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Results from the high Arctic Svalbard reindeer

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Thanks to my great mentors
– Bernt-Erik, Vebjørn and Brage –

and thanks to all the wonderful people
– my colleagues, friends, family and flat mates –

who guided me, challenged me, encouraged me, and comforted me
along this long journey.

This work had not been possible without the endless support from Brage
and the unconditional love of my family.

Contents

Preface

The field of ecology suffers from a never-ending need for empirical, long-term, spatially-replicated data. Breeding short-lived species in the lab can provide you with the required data (and a lot of it!) within a PhD-student lifespan, but global change and natural processes are happening outside the office, from your backyard to the most remote places on Earth. Thus, continuous wildlife monitoring remains essential to understand the dynamics of populations under anthropogenic pressure. However, empirical studies are prone to noise from observer errors, suboptimal field conditions, unaccounted or undetectable variables, copy-paste and data-punching mistakes in shared excel files, and so on. In an ideal world, we would have had perfect control over all variables that drive the dynamics of populations in space and time. Experiments are the closest we can get to a controlled environment with real-life organisms. Biomathematical models allow us to create our own "world" where we have full control of all parameters of interest, but translating and generalizing these digital results to natural situations requires, yet again, empirical validation. Furthermore, scientific conclusions can never be perfectly objective as long as they are founded on human subjectivity; the phrasing of a research question, the study design, the gathering of data, the choice of analyses, the structure of a model, the interpretation of results, and most (and worst?) of all, personal motives. Today's international academic community intends to improve the quality and correctness of scientific studies through critical article review and careful assessment of research proposals. We can always do better, but when is better good enough? There will always be someone who opposes your ideas, criticizes your methods, or thinks your research is just a waste of time and resources. The common playground of science is a crowded ballroom where people dance the boogie-woogie on mainstream pop music, but listen to their own favorite tune with noise-cancelling headphones. Nonetheless, as technological advances, international collaborations, and public outreach are flourishing in this digital era, there are also great opportunities for continuously increasing our knowledge, improving our approaches, and expanding our horizons, both in-depth and across disciplines. Also, who said fencing with knowledge can't be fun?

Summary

To prevent populations or species extinctions due to anthropogenic global change, we need a better mechanistic understanding of the interplay between intrinsic (e.g. resource competition, demographic structure) and extrinsic (e.g. climate change, exploitation) drivers of population dynamics. In this thesis, I demonstrate how interactive effects of climate change and harvesting can shape wildlife population dynamics in time and space. I adopted an interdisciplinary approach combining theoretical and empirical models with time-series data and genetic samples from the high Arctic Svalbard reindeer. I present empirical evidence of the causal links between midwinter rain-on-snow events and basal ice encapsulating the tundra vegetation. These events have become more frequent under recent climate change and can strongly affect resource availability with multiplicative effects on reindeer survival and fecundity at high population densities. Density-dependent effects of rain-on-snow contributed to large-scale spatial synchrony in population fluctuations. However, local populations showed contrasting trends in abundance, which was attributed to spatial heterogeneity in the effects of climate change. This spatial decoupling of population dynamics in the long-run is expected to improve the sub-species' resilience to climate change. In contrast, analysis of landscape genetics across Svalbard revealed that the rapid loss of sea ice due to climate change leads to increased genetic isolation and, thereby, higher local extinction risk. Moreover, local and regional extinctions due to historical overexploitation and subsequent reintroduction programs modified the observed genetic structure linked to sea ice connectivity and landscape barriers. However, I provide theoretical and empirical-based evidence for a wide range of life histories, with Svalbard reindeer as a case-study, that *sustainable* harvesting can mitigate over-compensatory responses to weather-induced resource limitation. Thus, harvesting can be used as a management tool to avoid overabundant populations, thereby increasing population stability and resilience to climate change. In conclusion, the results from this thesis demonstrate how anthropogenic stressors can interact to shape population dynamics and genetics in time and space. Accounting for the interplay between different extrinsic and intrinsic drivers could significantly improve the conservation and management of wildlife populations under climate change and harvesting.

List of papers

I. **Peeters B**, Pedersen ÅØ, Loe LE, Isaksen K, Veiberg V, Stien A, Kohler J, Gallet J-C, Aanes R, Hansen BB (2019) Spatiotemporal patterns of rain-on-snow and basal ice in high Arctic Svalbard: detection of a climate-cryosphere regime shift. *Environmental Research Letters*, doi: 10.1088/1748-9326/aaefb3

II. Hansen BB, Pedersen ÅØ, **Peeters B**, Le Moullec M, Albon S, Herfindal I, Sæther B-E, Grøtan V, Aanes R. (in press) Spatial heterogeneity in climate change effects decouples the long-term dynamics of wild reindeer populations in the high Arctic. *Global Change Biology*.

III. **Peeters B**, Le Moullec M, Raeymaekers JAM, Marquez JF, Røed KH, Pedersen ÅØ, Veiberg V, Loe LE, Hansen BB. Sea ice loss increases genetic isolation in a high Arctic ungulate metapopulation. *In review*.

IV. **Peeters B**, Grøtan V, Gamelon M, Veiberg V, Lee A, Albon S, Fryxell JM, Sæther B-E, Engen S, Loe LE, Hansen BB. Harvesting can increase population viability by modifying climate change effects. *Manuscript*.

Declaration of contributions

Paper I: BBH and BP designed the study. JK, LEL, ÅØP, BBH, VV, RA and JCG collected snowpack data. BP analyzed the data and wrote the manuscript, which was reviewed and commented by ÅØP, LEL, KI, VV, AS, JK, JCG, RA and BBH.

Paper II: BBH designed the study. RA and ÅØP conducted field work with help from BBH, BP and MLM. BP and BBH analyzed the data with input from MLM, IH and VG. BBH wrote the manuscript, which was reviewed and commented by ÅØP, BP, MLM, SA, IH, BES, VG and RA.

Paper III: BBH, BP and MLM designed the study. MLM, BBH, ÅØP, LEL, VV and KHR provided samples. BP conducted DNA extraction and genotyping with help from KHR. BP analyzed the data with help from JFM, JAMR and KHR. BP wrote the manuscript, which was reviewed and commented by all co-authors.

Paper IV: BP, BBH and VG designed the study and conceptual ideas with significant contributions from MG, VV, BES and JMF. BP conducted all empirical and theoretical analyses with input from BBH, VG, MG and AL. VG and SE developed the theoretical models. SA, LEL and VV collected the Svalbard reindeer data. BP wrote the manuscript, which was reviewed by all co-authors.

1| Objective of the thesis

The anticipated and unknown implications of anthropogenic climate change call for a clear, unambiguous understanding of how intrinsic (e.g. resource competition, age structure) and extrinsic (e.g. weather, harvesting) forces drive the dynamics of wildlife populations. The general assumption that environmental variability affects populations independently of intrinsic mechanisms has been opposed by multiple empirical studies (e.g. Bonenfant et al., 2009, Coulson et al., 2001, Gamelon et al., 2017, Hansen et al., 2019). However, disentangling the often complex, yet fundamental, interactions among intrinsic and environmental drivers of individual fitness and population dynamics remains a continuous challenge. The relative importance of extrinsic drivers often varies in space and time, and their ecological responses depend on both the species' life history and the state of the population (Sæther, 1997). Furthermore, direct modifications of population structure and size through harvesting may cause unforeseen responses to environmental perturbations (Anderson et al., 2008, Lande et al., 1995).

One urgent question in ecology and evolution, with huge management implications, is how populations respond to harvesting under climate change, and vice versa. Past population collapses and local, regional, and global extinctions of species due to unregulated harvesting have taught us much about our responsibility to manage and conserve viable populations in the wild (Lande et al., 1995). Today, methods for population monitoring and sustainable harvesting are available and continuously improving, but the anticipated environmental consequences of climate change are posing new questions. How will ecological and evolutionary responses to multiple anthropogenic drivers vary in space and time? How will species and populations respond to a rapidly changing environment, and will they be able to persist? Ultimately, how will this affect us, humans, in a world with a constantly growing need for food and desire for wealth?

In this thesis, I use monitoring data from a high Arctic study system to assess **how climate change and harvesting, and their interactions, can drive the dynamics of populations in space and time.** My model species, the high Arctic Svalbard reindeer (*Rangifer tarandus platyrhynchus*, Figure 1), suffered from overexploitation in the past and is now facing a rapidly changing environment due to global warming (Post et al., 2009). This represents a unique opportunity to examine ecological and evolutionary implications of anthropogenic change, made possible thanks to the extensive, long-term monitoring and sampling efforts of multiple populations (Figure 2). I adopted an integrative approach by combining theoretical models with genetic samples and empirical time-series data on the reindeer and their environment. Specifically, my research focused primarily on:

- the causal links between climate change, weather variability and density-dependent population processes (**Papers I, II & IV**),
- climate change effects on spatial variation in population dynamics and genetics over annual, decadal and evolutionary time scales (**Papers II & III**),
- how consequences of harvesting can modify climate change effects on population dynamics (**Papers III & IV**).

Figure 1. A Svalbard reindeer bull sniffs the air to catch the scent of an approaching PhD-student. Photo: B. Peeters.

2| Climate change and the Arctic ecosystem

Since the industrial revolution, we have experienced an exponential increase in anthropogenic greenhouse gas emissions (IPCC, 2013). As our planet is warming, life on Earth has to cope with rising sea levels and more extreme floods, droughts, storms and heat waves (Diffenbaugh et al., 2017, Easterling, 2000, IPCC, 2013). The Arctic is changing more rapidly than any other biome on Earth. Warmer oceanic and atmospheric temperatures increase the amount of rain- instead of snowfall and induce the melting of glaciers, snowpacks and sea ice (Bintanja and Andry, 2017, Diffenbaugh et al., 2017, Radic et al., 2014). Climate change in the Arctic is further accelerated by the decrease in the amount of solar radiation reflected by snow and ice, a physical process known as 'albedo' (Serreze and Barry, 2011). This positive feedback mechanism between geophysical processes leads to an 'Artic amplification' of global warming. Consequently, even if we manage to restrict global temperature rise by 2°C towards the end of the 21st Century, the Arctic would likely still experience a warming of 4-5°C (IPCC, 2013).

Climate change in the Arctic has far-reaching biological consequences (Post et al., 2009). Sea ice loss will change ecological and evolutionary responses across trophic levels, from primary producers to apex predators, in both marine and terrestrial ecosystems (Post et al., 2013). On land, warmer ambient temperatures lead to earlier snowmelt and spring phenology, and an overall greening of the Arctic tundra (Assmann et al., 2019, Van der Wal and Stien, 2014, Vickers et al., 2016). Extreme rain-on-snow (ROS) events, leading to thick ice-layers covering large tracts of tundra vegetation, have been linked to catastrophic population collapses in Arctic ungulates, such as muskox (*Ovibos moschatus*), Peary caribou (*R. t. pearyi*) and Svalbard reindeer (Forchhammer and Boertmann, 1993, Kohler and Aanes, 2004, Miller and Gunn, 2003, Parker et al., 1975, Rennert et al., 2009). Scavengers like the Arctic fox (*Vulpes lagopus*) may benefit from the abundance of carcasses but consequently induce a higher predation pressure on small herbivores and migratory birds (Bêty et al., 2002). Therefore, extreme climate events like ROS may strongly affect the dynamics of species across the terrestrial community (Hansen et al., 2013, Stien et al., 2012).

