid species. Lichen is the preferred food source during winter due to high energy content and digestibility (Danell et al., 1994) and at the re-introduction of reindeer, there was a high abundance of lichens on Brøggerhalvøya (Brattbakk, 1986). However, on Brøggerhalvøya the plant group was largely depleted in 2000 – 2005 (Hansen et al., 2007) and a decline in lichen cover has also been observed between 2000 and 2005 at the formerly lichen rich Sarsøyra (Hansen et al., 2010b). Common vascular species in the study area consumed by reindeer during summer are the woody *Saxifraga oppositifolia*, the dwarf willow *Salix polaris*, and different graminoid species. The reindeer also prefer the annual and less common forbs *Oxyria digyna* and *Bistorta vivipara* (Staaland, 1986). *S. polaris* and *Dryas octopetala* are found in the reindeer diet during winter, in addition to non-vascular plants like mosses (Staaland, 1986). In addition to reindeer, pink-footed geese (*Anser brachyrhynchus*), Svalbard rock ptarmigans (*Lagopus muta hyperborea*) and barnacle geese (*Branta leucopsis*) are present in the study area. Based on personal observations and field observations by Hansen et al. (2007), these herbivores are, however, expected to have a minor effect on the vegetation in the study area except around Ny-Ålesund, where barnacle geese nest around lakes.

Data collection

Changes in vegetation composition were studied based on subsamples from randomly distributed sampling frames at Brøggerhalvøya, Sarsøyra and Kaffiøyra in 2000, 2005 and 2013. In 2000, vegetation point transects were performed at Brøggerhalvøya and Sarsøyra, with vegetation analysed at 623 and 363 plots, respectively (Hansen et al., 2007). There was a distance of 300 meters between each plot (i.e. a semi-random grid system design) and the analyses were performed below 200 m a.s.l. due to little or no vegetation at higher altitudes. In order to estimate the abundance of reindeer forage plants and other

common plants found in the study area, a sampling frame (1 x 1 m) divided into 10 x 10 smaller squares was used at each plot (Hansen et al., 2007).

The vegetation analysis was performed by visually recording cover and frequency of species and species groups. In the cover recordings, the number of small squares where more than half was covered by a particular species or species group were counted and summed up. However, due to scattered abundances, many plant species were measured by frequency recordings. Recording frequency involved estimating presence/absence of species or species groups in each of the 100 small squares, and the number of squares with presence was then summed up. In 2005, a random subsample of the plots with >10 % total plant cover was revisited (83 plots on Brøggerhalvøya and 92 at Sarsøyra). Mean dates of sampling in 2005 were 18th of July (SD = 3 days) at Sarsøyra and 29th of July at Brøggerhalvøya (SD = 5 days). Vegetation analyses were also performed on Kaffiøyra in 2004-05, where 351 vegetation plots were analysed in a 300 m grid system according to the design from Brøggerhalvøya and Sarsøyra in 2000 (B.B. Hansen, unpublished data).

In 2013, I re-analysed the vegetation plots analysed in 2005 at Brøggerhalvøya and Sarsøyra, and a subsample of the 2004-05 sampling sited at Kaffiøyra. Vegetation composition was recorded in 80 plots at Brøggerhalvøya, 92 at Sarsøyra and 100 at Kaffiøyra. This was done during July and early August 2013, where mean dates of sampling were 20th of July (SD = 3 days) at Sarsøyra, 25th – 26th of July (SD = 2 days) at Kaffiøyra, and 30th of July (SD = 3 days) at Brøggerhalvøya. The sampling dates thus corresponded well with the mean sampling dates in previous years (Hansen et al., 2007). Four different observers performed the vegetation analysis in 2013, with instructions given by one of the observers who performed the analyses in 2000, 2004 and 2005. A sampling frame (50 x 50 cm), further divided into 5x5 smaller squares, was used to measure the cover and frequency as described above. In the present analysis, the choice of species to record was restricted to the most common plants and plants central in reindeer diet. This included (i) the lichen genus *Cetraria* sp.; (ii) mosses; (iii) graminoids; and (iv) the vascular plants *S. polaris*, *O. digyna* and *B.*

vivipara. Species or species groups were included in the vegetation analysis if their living aboveground parts extended into the square, independent of where they were rooted. The plots were previously not marked, and relocations therefore had an inaccuracy associated with the use of GPS (global positioning system) for relocation. The sampling frame was laid down when the GPS arrived at the vegetation plot and displayed 0 m. During the analysis performed in 2013, the locations were marked with sink plates and nails for future analyses.

Estimating population size of reindeer

The reindeer density in the three study areas has been monitored annually during winter since the re-establishment of the three sub-populations (Aanes et al., 2000, 2002, Kohler and Aanes, 2004). No winter count was performed in 2009, and instead the population size (≥ 1 year old) counted in July was used in the analysis. To evaluate the effect of accumulated grazing pressure on vegetation changes, I calculated total animal density over the last 3, 5, 10 and 20 years per vegetated area.

Evaluating vegetation type

The vegetation in the study area was classified into seven habitat types determined in field and modified from Hansen (2008): 1) “Ridge” is found on dry, elevated and exposed ridges with an early snowmelt and a scattered vegetation characterized by *D. octopetala* and *S. polaris*. 2) “Moderate snowbed with a dominance of *Saxifraga oppositifolia*” is located in flat areas with vegetation dominated by *S. oppositifolia*, mosses and *S. polaris*. 3) “Moderate snowbed with a dominance of *Luzula* sp.” is similar to the latter habitat, but with a dominance of *Luzula* sp. instead of *S. oppositifolia*. 4) “Late snowbed” is found in areas with prolonged snow cover, relatively moist soil and with a high abundance of mosses and forbs, i.e. *O. digyna*. 5) “Sparse habitat” is sparsely vegetated and located in moraines, riverbeds, polar deserts, and erosive areas. 6) “Tundra mire” is moist and consists mainly of mosses and *Deschampsia alpina*. 7)

“Moss tundra” is only found on Brøggerhalvøya where it is associated with bird cliffs. Here, the wet and fertilised area is characterized by a high plant cover, consisting of graminoids, forbs and thick mats of mosses.

Observer test

To test for the effect of different observers, vegetation observer tests were performed two times on Sarsøyra during the summer 2013. The four observers analysed the same sampling frames (24 sampling frames in the first observer test, and 28 in the second), and the frames were laid down randomly and analysed by each observer sequentially. Cover of *Cetraria* sp. and mosses, as well as frequency of presence of graminoids were recorded. To randomize the procedure, observers closed their eyes upon arrival at the vegetation type and took three steps in different directions and then laid down the frame to do the analysis. The test was done in different vegetation types to get as much variation as possible.

Data analysis

Changes in plant cover and frequency were analysed using a generalized linear mixed model (GLMM) with a binomial family and a logit link. I ran separate GLMM's for each area when looking at changes in species or species groups between years, using year of survey and vegetation type as fixed variables, and vegetation plot id as a random variable (random intercept). This model was used for mosses and graminoids, while models for other species and species groups showed non-normality in residuals and are not included. Where a GLMM could not be fitted to the species, mainly due to data inflated by zeros, non-parametric tests were applied. In these tests, the vegetation data from 2000 and 2005 (collected using 1m x 1m frames) were divided by a factor of four for direct comparisons with the data collected in 2013 (which were collected using a 50x50 cm sized frame). When evaluating differences in plant abundance between years, a paired Wilcoxon rank sum test was used, while year-specific

differences in plant abundance between the three areas were assessed using a Mann – Whitney U test.

Likewise, a GLMM procedure was run when looking at the effect of accumulated grazing pressure (area-specific) on the vegetation to see if the spatiotemporal effects in different forage species could be described quantitatively by replacing the spatial and temporal variables with accumulated grazing pressure, using a binomial family and a logit link. The models for lichens and mosses indicated pronounced non-normality in the residuals and are not shown. Different effects were tested, including three, five, ten and twenty years of accumulated grazing pressure by reindeer. I ran model selection with AICc (Akaike`s information criterion corrected for small sample size) as criteria (Burnham and Anderson, 2002). Accumulated grazing pressure, area and vegetation type were included as fixed variables, while vegetation plot id was included as random factor. All statistical analyses were performed in R for Windows version 3.0.2 (R Development Core Team, 2013), with 0.05 as the level of significance.

Results

Lichen cover

The overgrazed Brøggerhalvøya (Hansen et al., 2007) was largely depleted of *Cetraria* sp. already in 2000 and did not show any significant change in cover during 2000 – 2005 and 2005 – 2013 (Table 1, Figure 2a). At the more recently occupied Sarsøyra, there was a strong reduction in the cover of *Cetraria* sp. during 2000 – 2005, which continued throughout 2005 – 2013 (Table 1, Figure 2b). During 2005 – 2013, the strongest decrease was observed on Kaffiøyra (Table 1, Figure 2c), where the reindeer population had been established a few years later than Sarsøyra. The cover of *Cetraria* lichens was significantly higher at Sarsøyra in 2000 compared to Brøggerhalvøya, which was also the case in 2005 (Table 1, see Fig. 2). In 2005, Kaffiøyra had a higher *Cetraria* cover compared to both Brøggerhalvøya and Sarsøyra. Despite the strong decreases on both Sarsøyra and Kaffiøyra, the *Cetraria* cover in the two areas was still higher than on the overgrazed Brøggerhalvøya in 2013. However, this year there was no longer a significant difference between Kaffiøyra and Sarsøyra (Table 1, see Fig. 2).

Table 1: Median cover of *Cetraria* sp. (with 25th and 75th percentiles) during the period 2000 – 2013. B = Brøggerhalvøya, S = Sarsøyra and K = Kaffiøyra. A paired Wilcoxon rank sum test is used to compare years, while a Mann – Whitney U test is used to compare areas.

| <i>Cetraria</i> sp. | | | | | | |
|---------------------|-------------------------|--------------------------|-------------------------|-------------------------|-------------------------|-------------------------|
| | 2000 | 2005 | 2013 | 2000 - 2005 | 2000 - 2013 | 2005 - 2013 |
| B | 0.00 (0.00-0.00) | 0.00 (0.00-0.00) | 0.00 (0.00-0.00) | V = 6.0 p = 0.850 | V = 3.0 p = 1.00 | V = 6.0 p = 0.850 |
| S | 0.25 (0.00-3.13) | 0.25 (0.00-1.81) | 0.00 (0.00-1.00) | V = 1238.0 p < 0.001 | V = 1235.5 p < 0.001 | V = 916.5 p < 0.01 |
| K | - | 0.75 (0.00-4.75) | 0.00 (0.00-1.00) | - | - | V = 1663.5 p < 0.001 |
| B-S | W = 1693.5 p < 0.001 | W = 1839.5, p < 0.001 | W = 2762.0 p < 0.001 | | | |
| B-K | - | W = 1664.5 p < 0.001 | W = 2925.5 p < 0.001 | | | |
| S-K | - | W = 3791.5 p < 0.05 | W = 4501.0 p = 0.743 | | | |

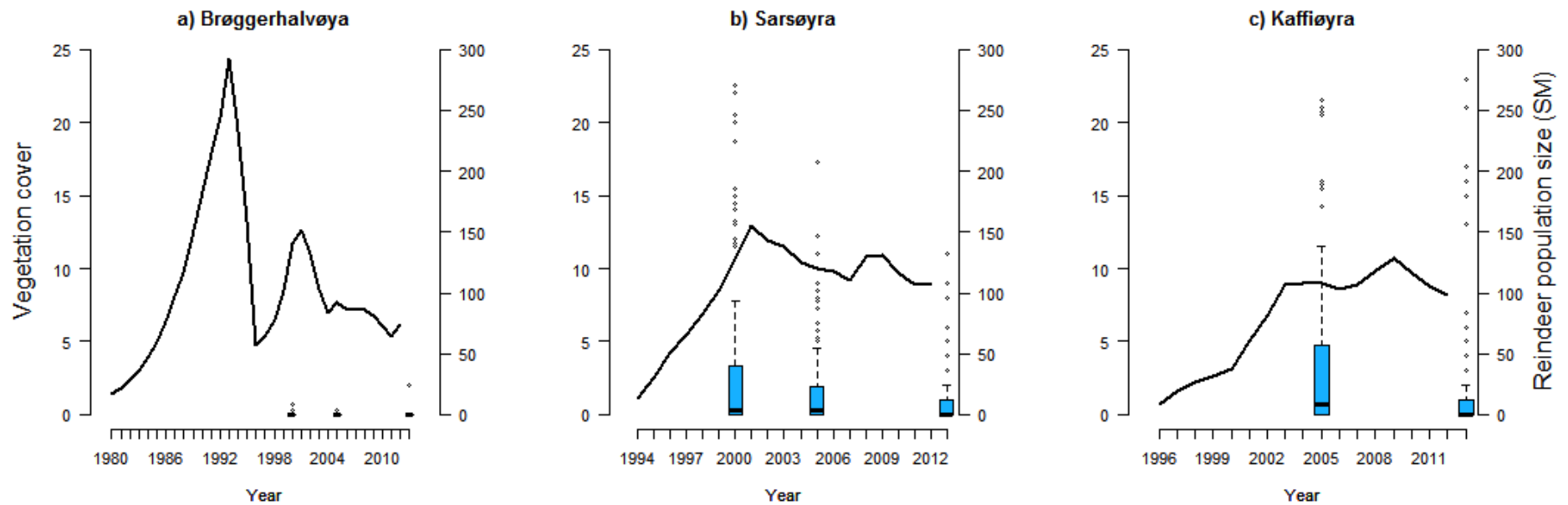


Figure 2: Cover of *Cetraria* sp. at a) Brøggerhalvøya, b) Sarsøyra and c) Kaffiøyra. Boxplots represent cover of *Cetraria* in 2000, 2005 and 2013, showing median values and *whiskers*, which indicate the 25th and the 75th percentile. The solid lines show fluctuations in reindeer population size during 1979 – 2012 at Brøggerhalvøya, 1994 – 2012 at Sarsøyra and 1996 – 2012 at Kaffiøyra, represented as three years sliding mean (SM). This is shown to relate changes in *Cetraria* sp. to changes in population size. Note that observations from 2000 and 2005 are divided by a factor of four for comparisons (see Methods)

Moss cover

During 2000 – 2005 and 2005 – 2013, the moss cover showed a significant decline on Brøggerhalvøya (Table 2, Figure 3a). No significant change was observed on Sarsøyra during 2000 – 2005, but during 2005 - 2013, there was a decline in the cover of moss also in this area (Table 2, Figure 3b). Kaffiøyra also showed a decrease between 2005 and 2013 (Table 2, Figure 3c). The decline in moss cover was most prominent on Brøggerhalvøya, followed by Sarsøyra, while the least decline was observed on Kaffiøyra. In addition, Brøggerhalvøya had a higher cover of mosses than Sarsøyra in 2000, while in 2005 and 2013 there was no longer a difference. Both areas had, however, a higher cover compared to Kaffiøyra both these years.

Table 2: Change in moss cover in the three study areas, with year 2000 used as intercept for Brøggerhalvøya and Sarsøyra, and year 2005 as intercept for Kaffiøyra. The vegetation type (Veg) “Moderate snowbed – *Saxifraga oppositifolia*” is used as intercept for all the areas

| Fixed effects | Brøggerhalvøya | Sarsøyra | Kaffiøyra |
|------------------------|--------------------------------------|--|--------------------------------------|
| Intercept | - 1.68 (0.32), z = -5.22, p < 0.001 | - 2.19 (0.24), z = 9.14, p < 0.001 | - 2.95 (0.22), z = -13.19, p < 0.001 |
| 2005 | - 0.53 (0.04), z = -11.81, p < 0.001 | 0.04 (0.04), z = 0.94, p = 0.35 | / |
| 2013 | - 1.91 (0.09), z = -20.93, p < 0.001 | - 1.43 (0.09), z = -15.47, p < 0.001 | - 1.05 (0.12), z = -8.96, p < 0.001 |
| Veg – Moderate snowbed | | | |
| <i>Luzula</i> sp. | 0.55 (0.54), z = 1.03, p = 0.30 | - 0.43 (0.36), z = -1.18, p = 0.24 | - 0.40 (0.37), z = -1.09, p = 0.28 |
| Veg – Late snowbed | 2.21 (0.79), z = 2.80, p < 0.01 | 0.88 (1.42), z = 0.62, p = 0.54 | 0.49 (1.56), z = 0.31, p = 0.75 |
| Veg – Moss tundra | 4.23 (0.57), z = 7.37, p < 0.001 | NP | NP |
| Veg – Ridge | - 0.10 (0.66), z = - 0.15, p = 0.88 | - 15.20 (412.76), z = - 0.04, p = 0.97 | - 1.10 (1.25), z = -0.88, p = 0.38 |
| Veg – Sparse | - 0.46 (0.67), z = - 0.68, p = 0.49 | 0.81 (0.51), z = 1.60, p = 0.11 | 0.05 (0.48), z = 0.11, p = 0.92 |
| Veg – Tundra mire | 1.06 (0.65), z = 1.62, p = 0.10 | 1.99 (0.42), z = 4.70, p < 0.001 | NP |
| Random effects | SD and # Groups | SD and # Groups | SD and # Groups |
| Vegetation point | 1.60 and 81 | 1.40 and 92 | 1.51 and 101 |