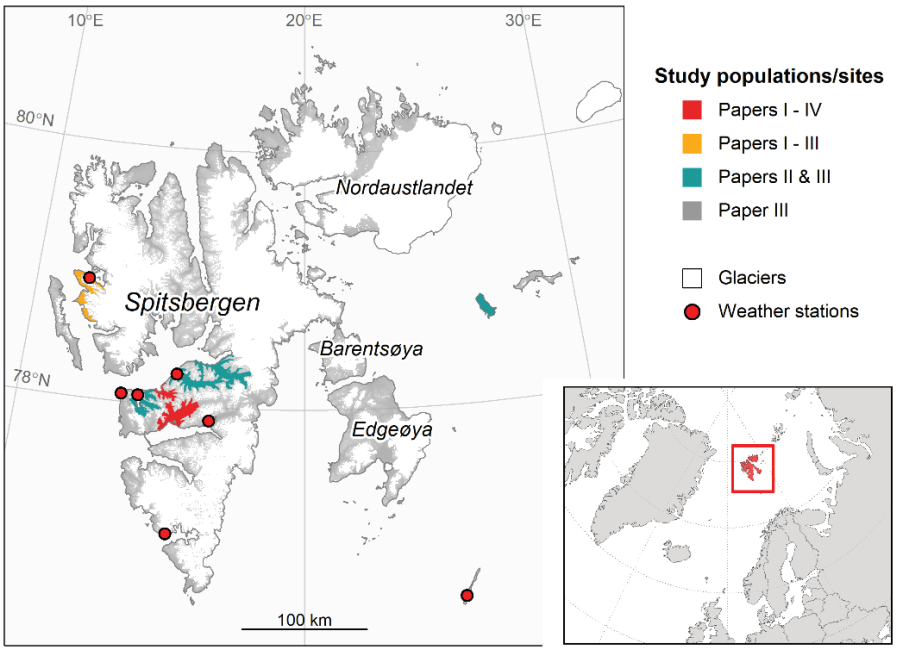

Figure 2. Svalbard is situated in the high Arctic north of Norway. Time-series data on snowpack measurements (**Paper I**) and abundance and vital rates in Svalbard reindeer (**Papers II & IV**) were obtained from populations in central and west-coastal Spitsbergen and east Svalbard. Samples for the study on metapopulation genetics (**Paper III**) covered approximately the entire range of Svalbard reindeer (grey land areas). Meteorological data was obtained from seven weather stations (red dots).

Rain-on-snow and basal ice

Recent advances in remote sensing and geophysical modelling have greatly improved the detectability of ROS events and our interpretation of how they influence snowpacks and wildlife (Bartsch et al., 2010, Forbes et al., 2016, Grenfell and Putkonen, 2008, Kohler and Aanes, 2004, Vikhamar-Schuler et al., 2013). Ecological responses of Arctic wildlife to ROS occur mainly through snowpack hardening and the formation of ice within, or at the base of, the snowpack. The latter type of ice is known as 'basal ice', but has often been referred to as 'ground ice' (e.g. Hansen et al., 2011, Kohler and Aanes, 2004) – which in cryosphere terminology describes ice formed in the ground and is often part of the permafrost (e.g. Harris et al., 2009). Thick layers of basal ice often occur after winter warm spells and heavy ROS (Hansen et al., 2014). However, empirical evidence from the high Arctic on the causal links between ROS, basal ice, and climate change has been lacking.

In **Paper I**, we investigated spatiotemporal variation in ROS and basal ice using a unique time series of spatially-replicated snowpack measurements during the period 2000-2017, and meteorological data from seven manned weather stations across Svalbard (Figure 2). Our statistical models confirmed that both the occurrence and thickness of basal ice increased strongly with the amount of winter rain, as expected from cryosphere theory (e.g. Kohler and Aanes, 2004, Putkonen and Roe, 2003). Note that I deliberately used 'winter rain' to describe the weather variable, which essentially means the same as ROS when it falls on top of the snowpack. Moreover, a positive interaction between winter rain and cumulative snowfall supported the assumption that more basal ice is formed when large amounts of ROS fall on top of a thicker snowpack, because both rain and snowmelt water percolates through the snowpack and freezes on the ground (Putkonen and Roe, 2003, Woo et al., 1982). Predictions from these models, based on the historical weather data, revealed a marked regime shift in winter rain and basal ice linked with climate change. Rain- and ice-free winters have virtually not occurred in our study area since 1998.

3| Population dynamics under climate change

Density-dependent environmental drivers

Vital rates, such as survival and recruitment, often vary with population density through competition for resources (Royama, 1992). When the per-capita resource availability is also influenced by weather or other environmental conditions, we should expect nonlinear perturbation effects on births, deaths, and ultimately population growth rates (Royama, 1992). Extreme weather events that restrict the availability of resources may thus have dramatic consequences for populations at high density due to even stronger resource competition, while the consequences may be negligible for populations at low density (Figure 3). Density-dependent effects of weather or other environmental drivers have recently been found in a wide range of taxa and regions, and have also been integrated in theoretical population-dynamic models (see empirical examples in **Paper IV**; Ferguson and Ponciano, 2015). Furthermore, the dynamics of natural populations are often complicated by temporal variation in the age or stage structure, as well as age- or stage-specific variation in the strength of density dependence and sensitivity to environmental stochasticity (**Paper IV**; Caswell, 2001, Festa-Bianchet et al., 2003, Lande et al., 2002).

In Arctic herbivores, observed population crashes have generally been linked to mass starvation after heavy ROS events as the tundra vegetation became inaccessible by hardened snowpacks and basal ice (e.g. Forchhammer and Boertmann, 1993, Hansen et al., 2011, Parker et al., 1975, Rennert et al., 2009). Population crashes were likely associated with high population densities at the time of extreme weather events (Hansen et al., 2019, Tyler, 2010). In Svalbard reindeer, the risk of starvation from winter forage competition is strongly related to ROS (Albon et al., 2017), but resultant mortality rates are likely to increase multiplicatively only when densities are high (Hansen et al., 2019). Furthermore, the sex and age structure of a population can change considerably during harsh winters. Changes towards more female-biased adult sex ratios after harsh winter conditions have been linked to stronger increases in adult mortality in males than females (Peeters et al., 2017), which were likely related to seasonal differences in energy expenditure and reproductive strategy among sexes (Barboza et al., 2004). Survival and fecundity rates of prime-aged females are also more robust to high density–high ROS winters than vital rates of juvenile and senescent females (Hansen et al., 2019, Lee et al., 2015). This may lead to ‘demographic buffering’, i.e. a selection for reduced variation from environmental fluctuations in the vital rates that are most influential to

population growth (Bjørkvoll et al., 2016). Overall, the density-dependent effect of ROS is a key component of the population dynamics of Svalbard reindeer because of the mechanistic link between winter weather, snowpack properties (particularly basal ice) and resource availability (Hansen et al., 2019). However, in **Paper II** we demonstrated how the strength of the interaction between density and ROS can vary between populations due to spatial variation in climate and weather conditions.

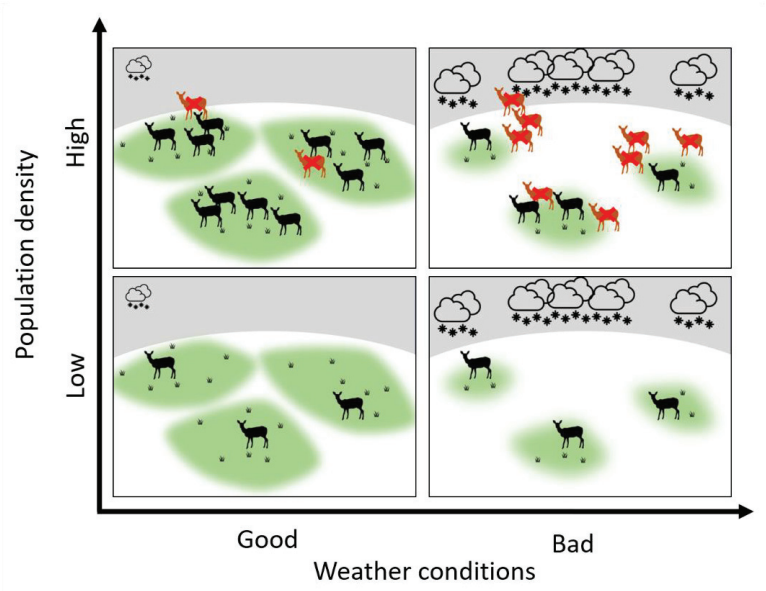

Figure 3. Contrasting levels of population density and weather conditions impact per-capita resource availability and ultimately vital rates, here illustrated by mortality (red animals). At low population density and good weather conditions, resource availability is high. At high population density and good weather conditions, density-dependent mechanisms impact vital rates by reducing the per-capita resource availability. At low population density and bad weather conditions, overall resource availability is restricted but may not cause a decline in vital rates at low population densities. The combined effect of high population density and bad weather has particularly strong impact through multiplicative effects on resource competition.

Spatial synchrony and heterogeneity

Weather is typically autocorrelated over large distances (Koenig, 2002). If two spatially segregated populations are driven by the same environmental drivers and same logistic density-dependent processes, they are expected to have the same correlation in annual abundances as the spatial autocorrelation in their environment (Moran, 1953). This phenomenon, called the 'Moran effect', has been described in general for populations driven by the same weather patterns (Koenig, 1999, Liebhold et al., 2004, Moran, 1953, Sæther, 1997). In our high Arctic study system, annual fluctuations in ROS and basal ice were strongly autocorrelated in space (**Paper I**). Thus, spatially segregated populations may experience similar winter conditions linked to ROS across large areas and can, therefore, experience synchronized fluctuations in abundances.

Spatial synchrony in population dynamics can also arise from biotic drivers such as dispersal or trophic interactions (Engen et al., 2002, Ims and Andreassen, 2000, Liebhold et al., 2004, Ranta et al., 1995). The persistence of populations and (sub-)species to climate change is likely determined by the relative impact of biotic and abiotic drivers on synchrony. Strong synchronizing effects of weather can cause simultaneous (quasi-)extinctions of populations, whereas sufficiently high migration rates may avoid local extinctions and increase the probability of recolonization (Engen et al., 2002, Heino et al., 1997, Sutcliffe et al., 1997). Furthermore, synchronous dynamics are not exclusively intraspecific, but can also occur between different species even though they do not have any direct trophic interactions (Liebhold et al., 2004). On Svalbard, ROS events have been shown to locally synchronize population abundances of the four resident vertebrate species, i.e. Svalbard reindeer, Svalbard rock ptarmigan (*Lagopus muta hyperborea*), sibling vole (*Microtus levis*), and the Arctic fox (Hansen et al., 2013).

In **Paper II**, we investigated how the synchrony in ROS and icing (**Paper I**) contributed to long-term trends and spatial synchrony in ten populations of Svalbard reindeer over distances of 8-324 km (Figure 2). Spatial synchrony in the dynamics of Svalbard reindeer was evident from pairwise correlations between populations in annual fecundity, mortality, and population growth rates. These pairwise correlations were generally positive and decreased with increasing distance between populations. We found that the spatially autocorrelated fluctuations in ROS, as a proxy for basal ice conditions (**Paper I**), contributed to the synchrony among populations. However, after accounting for the interaction between ROS and density, the reductions in pairwise correlations were only significant in mortality and marginally non-

significant in population growth rates. As Liebhold et al. (2004) pointed out, *"although the existence of spatial synchrony is often quite clear, the mechanisms behind synchrony are often murky*". Spatial synchrony describes autocorrelation in annual fluctuations, but it provides little information on mechanisms driving population trajectories in the long run. A progressively shorter winter season and 'greening' of the tundra vegetation associated with warmer summers have likely contributed to an overall increase in total reindeer abundance (Albon et al., 2017, Hansen et al., 2019, Le Moullec, 2019, Vickers et al., 2016), yet we show that local populations have highly contrasting trends over time. To explain these contrasting dynamics of synchronous annual fluctuations and diverging long-term trends, we need to understand how spatial heterogeneity in weather drivers and ecological responses can cause variation in populations subject to those very same drivers (Engen and Sæther, 2005).

Although weather is typically autocorrelated over large distances, spatial variation in weather on Svalbard is closely related to coupled geophysical processes in the ocean and atmosphere. Transitions in ambient temperature, pressure and moisture above land and sea are linked to temporal and spatial variation in, amongst others, topography, sea surface evaporation and sea ice extent (Van Pelt et al., 2016, Østby et al., 2017). The climate on Svalbard is strongly influenced by cold Arctic water in the east, and the northward flow of warm Atlantic water in the west (see **Paper III**, Figure 1). Furthermore, climatic gradients from the coast towards the island centers result in local variation in weather. In our study system, reindeer populations along the west coast experienced more precipitation, particularly during winter ROS events, than 'continental' populations in the center of Spitsbergen (Paper II; Van Pelt et al., 2016, Østby et al., 2017). Indeed, even the spatial occurrence and thickness of basal ice was highest along the coast (**Paper I**). Accordingly, we observed a stronger density-dependent response to ROS in the population growth rates of a 'coastal' compared to a 'continental' population. Both populations also experienced a regime shift in summer temperature around 1998 – i.e. coinciding with the regime shift in ROS and basal ice (**Paper I**), but only the population growth rates of the 'continental' population showed a significantly positive response to summer temperature. As a result, the coastal and continental population displayed negative and positive abundance trends, respectively, over the last couple of decades with strong warming temperatures.

Overall, spatial autocorrelation in weather can synchronize population dynamics, but at the same time, spatial heterogeneity in climate change effects can decouple the long-term population trends (Sæther et al., 2007). Although I used the Svalbard reindeer as a model species, the complex mechanisms of spatial synchrony, spatial heterogeneity and ongoing

climate change are likely ubiquitous in nature (Bjørnstad et al., 1999, Koenig, 1999, Liebhold et al., 2004). The observed patterns in **Paper II** are thus of relevance for most, if not all, metapopulations in the Arctic.

Eco-evolutionary consequences of sea ice loss

While climate change effects on population dynamics were apparent from changes in the Arctic landscape (**Paper I** and **II**), the fate of many Arctic species will also depend on the ongoing changes in sea ice patterns (Post et al., 2013). The iconic polar bear (*Ursus maritimus*), Arctic fox, walrus (*Odobenus rosmarus*), harp seals (*Pagophilus groenlandicus*), ivory gull (*Pagophila eburnean*), and many other Arctic species, depend on sea ice for foraging, migration, and/or breeding. Reindeer must have crossed sea ice over great distances to colonize Svalbard, likely more than 5000 years ago (Kvie et al., 2016, Van der Knaap, 1989). Even vascular plants depended on sea ice for postglacial colonization in the Arctic (Alsos et al., 2016). Climate change and the rapid loss of sea ice are therefore expected to have dramatic consequences for the viability and persistence of isolated populations (Jenkins et al., 2016, Post et al., 2013). In **Paper III**, we show how sea ice loss will affect extinction-colonization dynamics and evolutionary processes in Svalbard reindeer. We sampled 411 reindeer at 25 locations across the archipelago and genotyped them at 19 microsatellite loci (Figure 2). Microsatellites are DNA sequences characterized by motifs of typically two to five base pairs repeated in tandem (e.g. CACACA…CA for nucleotides C(ytosine) and A(denine); Jarne and Lagoda, 1996). Variation in microsatellite lengths, i.e. due to variation in the number of repeated motifs, informs us of the genetic variability within and between individuals, populations, or (sub-)species. Most genetic variation arises due to selection, (partial) isolation, random mutations and genetic drift (Kimura, 1968, Wright, 1949). Microsatellites are non-coding DNA and typically occur in neutral regions of the genome, meaning that they are not under selection – unless through e.g. genetic hitchhiking (Jarne and Lagoda, 1996). These theories have led to a large field in biology focusing on the effects of landscape on ecological and evolutionary processes (Manel and Holderegger, 2013).

We expected that gene flow between populations of Svalbard reindeer was strongly restricted by open water, glaciers and steep mountains, but mediated by sea ice cover in winter. Our landscape genetic analysis revealed significant 'isolation-by-distance' (IBD), but much stronger evidence for 'isolation-by-resistance' (IBR). Populations were, indeed, highly differentiated due to limited dispersal across glaciers as well as open water bodies that were

rarely covered by winter sea ice. Accordingly, we observed evolutionary source-sink dynamics with directional gene flow and, similarly, a negative gradient in genetic diversity from the center of Spitsbergen towards the range periphery. Sea ice has also been an important migration corridor for island-dwelling Peary caribou, although signatures of IBD and IBR in Peary caribou were of similar strength (Jenkins et al., 2016). However, sea ice around Svalbard has been less continuous in time and decreasing much faster than in the Canadian high Arctic (Comiso et al., 2017), particularly in the west and north of Svalbard (Figure 1b in **Paper III**; Onarheim et al., 2014). This likely contributed to the much stronger IBR than IBD in our study. Thus, climate change and the continued loss of sea ice, an essential dispersal corridor, will very likely increase the genetic isolation of island populations in *Rangifer* and other (sub-)species across the Arctic (Geffen et al., 2007, Jenkins et al., 2016, Mallory and Boyce, 2019, Post et al., 2013).

4| Harvest-climate interactions

Past extinctions and reintroductions

Like many other tasty species, Svalbard reindeer were harvested to the brink of extinction in the past (Lønø, 1959). Since they were protected from harvesting in 1925, they gradually expanded from four isolated remnant populations to recover their historical range (Le Moullec, 2019). Harvesting can be assumed to have reduced the genetic diversity of Svalbard reindeer (Côté et al., 2002), but a comparative analysis between modern and 'ancient' DNA would be required to quantify the loss of genetic variation. In a pilot study of fourteen ancient samples (200 – 4000 years old), we discovered three haplotypes in the control region of mitochondrial DNA (Peeters et al., unpubl.) whereas only one haplotype was found in contemporary samples (Kvie et al., 2016). This suggests a substantial loss of genetic variation since the pre-harvesting period. Indeed, the strong isolation from the mainland has likely contributed to the lower genetic diversity in Svalbard reindeer than other *Rangifer* subspecies, even before they were overharvested (Frankham, 1997, Røed, 2003, Yannic et al., 2013). However, some newly recolonized populations showed a mixed genetic origin from highly differentiated remnant populations, suggesting that reindeer populations were likely more connected and admixed before the local and regional extinctions from overharvesting (**Paper III**).

Recolonizations were in part facilitated by human-mediated reintroductions from Central to West Spitsbergen in the late 1970's (Aanes et al., 2000, Gjertz, 1995). Based on historical reports and the genetic structure observed in **Paper III**, we could deduce recolonization patterns and anthropogenic modifications of natural isolation. Notably, the recent lack of sea ice in West Svalbard has likely impeded gene flow between reintroduced and naturally recolonized populations, with very high (i.e. the highest observed) genetic differentiation (F_{ST} = 0.41) between populations only ~16 km apart. Without successful reintroduction by humans, there would likely be no reindeer in several locations of West Svalbard today due to past overharvesting and ongoing climate change.

Harvesting under climate change

Whether harvesting can amplify the effects of climate change on population dynamics is an ongoing debate (Gamelon et al., 2019). Specific types of harvest strategies, e.g. fixed quota or *constant* harvesting, are more likely to increase the risk of extinction or quasi-extinction than other strategies, e.g. fixed effort or *proportional* harvesting (Lande et al., 1995). For instance, harvest-induced changes in demographic structure can modify short-term population fluctuations and the capacity to buffer environmental stochasticity and perturbations (Hsieh et al., 2006, Rouyer et al., 2012). However, environmental stochasticity has been routinely integrated as a density-independent term in harvest models (Beddington and May, 1977, Fryxell et al., 2010, Lande et al., 1995, May et al., 1978). May et al. (1978) briefly discussed the potential importance of density-dependent environmental stochasticity in harvest models and suggested that stabilizing effects of harvesting can occur under over-compensatory or chaotic population fluctuations. We argue that, in resource-limited systems, climate-density interactions in population dynamics are more common than previously assumed (Figure 3; **Paper IV**). However, a theoretical framework and empirical-based evidence of how harvesting can modify resource-based environmental stochasticity in population dynamics has been lacking.

In **Paper IV**, we demonstrated how proportional harvesting can buffer climate-driven population fluctuations and, thereby, increase population stability and resilience to environmental perturbations. First, we defined a Ricker type model of population growth with environmental stochasticity in the strength of density dependence (Ferguson and Ponciano, 2015). Based on simulations from this model, we assessed harvest-induced changes in the quasi-extinction probability for a wide range of life histories and environmental variance effects. Then, we used an age-structured population model of demographic rates (i.e. survival, fecundity) in Svalbard reindeer (Hansen et al., 2019) to evaluate, by simulating population trajectories, how proportional harvesting can modify age-specific interaction effects of population density and ROS. These models have been developed based on the results from Integrated Population Models that combined long-term mark-recapture and population monitoring data from our study population in Central Spitsbergen (Figure 2; Bjørkvoll et al., 2016, Hansen et al., 2019, Lee et al., 2015).