NP = Not present in the study area

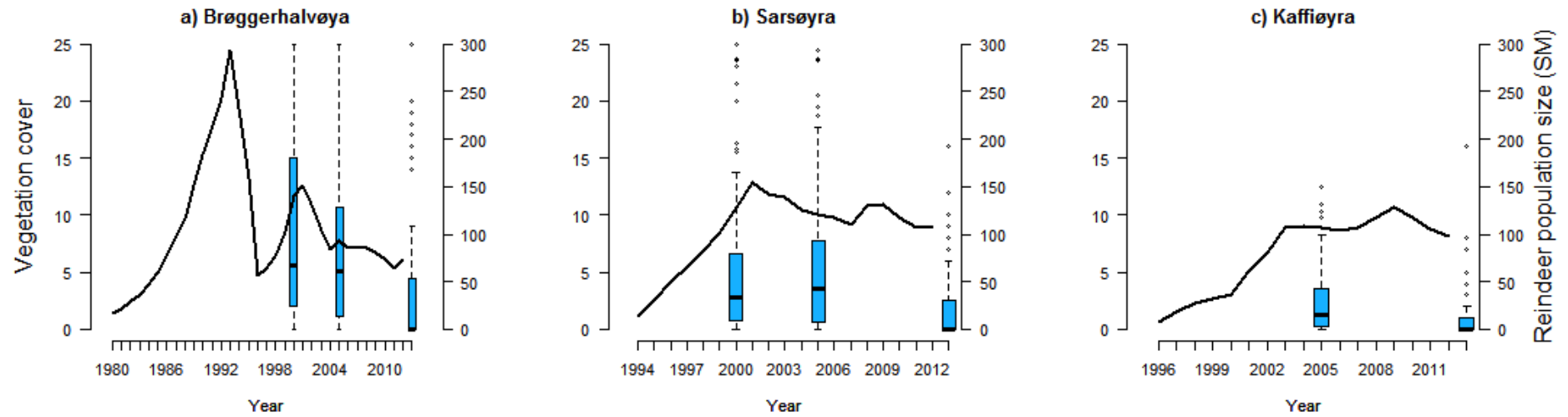


Figure 3: Cover of mosses at a) Brøggerhalvøya, b) Sarsøyra and c) Kaffiøyra. Boxplots represent cover of mosses in 2000, 2005 and 2013, showing median values and *whiskers*, which indicate the 25th and the 75th percentile. The solid lines show fluctuations in reindeer population size during 1979-2012 at Brøggerhalvøya, 1994-2012 at Sarsøyra and 1996-2012 at Kaffiøyra, represented as three years sliding mean (SM). Note that the observations from 2000 and 2005 are divided by a factor of four for comparisons (see Methods).

Graminoids

During 2000 – 2005, the frequency of presence of graminoids showed a significant increase at Brøggerhalvøya, while during 2005 – 2013, the frequency was reduced (Table 3, Figure 4a). On Sarsøyra, there was an increase in graminoids during 2000 - 2005, which continued during 2005 – 2013 (Table 3, Figure 4b). During 2005 – 2013, there was also an increase in graminoids on Kaffiøyra (Table 3, Figure 4c). Even though the median value showed a small decrease on Kaffiøyra during this period, there was an increase in the 75th percentile. The changes were also different between areas, where e.g. Sarsøyra showed the strongest increase of the three areas during 2000 – 2013.

Table 3: Change in frequency of presence of graminoids in the different areas, with year 2000 used as intercept for Brøggerhalvøya and Sarsøyra, and year 2005 used as intercept for Kaffiøyra. The vegetation type (Veg) “Moderate snowbed – *Luzula*” is used as intercept for all the areas.

| Fixed effects | Brøggerhalvøya | Sarsøyra | Kaffiøyra |
|-------------------------|-------------------------------------|-------------------------------------|-------------------------------------|
| Intercept | - 2.25 (0.51), z = -4.41, p < 0.001 | - 1.11 (0.22), z = -5.02, p < 0.001 | - 1.27 (0.26), z = -4.94, p < 0.001 |
| 2005 | 0.47 (0.05), z = 8.77, p < 0.001 | 0.42 (0.04), z = 10.88, p < 0.001 | / |
| 2013 | 0.37 (0.08), z = 4.40, p < 0.001 | 0.86 (0.57), z = 15.16, p < 0.001 | 0.24 (0.06), z = 3.80, p < 0.001 |
| Veg – Moderate snowbed | | | |
| <i>S. oppositifolia</i> | - 1.45 (0.64), z = -2.27, p < 0.05 | - 1.09 (0.29), z = -3.69, p < 0.001 | - 1.17 (0.33), z = -3.57, p < 0.001 |
| Veg – Late snowbed | - 0.75 (0.99), z = -0.76, p = 0.45 | - 2.44 (1.22), z = -2.00, p < 0.05 | 0.78 (1.46), z = 0.53, p = 0.59 |
| Veg – Moss tundra | 2.30 (0.75), z = 3.07, p < 0.01 | NP | NP |
| Veg – Ridge | - 2.08 (0.87), z = -2.39, p < 0.05 | - 2.22 (1.21), z = -1.83, p = 0.07 | - 2.39 (1.17), z = 2.05, p < 0.05 |
| Veg – Sparse | - 1.09 (0.85), z = -1.28, p = 0.20 | - 0.91 (0.43), z = -2.12, p < 0.05 | - 1.05 (0.48), z = -2.20, p < 0.05 |
| Veg – Tundra mire | 0.50 (0.84), z = 0.60, p = 0.55 | 0.17 (0.36), z = 0.47, p = 0.64 | NP |
| Random effects | SD and # Group | SD and # Group | SD and # Group |
| Vegetation point | 1.87 and 81 | 1.15 and 92 | 1.43 and 101 |

NP = Not present in the study area

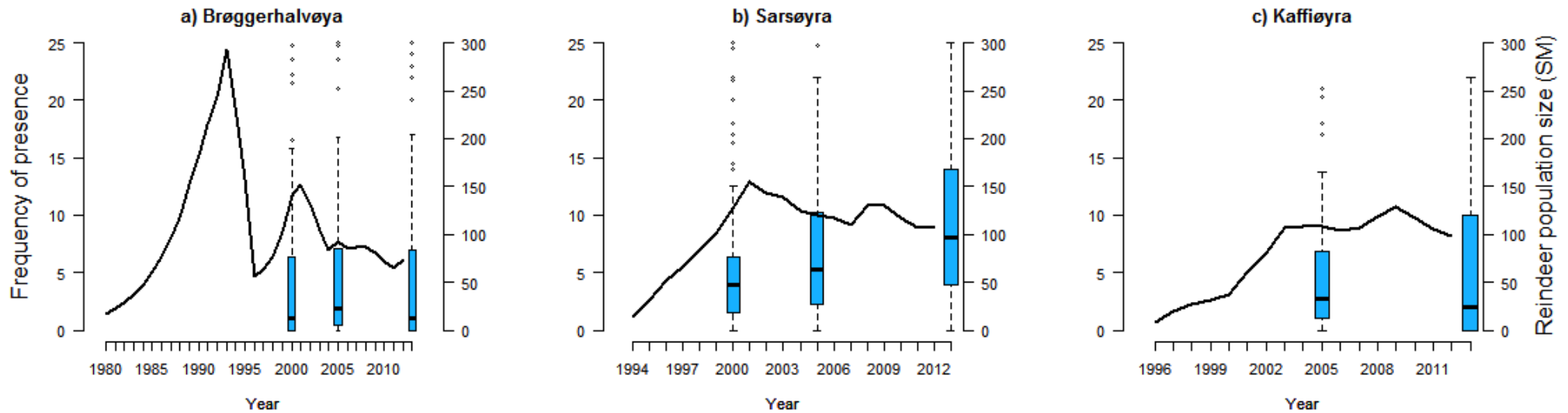


Figure 4: Frequency of presence of graminoids at a) Brøggerhalvøya, b) Sarsøyra and c) Kaffiøyra. Boxplots represent cover of mosses in 2000, 2005 and 2013, showing median values and *whiskers*, which indicate the 25th and the 75th percentile. The solid lines show fluctuations in reindeer population size during 1979-2012 at Brøggerhalvøya, 1994-2012 at Sarsøyra and 1996-2012 at Kaffiøyra, represented as three years sliding mean (SM). Note that the observations from 2000 and 2005 are divided by a factor of four for comparisons (see Methods).

Model selection suggested that twenty years accumulated grazing pressure, area and vegetation type should be included in the model describing the effect herbivores had on the graminoid vegetation. Models with three, five and ten years of accumulated grazing pressure had $\Delta AICc > 80$. Twenty years accumulated grazing pressure had a significant effect on the frequency of graminoids, showing an increase in graminoids with an increase in grazing pressure by reindeer (Table 4, Figure 5).

Table 4: Parameter estimates and test statistics for the effect of twenty years accumulated grazing pressure on graminoids, including “Vegetation point” as a random effect. The vegetation type (Veg) “Moderate snowbed – *Luzula*” is used as an intercept. Estimates are on a logit scale.

| Fixed effects | β (SE) | z - value | p - value |
|---|--------------------------------|------------------|------------------|
| Intercept | -2.80 (0.25) | z = -10.87 | p < 0.001 |
| Grazing pressure – twenty years | 0.0113 (0.00) | z = 16.32 | p < 0.001 |
| Area – Sarsøyra | 1.57 (0.25) | z = 6.20 | p < 0.001 |
| Area – Kaffiøyra | 1.09 (0.25) | z = 4.29 | p < 0.001 |
| Veg – Moderate snowbed – <i>S. oppositifolia</i> | -1.20 (0.23) | z = -5.30 | p < 0.001 |
| Veg – Late snowbed | -0.74 (0.61) | z = -1.22 | p = 0.22 |
| Veg – Moss tundra | 2.30 (0.50) | z = 4.55 | p < 0.001 |
| Veg – Ridge | -2.05 (0.53) | z = -3.89 | p < 0.001 |
| Veg – Sparse | -1.01 (0.32) | z = -3.14 | p < 0.001 |
| Veg – Tundra mire | 0.28 (0.36) | z = 0.78 | p = 0.44 |
| Random effects | SD | #Groups | |
| Vegetation point | 1.48 | 274 | |

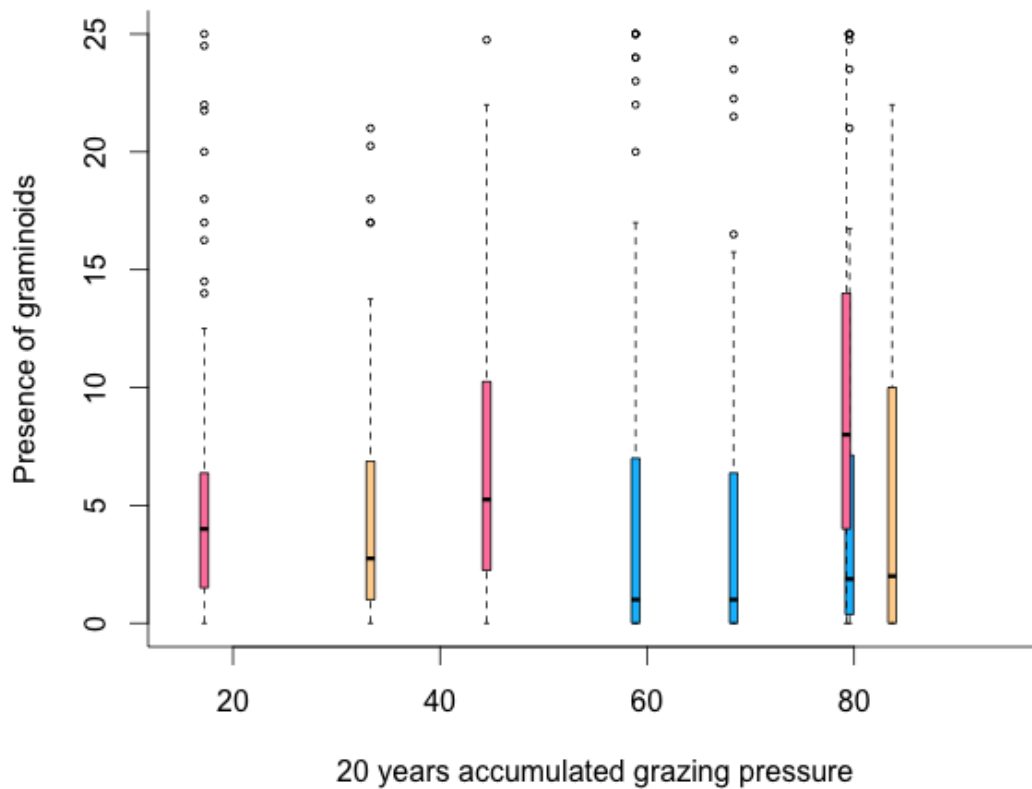


Figure 5: Change in the frequency of presence of graminoids with twenty years accumulated grazing pressure by reindeer. Accumulated grazing pressure is calculated as the total reindeer density over the last twenty years divided by vegetated area (see Methods). Blue = Brøggerhalvøya, pink = Sarsøyra, and yellow = Kaffiøyra. Note that graminoids at the accumulated grazing pressures 17.2 (year 2000 Sarsøyra), 33.3 (year 2005 Kaffiøyra), 44.5 (year 2005 Sarsøyra), 68.4 (year 2000 Brøggerhalvøya), and 79.55 (year 2005 Brøggerhalvøya) are divided by a factor of four for direct comparisons.

Other important reindeer food plants

At Brøggerhalvøya during 2000 - 2005, the relatively abundant *S. polaris* increased in abundance, while during 2005 - 2013, no significant change in the species was observed (Table 5, Appendix 1). At Sarsøyra the species showed no significant change in frequency during 2000 - 2005 or during 2005 - 2013. From 2005 to 2013, there was also no significant change in the species at Kaffiøyra.

From 2000 to 2005, there was also an increase in the forb *O. digyna* on Brøggerhalvøya, while no change of the species was observed between 2005 and 2013 (Table 6, Appendix 2). On Sarsøyra there was no change in *O. digyna* during 2000 - 2005, which was also found during 2005 - 2013. There was also no significant change in the species at Kaffiøyra during 2005 - 2013.

During 2000 - 2005, the frequency of presence of *B. vivipara* at Brøggerhalvøya showed no significant change, while during 2005 - 2013 there was a small increase of the species (Table 7, Appendix 3). At Sarsøyra a similar change in *B. vivipara* was observed, with no change in the species during 2000 - 2005, and an increase during 2005 - 2013. At Kaffiøyra, there was also a small increase of *B. vivipara* during 2005 - 2013.

Table 5: Frequency of presence of *S. polaris* (with 25th and 75th percentiles) during the period 2000 – 2013. B = Brøggerhalvøya, S = Sarsøyra and K = Kaffiøyra. A paired Wilcoxon rank sum test is used to compare years.

| <i>S. polaris</i> | | | | | | |
|-------------------|----------------------|-----------------------|-----------------------|------------------------|------------------------|------------------------|
| | 2000 | 2005 | 2013 | 2000 - 2005 | 2000 - 2013 | 2005 - 2013 |
| B | 6.00 (0.00-17.56) | 11.63 (0.50-19.81) | 11.50 (0.00-22.25) | V = 503.5 p < 0.001 | V = 601.5 p < 0.01 | V = 923.5 p = 0.332 |
| S | 5.13 (0.00-17.81) | 6.38 (0.00-18.38) | 2.50 (0.00-22.00) | V = 880.5 p = 0.503 | V = 841.0 p = 0.455 | V = 849.5 p = 0.632 |
| K | - | 0.88 (0.00-13.06) | 0.00 (0.00-13.25) | - | - | V = 952.0 p = 0.704 |

Table 6: Frequency of presence of *O. digyna* (with 25th and 75th percentiles) during the period 2000 – 2013. B = Brøggerhalvøya, S = Sarsøyra and K = Kaffiøyra. A paired Wilcoxon rank sum test is used to compare years.

| <i>O. digyna</i> | | | | | | |
|------------------|---------------------|---------------------|---------------------|-------------------------|-------------------------|-------------------------|
| | 2000 | 2005 | 2013 | 2000 - 2005 | 2000 - 2013 | 2005 - 2013 |
| B | 0.00 (0.00-0.81) | 0.00 (0.00-1.13) | 0.00 (0.00-1.25) | V = 160.5 p < 0.05 | V = 116.5 p < 0.05 | V = 324.5 p = 0.883 |
| S | 0.50 (0.00-2.25) | 0.75 (0.00-2.75) | 0.00 (0.00-2.00) | V = 1047.5 p = 0.340 | V = 1080.0 p = 0.792 | V = 1310.0 p = 0.192 |
| K | - | 0.25 (0.00-2.00) | 0.00 (0.00-0.25) | - | - | V = 827.0 p = 0.325 |

Table 7: Frequency of presence of *B. vivipara* (with 25th and 75th percentiles) during the period 2000 – 2013. B = Brøggerhalvøya, S = Sarsøyra and K = Kaffiøyra. A paired Wilcoxon rank sum test is used to compare years.

| <i>B vivipara</i> | | | | | | |
|-------------------|---------------------|---------------------|---------------------|------------------------|---------------------|-----------------------|
| | 2000 | 2005 | 2013 | 2000 - 2005 | 2000 - 2013 | 2005 - 2013 |
| B | 0.00 (0.00-2.06) | 0.25 (0.00-4.81) | 0.00 (0.00-5.00) | V = 364 p = 0.084 | V = 263 p < 0.05 | V = 300 p < 0.05 |
| S | 0.00 (0.00-0.31) | 0.00 (0.00-0.50) | 0.00 (0.00-2.25) | V = 234.5 p = 0.285 | V = 64 p < 0.001 | V = 84.5 p < 0.001 |
| K | - | 0.00 (0.00-0.25) | 0.00 (0.00-0.25) | - | - | V = 101.5 p < 0.01 |

Observer test

The vegetation observation tests showed that there was a strong correlation between all the four observers in both observer tests (i.e. early and mid summer, Table 8, Appendix 4 – 6). All correlation tests had $p < 0.001$.

Table 8: Pearson`s correlation coefficients for the four different observers in summer 2013. The estimates are from sampling frames in 24 point sites (in six different vegetation types) in the first observer test, and in 28 point sites (in six different vegetation types) in the second observer test. *** indicates $p < 0.001$.

| | | 1. Observer test | | | | 2. Observer test | | | |
|---------------------|----------|------------------|---------|---------|---------|------------------|---------|---------|---------|
| | Observer | 1 | 2 | 3 | 4 | 1 | 2 | 3 | 4 |
| <i>Cetraria</i> sp. | 1 | | 1.00*** | 0.84*** | 0.95*** | | 0.96*** | 0.87*** | 0.87*** |
| | 2 | | | 0.82*** | 0.93*** | | | 0.97*** | 0.96*** |
| | 3 | | | | 0.95*** | | | | 0.99*** |
| | 4 | | | | | | | | |
| Mosses | 1 | | 0.95*** | 0.87*** | 0.82*** | | 0.76*** | 0.74*** | 0.79*** |
| | 2 | | | 0.94*** | 0.75*** | | | 0.85*** | 0.94*** |
| | 3 | | | | 0.72*** | | | | 0.95*** |
| | 4 | | | | | | | | |
| Graminoids | 1 | | 0.99*** | 0.96*** | 0.99*** | | 0.95*** | 0.99*** | 0.98*** |
| | 2 | | | 0.97*** | 0.99*** | | | 0.98*** | 0.97*** |
| | 3 | | | | 0.96*** | | | | 0.98*** |
| | 4 | | | | | | | | |

Discussion

This study has demonstrated how high-Arctic herbivores are able to modify species abundance and composition in a low-productivity environment free from predators. Long-term changes in the abundance of important forage plants of reindeer were compared within and between three neighbouring areas, showing an overall decline in lichen and partly also moss cover, and an increase in graminoids in the two areas with a more recent establishment of reindeer and a lack of irruptive dynamics. This demonstrates how vegetation abundance may vary in areas that have faced contrasting grazing pressure by reindeer. The study further supports the prediction that reindeer herbivory can cause vegetation state transitions (Van der Wal 2006) and that their influence on vegetation in resource-limited areas may be described as a top-down control, in the absence of predators (Fretwell, 1977, Oksanen et al., 1981).