Stochastic simulations of our theoretical and empirical-based population models revealed that even modest harvest proportions can have large stabilizing effects on fluctuations in population size and age structure, with only minor reductions in long-run average population

sizes. Thus, by modifying population density and, thereby, the strength of density-dependent environmental effects, proportional harvesting reduced the risk of quasi-extinction and population crashes. This result is linked to the modelled assumption of bad environmental conditions with multiplicative effects at high densities (Figure 2). Under such circumstances, harvesting could therefore be implemented as a strategy to buffer against increased environmental variation and higher frequencies of perturbations predicted due to global climate change (e.g. Diffenbaugh et al., 2017). Indeed, populations can become more sensitive to temporal variation in the environment in cases with, e.g., strong density-independent stochastic mechanisms (May et al., 1978) or secondary consequences of selective harvesting (Festa-Bianchet et al., 2017), such as increased bias in sex and age structure (Hsieh et al., 2006, Solberg et al., 1999) and artificial selection by trophy hunting (Pigeon et al., 2016). Making sustainable harvesting decisions will therefore depend on continuous monitoring with reliable population observations and careful assessment of the causal mechanisms of population responses to environmental drivers. Nevertheless, I have demonstrated that (proportional) harvesting can buffer against unforeseen changes in population dynamics following increasing environmental variability due to climate change.

5| Prospects and concluding remarks

Accounting for the density-dependent population responses to weather conditions (Figure 3) and increased stability through harvesting are essential for correctly estimating the maximum sustainable yield and optimal criteria for different harvest strategies. Existing theoretical and empirical-based harvest models often account for the magnitude of environmental stochasticity, density dependence, and demographic structure (e.g. Beddington and May, 1977, Lande et al., 1995, Solberg et al., 1999, Sæther et al., 1996). However, these models have generally overlooked the potential for strong density-dependent population responses to environmental effects on resource availability. Finding the right balancing point between climate-driven and harvest-induced fluctuations in population size will likely become a major goal in the future design of sustainable wildlife management under climate change.

The observed interactive effects of extreme weather events, climate change, and harvesting on single-species population dynamics may also have wider community-dynamic implications. For instance, ROS events have been shown to synchronize the population dynamics of the few vertebrate species overwintering on the Svalbard tundra (Hansen et al., 2013). Because the reindeer and its annual fluctuations in mortality rates are a key factor in these trophic co-fluctuations, a modification of climate change effects on reindeer population stability, through harvesting, may cascade throughout the food web. However, assessing the community-dynamic implications of interacting anthropogenic stressors on single key species requires complex multi-species modelling combined with rarely available long-term data of high quality across trophic levels.

A major constraint inherent in population count data is that changes in population size cannot be accurately attributed to natural growth (births, deaths), predation or migration. In general, individual mark-recapture and movement data are needed to accurately estimate relative population changes due to mortality, reproduction and migration (Festa-Bianchet et al., 2017). Furthermore, effective migration rates can be estimated from modern genetic tools, such as single nucleotide polymorphism or whole genome sequencing. The two ongoing mark-recapture programs on Svalbard reindeer (Ny-Ålesund and the Reindalen valley system) present a unique opportunity to implement state-of-the-art molecular analyses and obtain high-resolution data on individual migration and effective gene flow. Ultimately, integrating individual mark-recapture data and genetic assignment analyses could enable an exhaustive investigation of the relative impacts of population density, climate forcing and dispersal, and their interactions (Hansen et al., 2019, Loe et al., 2016), on spatial synchrony. Furthermore,

modern genetic tools can provide important information on local adaptation and genome level changes under climate change, with huge relevance for the conservation of small isolated populations.

Overall, I have demonstrated how population responses to large-scale changes in their environment can be naturally buffered by spatial heterogeneity in the effects of climate change, but also artificially through harvesting. Because harvesting can reduce the spatial scale of population synchrony (Engen et al., 2018), it can also be used as a management tool to reduce the risk of unexpected population collapses over large areas. However, the risk of population bottlenecks and local extinctions is expected to increase as major dispersal corridors disappear due to climate change. Small isolated populations are therefore especially vulnerable as global warming is expected to generate more frequent and unprecedented extreme climatic events (Diffenbaugh et al., 2017, IPCC, 2013). Importantly, the demonstrated interplay between harvesting and climate change effects on temporal and spatial population dynamics are certainly not exclusive to Svalbard reindeer (Figure 4). The results from this thesis are therefore highly relevant for the future conservation and management of many harvested species.

Figure 4. Svalbard reindeer, a tasty herbivore in a climate change hotspot. Photo: B. Peeters.

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Paper I

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Spatiotemporal patterns of rain-on-snow and basal ice in high Arctic Svalbard: detection of a climate-cryosphere regime shift

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Spatiotemporal patterns of rain-on-snow and basal ice in high Arctic Svalbard: detection of a climate-cryosphere regime shift

Bart Peeters[1,7], **Åshild Ønvik Pedersen**[2], **Leif Egil Loe**[3], **Ketil Isaksen**[4], **Vebjørn Veiberg**[5], **Audun Stien**[6], **Jack Kohler**[2], **Jean-Charles Gallet**[2], **Ronny Aanes**[1,2] and **Brage Bremset Hansen**[1]

[1] Centre for Biodiversity Dynamics, Department of Biology, Norwegian University of Science and Technology, NO-7491 Trondheim, Norway
[2] Norwegian Polar Institute, Fram Centre, NO-9296 Tromsø, Norway
[3] Norwegian University of Life Sciences, Department of Ecology and Natural Resource Management, PO Box 5003, NO-1432 Ås, Norway
[4] Norwegian Meteorological Institute, PO Box 43, Blindern, NO-0313 Oslo, Norway
[5] Norwegian Institute for Nature Research, PO Box 5685, Torgarden, NO-7485 Trondheim, Norway
[6] Norwegian Institute for Nature Research, Fram Centre, NO-9296 Tromsø, Norway
[7] Author to whom any correspondence should be addressed.

E-mail: bart.peeters@ntnu.no

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Abstract

Arctic winters have become increasingly warmer and rainier. Where permafrost prevails, winter rain (or rain-on-snow) is known to occasionally cause extensive ice layers at the snow/ground interface, i.e. 'basal ice' or 'ground ice', with potentially large ecological and socio-economic implications. However, an overall lack of field data has so far restricted our predictive understanding of the environmental conditions shaping spatiotemporal variation in basal ice. Here, we use time-series of spatially replicated snowpack measurements from coastal (Ny-Ålesund area; 2000–2017) and central Spitsbergen (Nordenskiöld Land; 2010–2017), Svalbard, to analyze spatiotemporal patterns in basal ice and how they are linked with topography, weather, snowpack and climate change. As expected, both the spatial occurrence and thickness of basal ice increased strongly with the annual amount of winter rain. This effect was modified by accumulated snowfall; a deeper snowpack restricts ice formation following a minor rain event, but enhances ice formation following heavy rain due to an increased contribution of snowmelt. Accordingly, inter-annual variation in snow depth was negatively related to basal ice thickness. Annual fluctuations in basal ice thickness were strongly correlated in space (average correlation $\rho = 0.40$; 0–142 km distance between plots) due to strong spatial correlation in winter rain ($\rho = 0.62$; 14–410 km distance between meteorological stations). Models of basal ice based on meteorological time-series (1957–2017) suggested that ice-free winters (i.e. mean basal ice <0.1 cm) had virtually not occurred since 1998, whereas such winters previously (1957–1998) occurred every three–four years on average. This detected cryosphere regime shift was linked to a parallel climate regime shift with increased winter rain amounts. Svalbard is regarded a bellwether for Arctic winter climate change. Our empirical study may therefore provide an early warning of future changes in high-arctic snowpacks.

Introduction

In the Arctic, winter warm spells with near-surface air temperatures above 0 °C are becoming more frequent due to global warming (Moore 2016, Graham *et al* 2017). This warming, in combination with enhanced surface evaporation due to the loss of sea-ice cover and poleward atmospheric moisture transport, contributes to an overall increase in precipitation over Arctic land areas (4.5% increase per degree of temperature rise), particularly in late autumn and winter (Serreze *et al* 2009, Zhang *et al* 2012, Bintanja and Selten 2014). Recent climate models indicate that rainfall will likely become the dominant form of winter precipitation

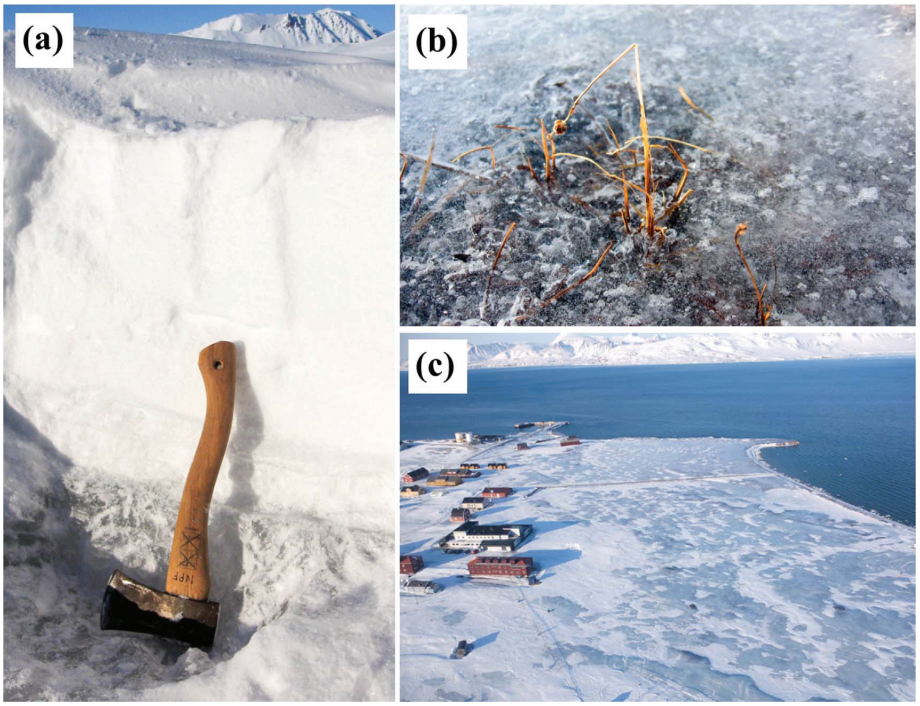

Figure 1. (a) Snow profile from a vegetated tundra site near Ny-Ålesund, Svalbard, showing a thick ice layer ('basal ice') at the bottom of the snowpack. (b) Because of the short-growing vegetation at such high latitudes, basal ice may encapsulate most of the plants. (c) In some winters, basal ice covers most of the tundra at low altitudes, such as the surroundings of Ny-Ålesund.

during the 21st century (Rennert *et al* 2009, Bintanja and Andry 2017). The rain-on-snow (ROS) phenomenon (Putkonen and Roe 2003) is of particular concern as it can lead to avalanches (Conway and Raymond 1993), increased ground surface temperature and near-surface permafrost thawing (Isaksen *et al* 2007, Westermann *et al* 2011), and ice-wedge cracking if water freezes after infiltrating the soil (Christiansen *et al* 2013). Furthermore, heavy ROS events can lead to thick ice layers within the snowpack or at the snow/ground interface, i.e. 'basal ice' or 'ground ice', across the landscape (figure 1; e.g. Vikhamar-Schuler *et al* 2013).