When reindeer populations occupy new and predator-free areas, lichens (which are highly preferred as forage during winter (Staaland, 1986)) are expected to decline in abundance with increased population densities due to herbivory (Klein, 1968). In addition, trampling may impede the recovery and even cause a further decline (Klein and Shulski, 2011). At Brøggerhalvøya, a reduction and subsequently a depletion of the lichen cover was reported following the reintroduction of reindeer in 1978 (Hansen et al., 2007). The reindeer's impact on the lichen cover was further supported by vegetation enclosures established at the reintroduction, which in 1999 showed a greater cover of lichens inside than outside these fences (Cooper and Wookey, 2001).

Lichens often lack the ability to compensate for the selective tissue removal by herbivores (Klein and Shulski, 2011), and in areas with continuous grazing by reindeer, regrowth is prevented and the lichens are kept at low abundances (Van der Wal 2006). This might also be the case in areas where the animal density is relatively low, if the reindeer are isolated and do not migrate seasonally to other ranges, which generally is the case in my study area (Hansen et al., 2007, but see Hansen et al., 2010a). This could be an explanation for the further depletion of

Cetraria sp. on Brøggerhalvøya during 2000 – 2013, which also coincides with earlier findings on changes in lichens in the area (e.g. Hansen et al., 2007). At the more recently established areas Sarsøyra and Kaffiøyra, there was a strong lichen decline during the same period, most likely due to the increase in reindeer density after the establishment, the lack of a subsequent population crash and a continuous and relatively high grazing pressure by the herbivores. Negative effects of reindeer herbivory on lichen cover resulting from introductions to new areas has also been reported by Klein (1968) on St. Matthews Island, by Lindsay (1973) on South Georgia, and by Henry and Gunn (1991) on Rideout Island. Here, irruptions of the island populations virtually caused an elimination of the preferred lichen species, further supporting the prediction of reindeer's ability to modify vegetation abundance and composition through herbivory and trampling (Van der Wal, 2006). It is important to note that figures in this study do not take pair-wise measurements into consideration and due to a major spread in cover and frequency in many species and species groups, the boxplots may be displayed with great variation. The tests, however, account for the pair-wise observations (which may give significant changes despite no observed changes in the figures).

Mosses are important components in Svalbard reindeer's winter diet despite a low digestibility (Staaland, 1986), and there was a decline in the cover of mosses at Brøggerhalvøya during 2000 – 2013 and at Kaffiøyra from 2005 to 2013. Even though the cover of mosses also declined at Sarsøyra between 2000 and 2013, no change was observed during 2000 – 2005. Mosses are less preferred as forage and are more resistant to grazing and trampling compared to lichens (Van der Wal, 2006), which may be a possible explanation for this observation. The decline in moss cover in the three areas may be due to the presence of non-migratory reindeer populations with a continuous grazing pressure, which prevents recovery of the grazed vegetation (Tyler and Øritsland, 1989). In addition, there have been no severe declines in reindeer density at Sarsøyra and Kaffiøyra after these populations reached a peak density in the early 2000's, which could also potentially have an effect on moss abundance due to a continuous and relatively high grazing pressure by the herbivores. Van der Wal

and Brooker (2004) reported of an increase in the extent and depth of the moss layer from reindeer exclusion by fencing, thus indicating that an increase in herbivore density may have a negative effect on moss cover and biomass in Arctic ecosystems (Van der Wal et al., 2001, Van der Wal and Brooker, 2004). This was also supported by Klein (1987) at St. Matthews Island, demonstrating an increase in the cover of moss following a release in grazing pressure by reindeer.

Within the vascular plant group, graminoids are most tolerant to herbivory, especially due to their basal meristems and sequential leaf growth, which enables them to compensate for grazing by reindeer (Wegener et al., 1992). Thus, they can counteract the negative effects of herbivory on aboveground biomass and even over-compensate with an increase in biomass (Van der Wal, 2006), which was partly supported by the findings at Brøggerhalvøya, Sarsøyra and Kaffiøyra during 2000 – 2013. At Sarsøyra and Kaffiøyra, there was an increase in the frequency of graminoids during the period, which was also the case at Brøggerhalvøya during 2000 - 2005. Also an increase in twenty years accumulated grazing pressure had a positive effect on the frequency of graminoids. In addition to graminoid's higher tolerance to herbivory and trampling and their ability to over-compensate from defoliation, the increases can be an effect of enhanced soil nutrient availability by faeces deposition and nutrient cycling, which is highly advantageous for the plant group (Olofsson et al., 2001). Also a reduction in the cover of lichens (Klein, 1987) and mosses (Van der Wal et al., 2001, Van der Wal and Brooker, 2004) from herbivory can cause an increase due to warmer soil temperatures (Brooker and Van der Wal, 2003). Klein (1987) also reported an increase in graminoids during the strong population increase of reindeer at St. Matthews Island, which further supports the prediction that an increase in reindeer density may have a positive effect on graminoid growth (Van der Wal, 2006).

S. polaris is one of the most common vascular plants in the study area and it is an important forage plant in the reindeer diet (Staal and White, 1991). In this study, an increase in the species was found at Brøggerhalvøya during 2000-2005,

which was likely due to a release in grazing pressure in the beginning of the century, implying that herbivory may regulate the abundance of *S. polaris*. Other preferred foraging species in reindeer diet are *O. digyna* and *B. vivipara* due to high nutrient contents (Staaland et al., 1983) and digestibility (Ekern and Kildemo, 1978). During 2000 – 2013, the only change in *O. digyna* was observed at Brøggerhalvøya with an increase between 2000 and 2005. *B. vivipara* showed no significant change during 2000-2005, while it increased in the three areas between 2005 and 2013. In addition to the impact of herbivory, the abundance of particular annual vascular plants may be influenced by natural community dynamics due to abiotic factors and short-term weather fluctuations, since vascular plants are seen to be more sensitive to these effects compared to other plant groups (e.g. Chapin et al., 1995), which could possibly explain the different changes in the vascular species in this study.

Van der Wal (2006) hypothesized that the Arctic tundra can occur in a sequential and relatively distinct lichen-, moss- or graminoid-dominated state, with transition between each state caused by changes in reindeer/caribou density. In this study, there was strong evidence of a shift from lichen-dominated to lichen-poor vegetation following an increase in accumulated reindeer grazing pressure. This shift occurred in a wave-like spatial pattern according to the sequential re-establishment of reindeer (see also Caughley, 1970). There was, however, no strong indication of a lichen – moss transition in any of the areas, as moss cover generally decreased over time. Although the moss decline in Brøggerhalvøya could potentially be due to the reduction in grazing pressure since ~2000, there was no sign of lichen re-establishment. As pointed out by Van der Wal (2006), the regrowth of lichens is a slow process and with a continuous presence of even low-density reindeer populations, no increase is expected. This was also observed on St. Matthews Island after the introduction of reindeer in 1957 (Klein, 1987). However, in Sarsøyra and Kaffiøyra, the reindeer population had reached peak densities when the vegetation measurements started (2000 and 2005, respectively), and it is therefore uncertain whether the initial population increase had caused changes in moss cover. Parallel to the declines in lichens and mosses, graminoids showed an overall increase in frequency at Sarsøyra and

Kaffiøyra, which is in line with the hypothesis made by Van der Wal (2006), indicating a vegetation transition towards a more graminoid-dominated state when the accumulated grazing pressure increases and the reindeer density is kept relatively high. This has also been reported in tundra ecosystems in northern parts of Norway, where reindeer have induced a vegetation transition from a moss-dominated state to a state dominated by graminoids (Olofsson et al., 2001, Olofsson et al., 2004).

Irruptions cause peak abundances that are unsupportable by the area and its vegetation, eventually leading to population crashes (Leopold, 1943). This is often the case when herbivores are introduced to predator-free and un-grazed areas, as shown by Klein (1987) at St. Matthews Island and by Hansen et al. (2007) at Brøggerhalvøya, reporting of irruptions with subsequent changes in vegetation cover. The potential long-term effect of irruption on the abundance of common forage plants was also demonstrated in this study, showing a difference in vegetation between the previously irrupted Brøggerhalvøya compared to Sarsøyra and Kaffiøyra, where the initial population increase was not followed by a clear population crash. Non-irruptive reindeer populations have also been observed in other areas after introductions to new ranges, e.g. at South Georgia where the population grew and later stabilized around 4 000 reindeer (Bonner, 1958). According to Klein (1968), the interaction between population's ability to self-regulate and certain characteristics of an environment (e.g. food supply) may prevent an irruption from occurring. Furthermore, the flat lowland areas on Sarsøyra and Kaffiøyra are often covered with ice during winter, which may block the access to food and cause poor winter foraging conditions (Hansen et al., 2011). This may have suppressed the reindeer density below the threshold for what is needed to cause overshoot of carrying capacity and strong vegetation transitions, and can be a possible explanation for the non-irruptive population dynamics observed at Sarsøyra and Kaffiøyra.