Several studies have documented negative effects of ROS and basal ice on small and large herbivores (Kausrud *et al* 2008, Stien *et al* 2012), soil invertebrates (Coulson *et al* 2000), vegetation growth and reproduction (Bjerke 2011, Preece *et al* 2012, Milner *et al* 2016, Bjerke *et al* 2017), and even whole vertebrate communities (Hansen *et al* 2013). The most noticeable consequences are the occasional die-offs of Arctic ungulates due to mass starvation, as the impenetrable layer of ice makes vegetation inaccessible (e.g. Parker *et al* 1975, Forchhammer and Boertmann 1993, Miller and Gunn 2003, Kohler and Aanes 2004, Hansen *et al* 2011, Langlois *et al* 2017). More frequent ROS and basal ice formation in space and time may therefore also have serious socio-economic impacts for reindeer herders (Bartsch *et al* 2010, Forbes *et al* 2016, Riseth *et al* 2016), but also for the tourism industry and local communities in the Arctic (Hansen *et al* 2014).

Basal ice is formed when liquid water, deriving from snowmelt and/or rainfall (ROS), pools at the bottom of the snowpack and freezes as latent heat is transferred to the surrounding snowpack and frozen ground (Woo *et al* 1982, Putkonen and Roe 2003, Westermann *et al* 2011). In winter, small amounts of rainfall or melted snow resulting from solar radiation and warm air temperatures (Hock 1999) can be absorbed within the snowpack, where it freezes along lateral flow channels (Marsh and Woo 1984). However, as the snowpack becomes saturated, sufficient amounts of rainfall can percolate vertically through the snowpack and freeze in contact with the frozen ground (Woo *et al* 1982, Marsh and Woo 1984, Conway and Benedict 1994). During ROS events, a considerable proportion of total snowpack runoff can be caused by snowmelt (27% on average in the Swiss Alps, Würzer *et al* 2016). Heat fluxes from warm, moist, and windy conditions can be responsible for the main snowmelt energy input (e.g. Marks *et al* 1998). However, advective heat from rain is a potentially large additional source for melt energy (Würzer *et al* 2016). This is particularly the case in the Arctic, where shortwave

radiation is not available for melting during the polar night, and near-surface air temperatures need to be several degrees above freezing point to sufficiently increase snowmelt rates (Hock 1999, Putkonen and Roe 2003). Accordingly, in high-arctic environments where permafrost prevails, the formation of basal ice layers is typically associated with heavy ROS and concurrent snowmelt during warm spells (Putkonen and Roe 2003, Kohler and Aanes 2004, Bartsch *et al* 2010, Vikhamar-Schuler *et al* 2013, Hansen *et al* 2014).

Because of a general lack of field data time-series from the high Arctic (but see Kohler and Aanes 2004, Hansen *et al* 2011 for Svalbard, and Bulygina *et al* 2010, for Northern Eurasia), our empirical understanding of the spatial and temporal variation in basal ice occurrence remains poor. Some studies have used proxies or simulations based on meteorological or satellite data (e.g. Grenfell and Putkonen 2008, Bartsch *et al* 2010, Vikhamar-Schuler *et al* 2013, Langlois *et al* 2017), without validation from *in situ* field data. Furthermore, little is known on the spatial extent of basal ice events and how they are linked to large-scale meteorological patterns (but see Bartsch *et al* 2010, Forbes *et al* 2016).

In this study, we address this by taking advantage of time-series of spatially replicated snow and basal ice measurements from coastal (Ny-Ålesund area; 2000–2017) and central Spitsbergen (Nordenskiöld Land, near Longyearbyen; 2010–2017), Svalbard, combined with data from local meteorological stations. First, we investigated combined effects of topography, temperature and precipitation patterns, and climate change on basal ice occurrence and thickness. To make our approach applicable across study areas and scientific disciplines, we built simple regression models based on commonly available data from meteorological stations and topographic information from digital elevation models. We then investigated how the spatial extent of basal ice events across our study area was linked to spatial correlation in winter rain. Finally, we modelled and predicted historical occurrence and thickness in basal ice using our regression models accounting for weather and topography, and investigated temporal changes linked with the recent warming in high Arctic Svalbard (Hansen *et al* 2014, Isaksen *et al* 2016).

Materials and methods

Study area

The two study areas are located in coastal and central Spitsbergen, Svalbard (74–81 °N, 10–35 °E; figure 2(a)). The coastal study area in North–West Spitsbergen, hereafter referred to as 'NW coast', consists of the mountainous peninsula Brøggerhalvøya, where the research settlement Ny-Ålesund is located, and the two peninsulas Sarsøyra and Kaffiøyra, which are characterized by flat coastal planes with steep mountains to the East (figure 2(b)). The study area in Central Spitsbergen is located 17–33 km south of the meteorological station at Svalbard Airport, Longyearbyen, and covers the valleys Colesdalen, Semmeldalen and Reindalen (figure 2(c)). The climate in these parts of the Svalbard archipelago, and particularly the NW coast, is influenced by the North-Atlantic current and the coupled sea-ice-ocean atmosphere system (Benestad *et al* 2002). Annual total precipitation and mean temperature for 1970–2015 were on average 417 mm and −5.1 °C for Ny-Ålesund, and 194 mm and −5.0 °C for Svalbard Airport.

In our study, winter was defined as the period between 1 November (preceding year) and 31 March, i.e. just prior to the basal ice measurements. The main reason for the 1 November cut-off is that the onset of ground surface freezing, although depending on the landform, generally occurs some time during October (Eckerstorfer *et al* 2017). In addition, during the study period (2000–2017), daily air temperatures were often <0 °C in November (mean ± SD = −6.5 ± 5.3 °C for Svalbard Airport and Ny-Ålesund combined), and less so in October (−3.2 ± 4.4 °C). Total winter precipitation and mean winter temperature were on average 204 mm and −11.2 °C in Ny-Ålesund, and 88 mm and −11.8 °C at Svalbard Airport. However, a strong winter warming has been identified during the last decades (Førland *et al* 2011), and warm spells with above-zero temperatures now occur more frequently (Hansen *et al* 2014, Vikhamar-Schuler *et al* 2016).

Climate-cryosphere data

Snow profiles and basal ice were sampled in April/early May (earliest 29 March, latest 9 May). Snow pits were dug manually using a spade and, if basal ice was present, an axe or drill was used to reach the ground surface (figure 1(a)). Snow depth, basal ice thickness and the total thickness of ice layers within the snowpack were measured. Data were collected for a total of $n = 2\ 539$ observations during the period 2010–2017 in Central Spitsbergen and 2000–2017 (except 2001 and 2009) in NW coast (figures 2(b)–(c), 3(a)–(b); see supplementary material 1, available online at stacks.iop.org/ERL/14/015002/mmedia). In Central Spitsbergen, sampling was conducted annually at the same sites ($n = 128$), which were spatially structured at eight different locations following a hierarchical block design (see Loe *et al* 2016). Plots at each location covered ridges and sub-ridges at the smallest scale (5 m apart), and valley bottoms and flat hilltops at the largest scale (500 m apart). On the NW coast, snow-ice data were combined from three studies with varying sampling design (see supplementary material 1 for details). These included both randomly placed snow pits along transect lines (2000, 2002–2007, 2010, 2012–2015; Kohler and Aanes 2004) and repeated measures at fixed sites following either a randomly placed grid system (2005–2012, except 2009; Hansen *et al* 2011) or a similar hierarchical block

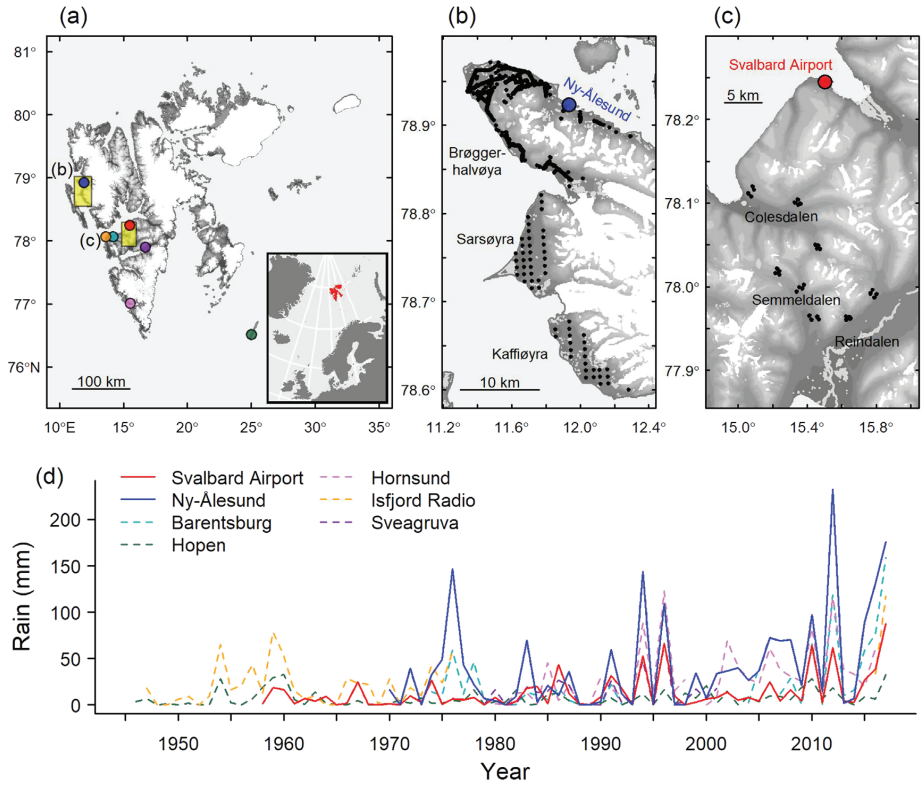

Figure 2. (a) Map of Svalbard (in red in the inset map), situated in the Arctic Ocean north of Norway. Coloured circles indicate the location of the seven meteorological stations used in this study. Yellow rectangles indicate study areas on (b) the NW coast near the meteorological station at Ny-Ålesund and in (c) Central Spitsbergen near the station at Svalbard Airport, Longyearbyen. Black dots in (b)–(c) indicate sample plot locations for cryosphere measurements. (d) Time-series of winter rain (November–March) for the seven meteorological stations across Svalbard.

design as in Central Spitsbergen (2013–2017; this study).

Daily average air temperature and amount of precipitation were obtained for seven meteorological stations across Svalbard (figure 2(a); table S1.2). All stations were used to analyze spatiotemporal patterns of winter rain, while only the meteorological stations in Ny-Ålesund and at Svalbard Airport were used for the basal ice analyses of the NW coast and Central Spitsbergen study areas, respectively. Winter (November–March) precipitation was classified as rain when daily average temperature $\geqslant 1\,^{\circ}\mathrm{C}$ (Stien *et al* 2012, Hansen *et al* 2013). Note that a large rain event (R. Aanes pers. obs.) occurred on 24 March 2007 in Ny-Ålesund (67.3 mm), however with air temperatures ranging from $-3.3\,^{\circ}\mathrm{C}$ to $3.8\,^{\circ}\mathrm{C}$ (mean $= -0.3\,^{\circ}\mathrm{C}$), which was included when calculating the variable Rain, i.e. total amount of winter rain (mm; figures 2(d), 3(c)). The 'peak rain event' for each winter was defined as the largest rainfall over a three-day period. Daily precipitation classified as snow (i.e. at temperatures $<1\,^{\circ}\mathrm{C}$) was then summarized from 1 November until this event to obtain the variable Snow_P, i.e. the accumulated amount of snowfall until the peak rain event (mm; figure 3(d)). Winter heat sum was calculated by accumulating daily temperatures $>0\,^{\circ}\mathrm{C}$ for November–March (figure 3(e)).

Data analysis

First, we compared annual basal ice occurrence (presence/absence, where presence $\geqslant$ 0.5 cm basal ice) and thickness (cm on natural logarithmic (hereafter log) scale) between the NW coast and Central Spitsbergen for the period in which the time-series overlap (2010–2017). We also investigated how average snow depth measured in late winter (April/early May) was related to average observed basal ice thickness, accounting for accumulated snowfall (November–March), in the two study areas (see supplementary material 2 for details on the data analysis).

Second, we used mixed-effects regression models to investigate the effects of climate and topography on the occurrence and thickness of basal ice. One major advantage of mixed models is that they can account for temporal and spatial autocorrelation as well as

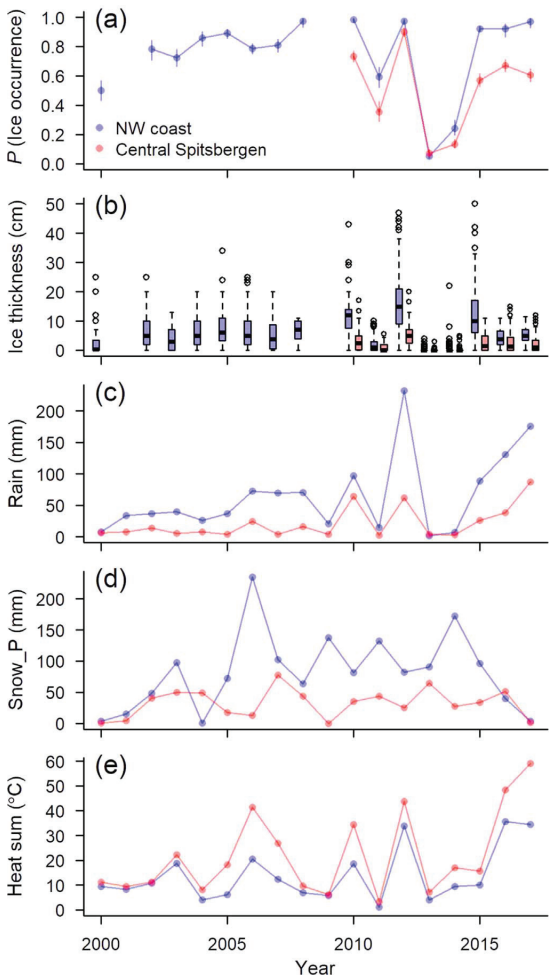

Figure 3. Time-series of data used in the basal ice analyses. (a) Basal ice occurrence, i.e. proportion of sampling sites with basal ice presence (mean ± SE). (b) Basal ice thickness (boxplots showing the median, 1st and 3rd quartile (box), with whiskers and dots indicating 1.5 times the interquartile range and outliers, respectively). (c) Amount of winter rain (November–March). (d) Accumulated amount of snowfall from 1 November until the peak rain event (Snow_P). (e) Winter heat sum, i.e. accumulated temperature above 0 °C (November–March). Basal ice data from the NW coast (2000, 2002–2008, 2010–2017) and Central Spitsbergen (2010–2017), and weather data from their local stations in Ny-Ålesund and at Svalbard Airport, are shown in blue and red, respectively.

unbalanced repeated observations (Cnaan *et al* 1997). *A priori*, we expected to find a positive effect of winter rain on ice occurrence and thickness (Putkonen and Roe, 2003), possibly modified by the amount of accumulated snowfall (Würzer *et al* 2016). We also tested for an effect of total accumulated heat sum as snowpack warming may lead to snow melting and refreezing at the bottom of the snowpack. Elevation (m a.s.l.) and Slope (degrees) at the sample plot level, derived from a Digital Elevation Model with a 20 m resolution (http://geodata.npolar.no), were included to account for topographic effects on basal ice. To evaluate the best fitting parameters, we performed model selection over candidate models using Akaike's information criterion (Burnham and Anderson 2002; see supplementary material 2 and 4).

Third, to quantify the spatial scales at which winter rain and basal ice occur, we analyzed spatial correlation in annual fluctuations of winter rain and ice thickness between pairs of meteorological stations or sampling sites, respectively. For this, we implemented a nonparametric covariance function on pairwise correlations (ρ) as a function of distance (Bjørnstad and Falck, 2001). To investigate the contribution of rain to the spatial correlation in basal ice, we first fitted log-linear models of basal ice thickness with rain as a predictor for every sampling site, and then analyzed the spatial correlation in annual fluctuations of the

Table 1. Parameter estimates (β) with standard errors (SE) of standardized fixed effects covariates from the generalized linear mixed model (GLMM) and linear mixed model (LMM) of basal ice occurrence (on logit scale) and thickness, respectively. Rain, Snow_P (i.e. accumulated snowfall until the peak rain event) and Ice thickness were log-transformed in the analysis. Standard deviations (SD) and number of groups (n) are given for random effects on the intercept. Marginal and conditional R^2 indicate variance explained by the fixed effects and by both fixed and random effects, respectively (Nakagawa and Schielzeth 2013).

	Ice occurrence (GLMM)		Ice thickness (LMM)	
Fixed effects	$\beta \pm SE$	P-value	$\beta \pm SE$	P-value
Intercept	0.904 ± 0.197	<0.001	1.180 ± 0.100	<0.001
Elevation	−0.527 ± 0.085	<0.001	−0.214 ± 0.024	<0.001
Slope	−0.162 ± 0.082	0.048	−0.142 ± 0.024	<0.001
Rain	1.675 ± 0.160	<0.001	0.493 ± 0.059	<0.001
Snow_P	−0.159 ± 0.109	0.143	0.034 ± 0.052	0.648
Rain : Snow_P	0.361 ± 0.129	0.005	0.227 ± 0.044	<0.001
Rain : elevation	—	—	−0.106 ± 0.017	<0.001
Random effects	SD	n	SD	n
Year	0.482	16	0.322	16
Location	0.441	13	0.175	13
Plot ID	0.339	1,282	0.239	1,282
R^2	Marginal	Conditional	Marginal	Conditional
	0.496	0.567	0.436	0.601

residuals from these models (see supplementary material 2 for details).

Finally, we investigated temporal changes in winter rain and basal ice. For this, we modelled and predicted past basal ice occurrence and thickness by using historical weather data (since 1958 and 1970 for Svalbard Airport and Ny-Ålesund, respectively) applied to our top-ranked regression models (supplementary material 4). Preliminary analyses suggested that changes over time were clearly not following linear trends. Thus, we tested for regime shifts (i.e. inter-decadal fluctuations in average levels; Overland *et al* 2006) in the time-series of winter rain and modelled basal ice (supplementary material 2).

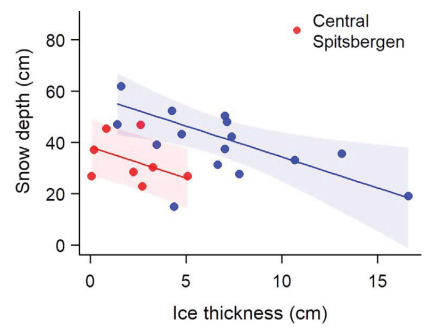

Figure 4. Relationship between average snow depth and basal ice thickness, measured at the same time in April, in the NW coast ($n = 16$ years; blue) and Central Spitsbergen ($n = 8$; red) study areas. Regression lines are shown with 95% CI (shaded areas; see table S3 for parameter estimates).

Results

The average amount of winter rain (mm; log scale) was more than twice higher on the NW coast than in Central Spitsbergen (paired t-test: $t = 4.27$, d.f. $= 47$, $P < 0.001$). Similarly, average basal ice thickness (cm; log scale) on the NW coast was on average twice the estimate for Central Spitsbergen (estimated ratio $= 2.0 \pm 0.7$; figure 3(b)), while the spatial occurrence of basal ice was also more extensive during most winters (figure 3(a)). Furthermore, late winter snow depth (measured in April/early May) was on average 53% deeper on the NW coast, and was more shallow in years with thick basal ice layers, independent of snowfall amount (figure 4, table S3).

Annual fluctuations in basal ice occurrence and thickness largely followed the fluctuations in winter rain (figure 3). Accordingly, the model selection for the regression analyses (supplementary material 4) indicated that the amount of winter rain was the strongest predictor of basal ice, with a positive effect on both occurrence and thickness (table 1, figure 5). As expected, there was a positive interaction between rain and accumulated snowfall (Snow_P) due to melting and refreezing processes in the snowpack (e.g. Woo *et al* 1982, Würzer *et al* 2016). Large amounts of snowfall (high Snow_P, i.e. presumably deep snow accumulation) prevented the formation of basal ice when there was only minor rainfall, but resulted in thicker basal ice when associated with major rain events. Accordingly, shallow late-winter snow depths recorded in years with particularly icy conditions (figure 4) were likely associated with more rain-induced snowmelt. At

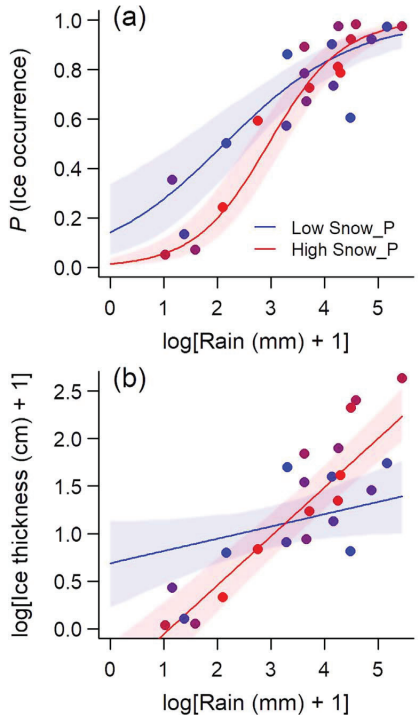

Figure 5. Annual variation in basal ice is explained by the interaction between winter rain and snow. Estimated effects (regression slopes) of winter rain (log scale) are shown for basal ice (a) occurrence (probability) and (b) thickness (log scale), and at low (blue; mean − 1SD) versus high (red; mean + 1SD) amounts of accumulated snowfall until the peak rain event (Snow_P). Shaded areas indicate 95% CI from 1000 parametric bootstrap iterations. Observed means (one dot per year and study area) follow a colour gradient from low (blue) to high (red) amounts of Snow_P.