This study has shown how herbivores in a predator-free and relatively unproductive environment may have the ability to alter vegetation composition and available phytomass, causing a depletion and decline in some important

forage plants (mainly lichens), while an increase in others (e.g. graminoids), which represents partial support for the hypothesis of vegetation state transitions in Arctic tundra ecosystems (Van der Wal, 2006). Furthermore, the results also partly support the “exploitation ecosystem hypothesis” (Fretwell, 1977, Oksanen et al., 1981) by suggesting that herbivory may suppress the vegetation, e.g. lichens, by a top-down control in moderately unproductive environments. Changes in grazing pressure is likely to become an increasingly important issue in Arctic ecological research, since grazing pressure in many Arctic regions has intensified and herbivore populations might expand their ranges northwards due to climate change and an overall greening effect (Klein, 1999, Van der Wal et al., 2001, Aanes et al., 2002, Van der Wal, 2006).

Acknowledgements

This master`s thesis was carried out at the Department of Biology at the Norwegian University of Science and Technology (NTNU) and the project was financed by The Svalbard Science Forum (SSF), Norwegian Polar Institute (NPI) and the Norwegian University of Science and Technology (NTNU).

I would like to offer my special thanks to Bernt-Erik Sæther (NTNU), Brage Bremset Hansen (NTNU) and Åshild Ønvik Pedersen (NPI) for their many advices and for supervising me during this thesis. This project would not have been possible without your help.

I would also like to thank Mathilde Le Moullec, Bart Peeters and Aino Luukonen for their good company while spending countless hours in the field and for their help in collecting the data for my thesis. A further thanks goes to the Logistic team in Ny-Ålesund.

Finally, I would like to express my greatest appreciation to my family and friends for support me during this project and for making these two years some of the best years so far.

References

- Augustine, D. J. & Mc Naughton, S. J. 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. *The Journal of wildlife management*, 62, 1165-1183.
- Beisner, B. E., Haydon, D. T. & Cuddington, K. 2003. Alternative stable states in ecology. *Frontiers in Ecology and the Environment*, 1, 376-382.
- Bonner, W. N. 1958. The introduced reindeer of South Georgia. *Falkland Island Dependencies Survey, Scientific Reports*, 22, 1-18.
- Brattbakk, I. 1986. Flora and vegetation. In: Øritsland, N. (ed.) *Svalbardreinen og dens livsgrunnlag*. Oslo: Universitetsforlaget.
- Brooker, R. & Van Der Wal, R. 2003. Can soil temperature direct the composition of high arctic plant communities? *Journal of Vegetation Science*, 14, 535-542.
- Burnham, K. P. & Anderson, D. R. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*, Springer.
- Caughley, G. 1970. Eruption of ungulate populations, with emphasis on Himalayan tahr in New Zealand. *Ecology*, 51, 51-72.
- Chapin, F. S., Shaver, G. R., Giblin, A. E., Nadelhoffer, K. J. & Laundre, J. A. 1995. Responses of arctic tundra to experimental and observed changes in climate. *Ecology*, 76, 694-711.
- Cooper, E. J. & Wookey, P. A. 2001. Field measurements of the growth rates of forage lichens, and the implications of grazing by Svalbard reindeer. *Symbiosis*, 31, 173-186.
- Danell, K., Mikael Utsi, P., Thomas Palo, R. & Eriksson, O. 1994. Food plant selection by reindeer during winter in relation to plant quality. *Ecography*, 17, 153-158.
- Derocher, A. E., Wiig, Ø. & Bangjord, G. 2000. Predation of Svalbard reindeer by polar bears. *Polar Biology*, 23, 675-678.
- Ekern, K. & Kildemo, K. 1978. *Svalbardreinenens ernæring*. Doctoral thesis, Institutt for Naturforvaltning, Norges Landbrukshøyskole, Ås.
- Forsyth, D. M. & Caley, P. 2006. Testing the irruptive paradigm of large-herbivore dynamics. *Ecology*, 87, 297-303.

- Fretwell, S. D. 1977. The regulation of plant communities by food chains exploiting them. *Perspectives in Biology and Medicine*, 20, 169-185.
- Fryxell, J. & Sinclair, A. 1988. Causes and consequences of migration by large herbivores. *Trends in Ecology & Evolution*, 3, 237-241.
- Hairston, N. G., Smith, F. E. & Slobodkin, L. B. 1960. Community structure, population control, and competition. *American Naturalist*, 94, 421-425.
- Hansen, B. B. 2008. *The Svalbard reindeer (Rangifer tarandus platyrhynchus) and its food base: plant-herbivore interactions in a high-arctic ecosystem*. Doctoral thesis, Norwegian University of Science and Technology, Trondheim.
- Hansen, B. B. & Aanes, R. 2012. Kelp and seaweed feeding by High-Arctic wild reindeer under extreme winter conditions. *Polar Research*, 31.
- Hansen, B. B., Aanes, R. & Sæther, B.-E. 2010a. Partial seasonal migration in high-arctic Svalbard reindeer (*Rangifer tarandus platyrhynchus*). *Canadian Journal of Zoology*, 88, 1202-1209.
- Hansen, B. B., Aanes, R. & Sæther, B.-E. 2010b. Feeding-crater selection by high-arctic reindeer facing ice-blocked pastures. *Canadian Journal of Zoology*, 88, 170-177.
- Hansen, B. B., Henriksen, S., Aanes, R. & Sæther, B.-E. 2007. Ungulate impact on vegetation in a two-level trophic system. *Polar Biology*, 30, 549-558.
- Hansen, B. B., Herfindal, I., Aanes, R., Sæther, B. E. & Henriksen, S. 2009. Functional response in habitat selection and the tradeoffs between foraging niche components in a large herbivore. *Oikos*, 118, 859-872.
- Hansen, B. B., Aanes, R., Herfindal, I., Kohler, J. & Sæther, B.-E. 2011. Climate, icing, and wild arctic reindeer: past relationships and future prospects. *Ecology*, 92, 1917-1923.
- Hansen-Bauer, I., Solås, M. & Steffensen, E. 1990. The climate of Spitsbergen. Klima 39/90. Oslo: Norwegian Meteorological Institute.
- Henry, G. & Gunn, A. 1991. Recovery of tundra vegetation after overgrazing by caribou in Arctic Canada. *Arctic*, 44, 38-42.
- Hobbs, N. T. 1996. Modification of ecosystems by ungulates. *The Journal of Wildlife Management*, 60, 695-713.

- Johansen, B., Tømmervik, H. & Karlsen, S. 2009. Vegetasjonskart over Svalbard basert på satellittdata. *NINA Rapport, Norsk institutt for naturforskning (NINA), Tromsø*, 456, 54 pp.
- Klein, D. R. 1968. The introduction, increase, and crash of reindeer on St. Matthew Island. *The Journal of Wildlife Management*, 32, 350-367.
- Klein, D. R. 1987. Vegetation recovery patterns following overgrazing by reindeer on St. Matthew Island. *Journal of Range Management*, 40, 336-338.
- Klein, D. R. 1999. The roles of climate and insularity in establishment and persistence of Rangifer tarandus populations in the high Arctic. *Ecological Bulletins*, 47, 96-104.
- Klein, D. R. & Shulski, M. 2011. The Role of Lichens, Reindeer, and Climate in Ecosystem Change on a Bering Sea Island. *Arctic*, 64, 353-361.
- Kohler, J. & Aanes, R. 2004. Effect of winter snow and ground-icing on a Svalbard reindeer population: results of a simple snowpack model. *Arctic, Antarctic, and Alpine Research*, 36, 333-340.
- Le Moullec, M. 2014. *Ungulate population monitoring in a tundra landscape: evaluating total counts and distance sampling accuracy*. Master's thesis, UiT - The Arctic University of Norway.
- Leopold, A. 1943. Deer irruptions. *Wisconsin Conservation Bulletin*, 8, 3-11.
- Lindsay, D. 1973. Effects of reindeer on plant communities in the Royal Bay area of South Georgia. *British Antarctic Survey Bulletin*, 35, 101-109.
- Manseau, M., Huot, J. & Crête, M. 1996. Effects of summer grazing by caribou on composition and productivity of vegetation: community and landscape level. *Journal of Ecology*, 84, 503-513.
- May, R. M. 1977. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. *Nature*, 269, 471-477.
- Mysterud, A. 2006. The concept of overgrazing and its role in management of large herbivores. *Wildlife Biology*, 12, 129-141.
- Noy-Meir, I. 1975. Stability of grazing systems: an application of predator-prey graphs. *Journal of Ecology*, 63, 459-481.
- Oksanen, L. & Oksanen, T. 2000. The logic and realism of the hypothesis of exploitation ecosystems. *The American Naturalist*, 155, 703-723.

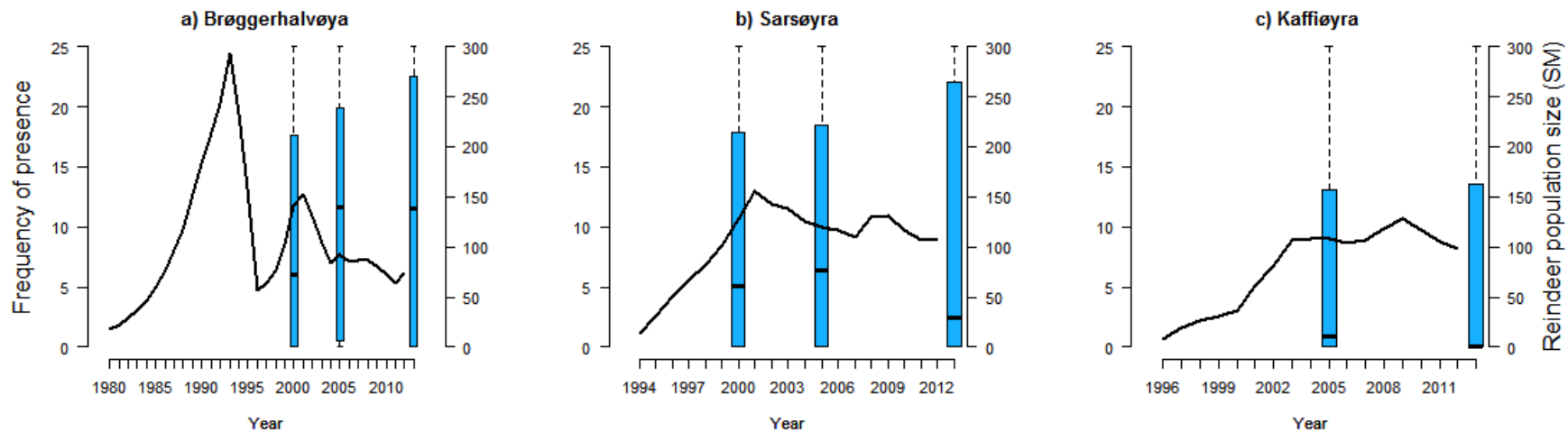
- Oksanen, L., Fretwell, S. D., Arruda, J. & Niemela, P. 1981. Exploitation ecosystems in gradients of primary productivity. *American Naturalist*, 118, 240-261.
- Olofsson, J., Stark, S. & Oksanen, L. 2004. Reindeer influence on ecosystem processes in the tundra. *Oikos*, 105, 386-396.
- Olofsson, J., Kitti, H., Rautiainen, P., Stark, S. & Oksanen, L. 2001. Effects of summer grazing by reindeer on composition of vegetation, productivity and nitrogen cycling. *Ecography*, 24, 13-24.
- R Development Core Team 2013. R: A Language and Environment for Statistical Computing. *In: Team, R. C. (ed.)*. Vienna, Austria: R Foundation for Statistical Computing.
- Riney, T. 1964. The impact of introductions of large herbivores on the tropical environment. *IUCN (International Union for the Conservation of Nature) Publication New Series*, 4, 261-273.
- Stien, A., Loe, L. E., Mysterud, A., Severinsen, T., Kohler, J. & Langvatn, R. 2010. Icing events trigger range displacement in a high-arctic ungulate. *Ecology*, 91, 915-920.
- Staaland, H. 1986. Svalbardreinenens ernæring. *In: NA, Ø. (ed.) Svalbardreinen og dens livsgrunnlag*. Oslo: Universitetsforlaget.
- Staaland, H. & White, R. G. 1991. Influence of foraging ecology on alimentary tract size and function of Svalbard reindeer. *Canadian Journal of Zoology*, 69, 1326-1334.
- Staaland, H., Brattbakk, I., Ekern, K. & Kildemo, K. 1983. Chemical composition of reindeer forage plants in Svalbard and Norway. *Ecography*, 6, 109-122.
- Tyler, N. & Øritsland, N. 1989. Why don't Svalbard reindeer migrate? *Ecography*, 12, 369-376.
- Van Der Wal, R. 2006. Do herbivores cause habitat degradation or vegetation state transition? Evidence from the tundra. *Oikos*, 114, 177-186.
- Van Der Wal, R. & Brooker, R. 2004. Mosses mediate grazer impacts on grass abundance in arctic ecosystems. *Functional Ecology*, 18, 77-86.
- Van Der Wal, R., Brooker, R., Cooper, E. & Langvatn, R. 2001. Differential effects of reindeer on high Arctic lichens. *Journal of Vegetation Science*, 12, 705-710.

- Van Der Wal, R., Bardgett, R. D., Harrison, K. A. & Stien, A. 2004. Vertebrate herbivores and ecosystem control: cascading effects of faeces on tundra ecosystems. *Ecography*, 27, 242-252.
- Wegener, C., Hansen, M. & Jacobsen, L. B. 1992. Effekter av reinbeite ved Kongsfjorden, Svalbard. *Norsk Polarinstitutt Meddelelser*.
- Øritsland, N. & Alendal, E. 1986. Svalbardreinen. Bestandens størrelse og livshistorie. In: NA, Ø. (ed.) *Svalbardreinen og dens livsgrunnlag*. Oslo: Universitetsforlaget.
- Aanes, R., Sæther, B. E. & Øritsland, N. A. 2000. Fluctuations of an introduced population of Svalbard reindeer: the effects of density dependence and climatic variation. *Ecography*, 23, 437-443.
- Aanes, R., Sæther, B. E., Smith, F. M., Cooper, E. J., Wookey, P. A. & Øritsland, N. A. 2002. The Arctic Oscillation predicts effects of climate change in two trophic levels in a high - arctic ecosystem. *Ecology Letters*, 5, 445-453.

Appendix

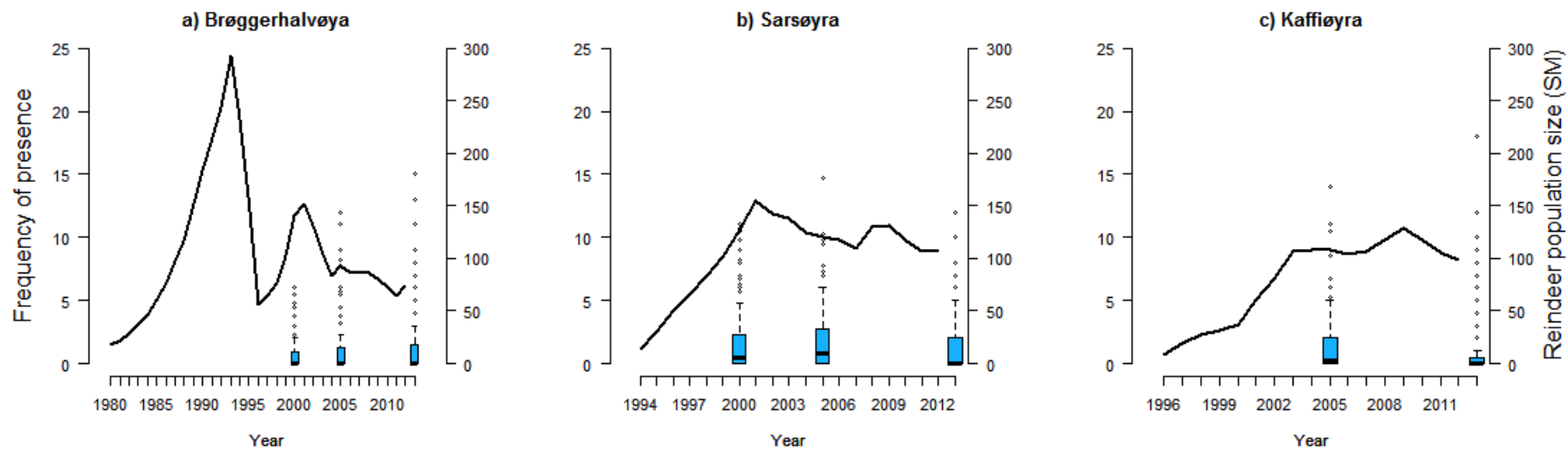
Appendix 1

Frequency of presence of *S. polaris* at a) Brøggerhalvøya, b) Sarsøyra and c) Kaffiøyra. Boxplots represent frequency of *S. polaris* in 2000, 2005 and 2013, showing median values and *whiskers*, which indicate the 25th and the 75th percentile. The solid lines show fluctuations in reindeer population size during 1979-2012 at Brøggerhalvøya, 1994-2012 at Sarsøyra and 1996-2012 at Kaffiøyra, represented as three years sliding mean (SM). Note that the observations from 2000 and 2005 are divided by a factor of four for comparisons (see Methods).