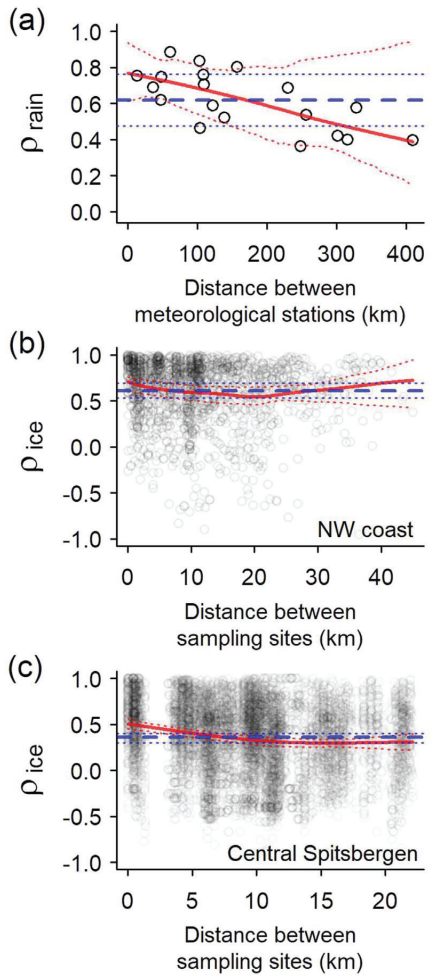

Figure 6. Spatial correlation in annual fluctuations of winter rain and basal ice thickness. (a) Correlation (ρ) in annual fluctuations of winter rain between meteorological stations across Svalbard ($n = 19$ pairwise correlations (circles) with at least five years overlap in time-series). (b)–(c) Correlation in basal ice thickness between sampling sites in (b) the NW coast study area ($n = 1\,676$ pairwise correlations) and (c) Central Spitsbergen ($n = 8\,035$ pairwise correlations). The average spatial, i.e. 'regional', correlation (dashed blue line) and nonparametric covariance of pairwise correlations as a function of distance (solid red line) are shown with 95% CI (dotted lines).

the local scale, basal ice occurrence and thickness decreased with higher elevation and steeper slopes (table 1). Furthermore, the positive effect of rain on basal ice thickness decreased with increasing elevation, because precipitation is more likely to fall as snow at higher altitudes.

Annual fluctuations in winter rain were strongly correlated over distances up to 410 km (i.e. the max distance between meteorological stations), with an average spatial or 'regional' correlation of $\rho = 0.62$ [95% CI: 0.48, 0.76] (figure 6(a)). However, the spatial correlation in winter rain gradually decreased with distance between the meteorological stations. Similarly, annual measurements of basal ice thickness were strongly correlated between sampling sites within and between the two study areas. The regional correlation in basal ice thickness was higher on the NW coast ($\rho = 0.61$ [95% CI: 0.53, 0.68]) than in Central Spitsbergen ($\rho = 0.36$ [95% CI: 0.31, 0.41]; figures 6(b)–(c)), but remained high across the two study areas ($\rho = 0.40$ [95% CI: 0.36, 0.45]; figure S6(a)). After accounting for the effect of rain, the regional correlation in basal ice thickness (i.e. the correlation in model residuals) was close to zero ($\rho = 0.06$ [95% CI: 0.02, 0.10]; figure S6(b)). Accordingly, and as expected, the strong spatial correlation in temporal variation of basal ice thickness across the landscape and study areas was mainly due to the strong spatial correlation in winter rainfall.

Historical weather data from Svalbard Airport and Ny-Ålesund (continuous time-series available since 1957 and 1969, respectively) indicated that winters with virtually no rain occurred approximately every third to fourth year until 1998 (figures 7(a)–(b)). Based

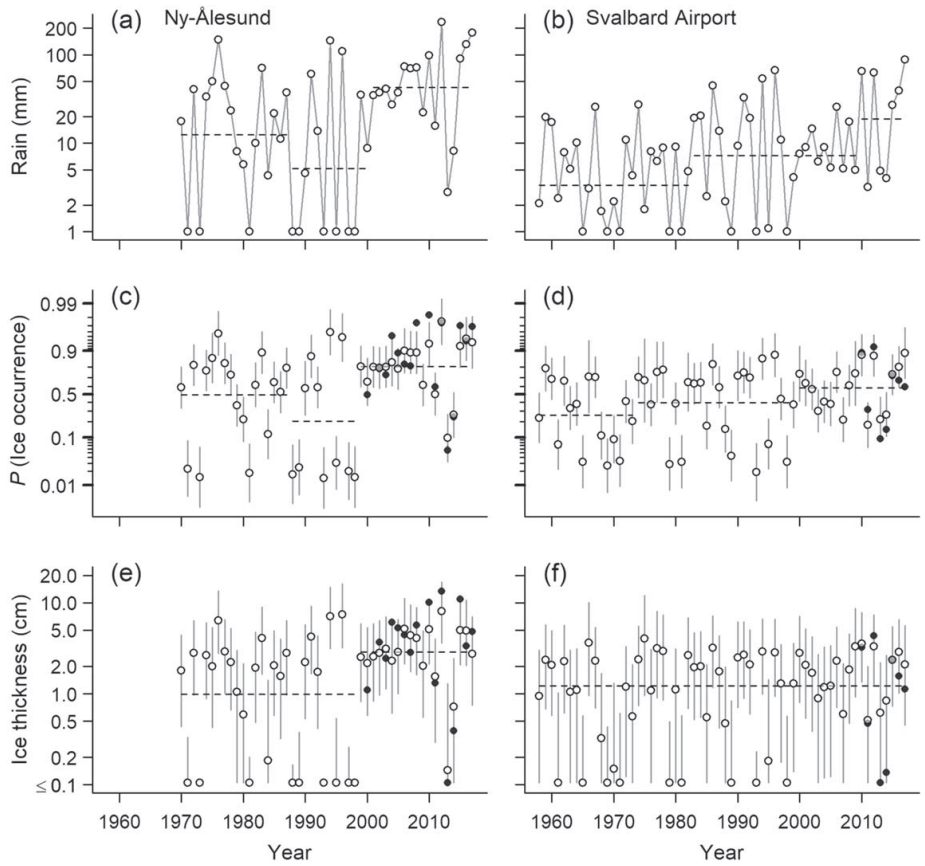

Figure 7. Regime shifts in (a)–(b) historical amount of winter rain (*y*-axis on log scale), and past modelled basal ice (c)–(d) occurrence (probability on logit scale) and (e)–(f) thickness (*y*-axis on log scale), for the meteorological stations in (a), (c), (e) Ny-Ålesund, NW coast, and at (b), (d), (f) Svalbard Airport, Central Spitsbergen. Estimated basal ice occurrence and thickness are shown for slope of 6° (i.e. average slope in sampling sites) at 50 m elevation (white dots; error bars show 95% prediction intervals). Average observed values up to 200 m elevation are indicated with black dots (or grey when overlapping with model estimates). Horizontal dashed lines indicate average values before and after observed change points, i.e. regime shifts ((a) 1987, 2000; (b) 1982, 2009; (c) 1987, 1998; (d) 1973, 1999; (e) 1998; (f) no change point observed).

on change point analyses, we detected a climate regime shift with an overall increase in the average amount of winter rain (log scale) around the turn of the century. Accordingly, when our best-ranked mixed-effects models were used to model basal ice occurrence and thickness based on historical weather data, we also detected a climate-related regime shift in the frequency of icy winters (figures 7(c)–(f)). Rain- and ice-free winters have virtually not occurred since 1998. On the NW coast (Ny-Ålesund), the modelled occurrence of basal ice in the landscape (at an arbitrary elevation of 50 m a.s.l.) was on average 49% before 1987, 20% between 1987 and 1998, and 80% after 1998 (figure 7(c)). Modelled average basal ice thickness increased almost three-fold from 0.99 to 2.88 cm before and after 1998, respectively (figure 7(e)). Also, for Central Spitsbergen (Svalbard Airport), a recent change point in the time-series of modelled basal ice occurrence was detected in 1999, when average ice occurrence increased from 40% to 58% before and after, respectively (figure 7(d)). Here, no change point was detected for ice thickness, but winters with very low ice thickness have been virtually absent since 1998 (figure 7(f)).

Discussion

In the present study, we used spatiotemporal modelling of long-term field data from the high Arctic archipelago of Svalbard to demonstrate the occurrence of a major climate-cryosphere regime shift (figure 7) linked to the recent rapid winter warming (Nordli *et al* 2014, Isaksen *et al* 2016, López-Moreno *et al* 2016). Previous remote-sensing studies have indicated a strong effect of Arctic winter rain on basal ice formation and snowpack hardening using satellite data (e.g. Grenfell and Putkonen, 2008, Bartsch *et al* 2010, Langlois *et al* 2017)

and snowpack simulations (e.g. Vikhamar-Schuler *et al* 2013). However, the very few long-term *in situ* studies in the high Arctic are from Svalbard (Kohler and Aanes 2004, Hansen *et al* 2011, Loe *et al* 2016). By combining these empirical time-series data, we have improved our predictive mechanistic understanding of the environmental conditions causing variation in basal ice in time and space. As expected, basal ice occurrence and thickness increased strongly with the amount of winter rain, particularly so when the accumulated snowfall until the largest rain event was high (figure 5, see also Putkonen and Roe 2003). Accordingly, for a given total snowfall amount, annual snow depths were negatively related to basal ice thickness (figure 4). Since ROS events generally occur over a substantial area (e.g. Rennert *et al* 2009) and are strongly correlated across Svalbard (figure 6(a)), observed basal ice thickness was also strongly correlated across sampling sites (figures 6(b)–(c), S6). This supports previous studies showing that icing events tend to occur across large spatial scales (Bartsch *et al* 2010, Hansen *et al* 2014, Forbes *et al* 2016).

The positive interaction effect of rain and accumulated snowfall on basal ice likely relates to the complex thermodynamic process of latent heat exchange as rain percolates through the snowpack (Woo *et al* 1982, Marsh and Woo 1984, Westermann *et al* 2011). For low amounts of rain falling on top of a deep snowpack, water may fill in the pore space between the snow grains and freeze, or may flow laterally through subsurface layers (Marsh and Woo 1984, Conway and Raymond 1993), thus forming ice layers within the snowpack rather than on the ground surface (supplementary material 7). In contrast, substantial quantities of rainfall during a warm spell will likely percolate through the entire snowpack, as it becomes saturated (Conway and Raymond 1993, Putkonen and Roe 2003, Westermann *et al* 2011). Furthermore, latent heat exchange between rain and snow may increase the cumulative water runoff (Würzer *et al* 2016), thus increasing the formation of basal ice as melted snow and rainwater freezes on the frozen ground.