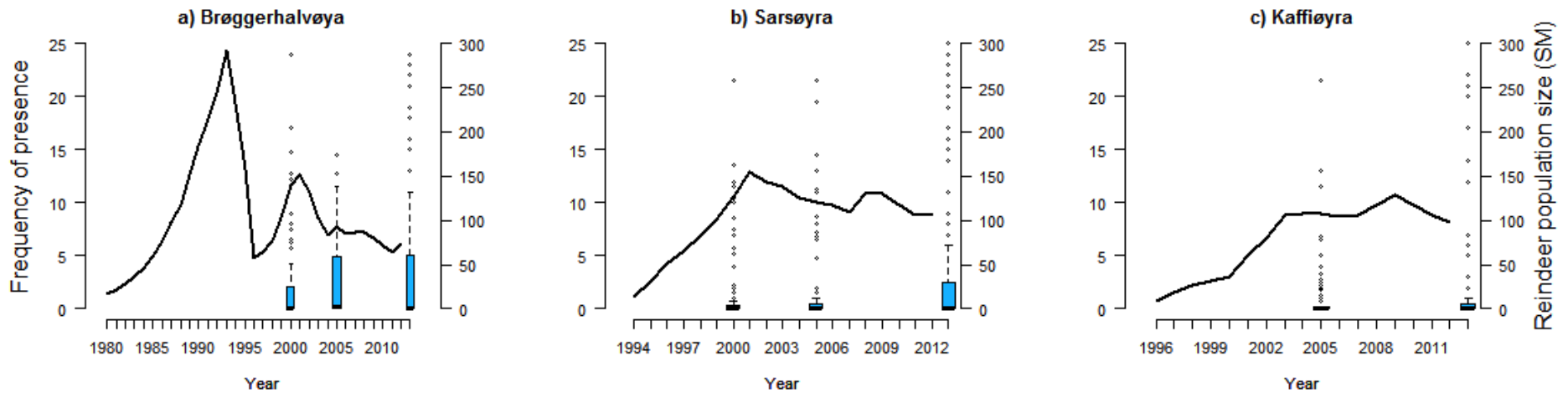
Appendix 2

Frequency of presence of *O. digyna* at a) Brøggerhalvøya, b) Sarsøyra and c) Kaffiøyra. Boxplots represent frequency of *O. digyna* in 2000, 2005 and 2013, showing median values and *whiskers*, which indicate the 25th and the 75th percentile. The solid lines show fluctuations in reindeer population size during 1979-2012 at Brøggerhalvøya, 1994-2012 at Sarsøyra and 1996-2012 at Kaffiøyra, represented as three years sliding. Note that the observations from 2000 and 2005 are divided by a factor of four for comparisons (see Methods).



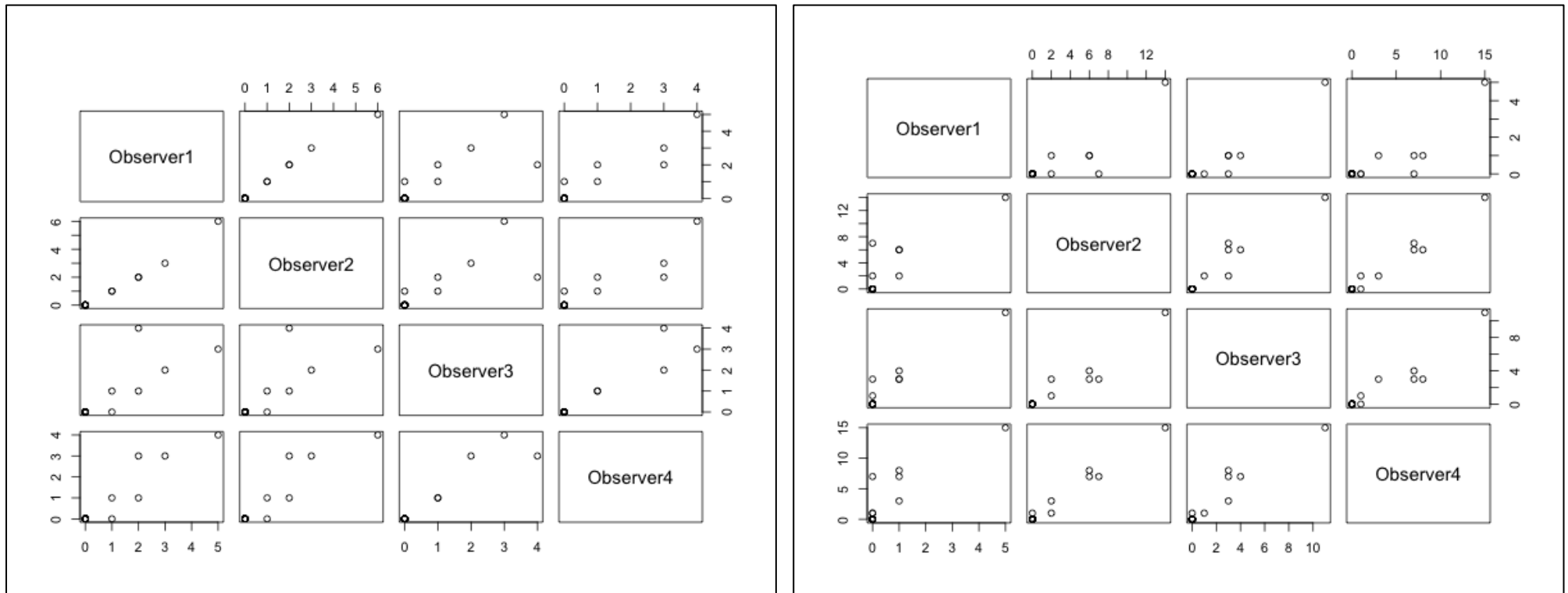
Appendix 3

Frequency of presence of *B. vivipara* at a) Brøggerhalvøya, b) Sarsøyra and c) Kaffiøyra. Boxplots represent frequency of *B. vivipara* in 2000, 2005 and 2013, showing median values and *whiskers*, which indicate the 25th and the 75th percentile. The solid lines show fluctuations in reindeer population size during 1979-2012 at Brøggerhalvøya, 1994-2012 at Sarsøyra and 1996-2012 at Kaffiøyra, represented as three years sliding mean. Note that the observations from 2000 and 2005 are divided by a factor of four for comparisons (see Methods).



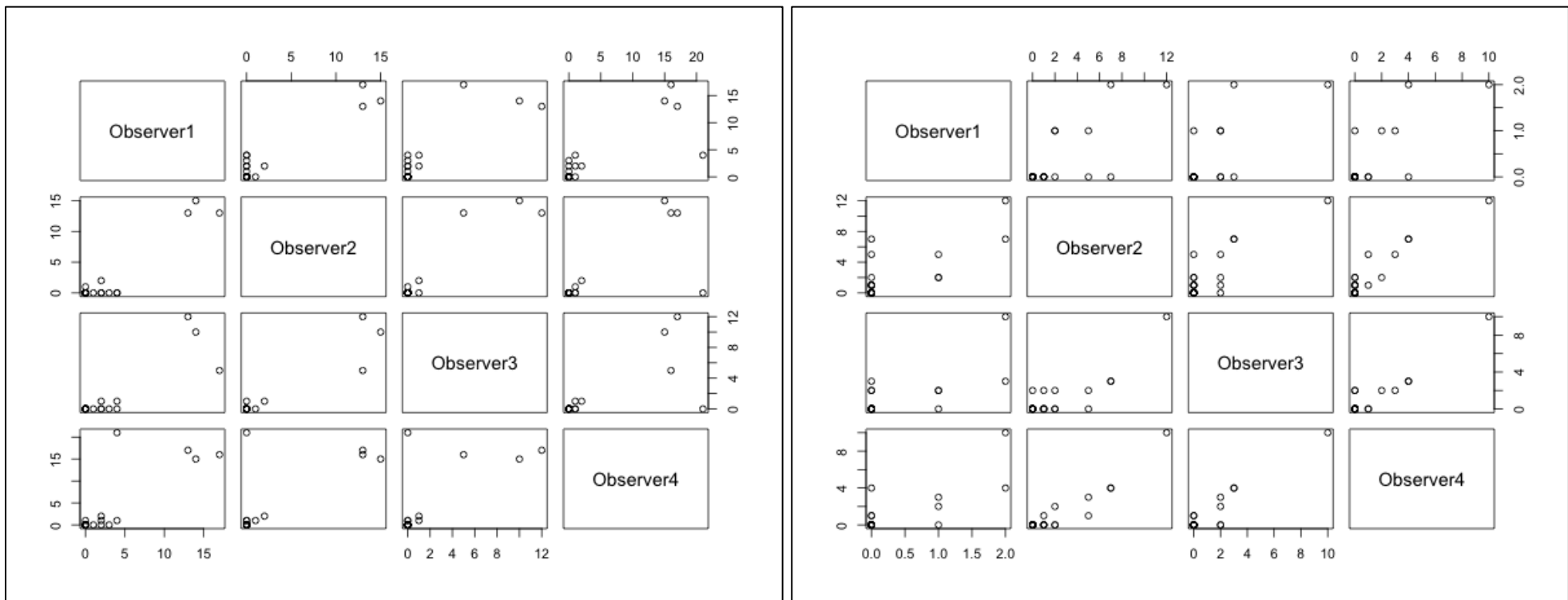
Appendix 4

Correlation between the four different observers concerning *Cetraria* sp. in the first observer test (to the left, performed in 24 sampling frames) and the second observer test (to the right, performed in 28 sampling frames).



Appendix 5

Correlation between the four different observers concerning mosses in the first observer test (to the left, performed in 24 sampling frames) and the second observer test (to the right, performed in 28 sampling frames).



Appendix 6

Correlation between the four different observers concerning graminoids in the first observer test (to the left, performed in 24 sampling frames) and the second observer test (to the right, performed in 28 sampling frames).