Winter rain may occur at near-surface temperatures below 0 °C (i.e. 'freezing rain') due to vertical isothermal gradients in the atmosphere with melting layers at higher altitudes and sub-freezing layers towards the ground (Roberts and Stewart 2008). Particularly in coastal regions such as Ny-Ålesund, warmer moist air from the sea may be transported to higher atmospheric layers above land. However, most heavy rain events occur during extreme warm spells coupled with increased wind and air moisture (Hansen *et al* 2014), which boost turbulent fluxes and snowmelt. Therefore, our winter rain variable based on a 1 °C threshold is likely to capture the combined effect of rain and increased temperature on basal ice. The western and southern coastal regions of Spitsbergen generally experience more rainfall (Van Pelt *et al* 2016), and thus heavier basal ice formation, compared to the inner fjord areas of Svalbard. Furthermore, on a more local scale, the positive effect of rainfall amount on basal ice thickness decreased at higher elevations (table 1), because winter precipitation is more likely to fall as snow due to lower ambient temperature at higher altitudes (see also Van Pelt *et al* 2016). Such an effect has also been proposed as a main explanation for why reindeer tend to climb up steep mountain slopes to forage when pastures at lower elevations are covered by ice (Hansen *et al* 2010).

Our models suggest that heavy rainfall that occurs early in winter is less likely to result in basal ice, as little snow has accumulated early in the season. Furthermore, the effect of winter rain on basal ice depends not only on snow cover, but also on other snowpack properties, such as initial liquid water content (Würzer *et al* 2016), linked with variation in air and ground temperatures as well as past icing events. Indeed, increased water run-off and drainage, rather than ice development, would be expected when ground temperatures are close to or above zero and/or air temperatures are not sufficiently low following warm spells. We should therefore expect more complex, non-linear relationships—especially under future winter climate scenarios (Bintanja and Selten 2014, Moore 2016, Bintanja and Andry 2017)—than those explored here.

While recent winters in Svalbard have become increasingly icy (figure 7), this has mainly been evident through a reduction in the frequency of ice-free winters, rather than increased average ice thickness. With continuously warmer and wetter winters, particularly for the early snow season (López-Moreno *et al* 2016, Bintanja and Andry 2017), and increased permafrost temperatures (Etzelmüller *et al* 2011), rapidly warming sites like Svalbard may soon pass a tipping point where extreme winter rainfall actually results in less basal ice. Nevertheless, the increased frequency in ROS events and the coupled increase in basal ice, leading to a recent climate-cryosphere regime shift, are strong indicators of ongoing and near-future changes in high-arctic terrestrial environments, with potentially wide ecological and socio-economic implications.

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with logistics, and numerous people for digging snow pits.

ORCID iDs

Bart Peeters https://orcid.org/0000-0002-2341-1035
Leif Egil Loe https://orcid.org/0000-0003-4804-2253
Ketil Isaksen https://orcid.org/0000-0003-2356-5330
Vebjørn Veiberg https://orcid.org/0000-0003-1037-5183
Audun Stien https://orcid.org/0000-0001-8046-7337
Jack Kohler https://orcid.org/0000-0003-1963-054X
Jean-Charles Gallet https://orcid.org/0000-0002-6153-1361
Brage Bremset Hansen https://orcid.org/0000-0001-8763-4361

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SUPPLEMENTARY MATERIAL

Spatiotemporal patterns of rain-on-snow and basal ice in high Arctic Svalbard: detection of a climate-cryosphere regime shift

Bart Peeters*, Åshild Ønvik Pedersen, Leif Egil Loe, Ketil Isaksen, Vebjørn Veiberg, Audun Stien, Jack Kohler, Jean-Charles Gallet, Ronny Aanes, Brage Bremset Hansen

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1. Data overview

Data collection

In Central Spitsbergen, sampling was conducted annually at the same sites (n = 128), which were spatially structured following a hierarchical block design across eight different locations (figure 2(c), table S1.1). At each location, sample plots covered two different vegetation types (ridge and sub-ridge) approximately 5 m apart, replicated at 50 m and 500 m distance, as well as two elevations covering the valley bottom and flat hilltops (mean = 112 and 203 m above sea level (a.s.l.), respectively), i.e. 2 x 2 x 2 x 2 = 16 plots (see Loe et al., 2016).

On the NW coast, data collection from 2013-2017 followed a similar hierarchical design as in Central Spitsbergen with n = 16 and 24 plots at the southern and northern side of Brøggerhalvøya, respectively, covering three elevations: valley bottom, flat hilltop, and mountain summit (mean = 34, 179 and 444 m a.s.l., respectively). From 2005-2012 (except 2009), sampling was conducted at fixed sites in a randomly placed grid system covering vegetated terrain < 200 m a.s.l. in Brøggerhalvøya (n = 14-28 plots), Sarsøyra (n = 22-33) and Kaffiøyra (n = 13-18) (figure 2(b); Hansen et al., 2011). In addition, as part of another study (see Kohler and Aanes, 2004), cryosphere data was collected in Brøggerhalvøya (total n = 1,031 over the years 2000, 2002-2007, 2010, 2012-2015) along transect lines with sampling locations varying among years. For simplicity, sampling sites in Brøggerhalvøya were grouped in three main locations: the flat, rocky shore at Kvadehuken in North-West Brøggerhalvøya, and the coastlines of North and South Brøggerhalvøya. Thus, sampling sites were grouped into thirteen locations: eight locations in Central Spitsbergen following the hierarchical sampling design, and five locations on the NW coast, i.e. Sarsøyra, Kaffiøyra and three locations on Brøggerhalvøya (table S1.1).

Table S1.1: Number of sample plots for snow and basal ice measurements (April/early May) per year and location.

Study Area	Area	Location	Latitude	Longitude	2000	2002	2003	2004	2005	2006	2007	2008	2010	2011	2012	2013	2014	2015	2016	2017
NW coast	Brøggerhalvøya	Kvadehuken	78.95 N	11.45 E	19	13	21	16	13*	22*	15*	-	21*	4	59*	94*	13*	98*	-	-
		North Brøgger	78.94 N	11.78 E	21	10	23	11	14*	64*	14*	-	28*	5	61*	96*	32*	118*	22	20
		South Brøgger	78.88 N	11.60 E	16	14	18	23	14*	10	18*	-	34*	5	44*	71*	25*	79*	16	16
	Sarsøyra	Sarsøyra	78.75 N	11.70 E	-	-	-	-	33	22	22	22	22	22	22	-	-	-	-	-
	Kaffiøyra	Kaffiøyra	78.64 N	11.95 E	-	-	-	-	18	18	18	16	15	13	15	-	-	-	-	-
Central Spitsbergen	Colesdalen	Colesbay	78.11 N	15.06 E	-	-	-	-	-	-	-	-	16	16	16	16	16	16	16	16
		Fardalen-Bødalen	78.10 N	15.34 E	-	-	-	-	-	-	-	-	16	-	16	16	16	16	16	16
		Medalen	78.05 N	15.46 E	-	-	-	-	-	-	-	-	16	16	16	16	16	16	16	15
	Semmeldalen	Istjørndalen	78.02 N	15.23 E	-	-	-	-	-	-	-	-	16	-	-	16	16	16	16	16
		Semmelbu	78.00 N	15.36 E	-	-	-	-	-	-	-	-	16	-	15	16	16	16	16	16
		Semmeldalen	77.96 N	15.44 E	-	-	-	-	-	-	-	-	16	-	16	16	16	14	16	8
	Reindalen	Gangdalen	77.99 N	15.78 E	-	-	-	-	-	-	-	-	16	-	16	16	16	16	16	16
		North Reindalen	77.96 N	15.64 E	-	-	-	-	-	-	-	-	16	16	16	16	16	16	16	16

* Sample size is a combination of snow pits randomly placed along transect lines, and annually repeated snow pits at fixed points from either a randomly placed grid (2005-2007, 2010, and 2012) or the hierarchical block design (2013-2015).

Table S1.2: Information on meteorological stations with the period (years) for which data on both daily average temperature and total precipitation were available. Altitude is given in meters above sea level.

Meteorological station	Period	Altitude	Latitude	Longitude	Source	URL
Ny-Ålesund [a]	1969-2017	8 m	78.92 N	11.93 E	Norwegian Meteorological Institute	eklima.met.no
Svalbard Airport [a, b]	1957-2017	28 m	78.25 N	15.50 E	Norwegian Meteorological Institute	eklima.met.no
Hopen	1945-2017	6 m	76.51 N	25.01 E	Norwegian Meteorological Institute	eklima.met.no
Isfjord Radio	1946-1976; 2015-2017	7 m	78.06 N	13.62 E	Norwegian Meteorological Institute	eklima.met.no
Sveagruva	1978-2001	9 m	77.90 N	16.72 E	Norwegian Meteorological Institute	eklima.met.no
Barentsburg	1973-1992; 2003-2017	40 m	78.06 N	14.21 E	Tutiempo Network, S.L.	https://en.tutiempo.net/climate/ws-201070.html
Hornsund	1979-2016	10 m	77.00 N	15.54 E	Institute of Geophysics, Polish Academy of Sciences	–

a - Meteorological stations used for the basal ice analyses at the NW coast (Ny-Ålesund) and Central Spitsbergen (Svalbard Airport) study areas; b - the Svalbard Airport composite series (1957-2017) comprises data from the nearby meteorological station in Longyearbyen (1957-1975) and at Svalbard Airport (1975-2017), and is considered to be homogenous (collectively referred to as Svalbard Airport) (Nordli et al., 2014).

2. Details on the data analysis

Regression analyses

We compared annual basal ice occurrence (presence/absence, where presence ≥ 0.5 cm basal ice) between the study areas for the period 2010-2017 by using a generalized linear model (GLM; binomial distribution and logit link function) with the categorical variables Study Area and Year, and their interaction, as predictor variables. Similarly, we compared annual basal ice thickness (cm, log-transformed after adding one to avoid log of zero) between the study areas using an ANOVA with the same predictors.

We used a multiple linear regression model (LM) to analyze how average snow depth measured in late winter (April/early May) for the NW coast (n = 16 years) and Central Spitsbergen (n = 8 years) is correlated with average basal ice thickness. Here, we included average observed basal ice thickness and Study Area as predictor variables, also accounting for cumulative snowfall (November-March).

To analyze the effects of climate and topography on the occurrence of basal ice, we used generalized linear mixed models (GLMM) with binomial distribution (presence/absence) and logit link function. For the analysis of basal ice thickness, we used linear mixed models (LMM) with Gaussian distribution. Mixed-effects models were implemented using the *lme4* package (Bates et al., 2015) in R version 3.3.2 (R Core Team, 2016). Since the ice data covered only 16 years, we avoided over-parameterization by restricting the number of climate parameters (including intercept) to be estimated by the model to four. The fixed climate effects considered in the model were either Rain, Snow_P and their interaction, or Rain, Heat sum and their interaction. Elevation (m a.s.l.) and Slope (degrees) at the plot-level, derived from a Digital Elevation Model with a 20 m resolution (http://geodata.npolar.no), were also included as fixed effects to estimate topographic effects on basal ice. Since precipitation is more likely to fall as snow at higher altitude (van Pelt et al., 2016), we also considered a two-way

interaction between Rain and Elevation. In both models, we included the following variables as random effects on the intercept: Year (n = 16), to account for dependency of observations taken within the same year; Location (n = 13; table S1.1), to account for spatial autocorrelation and different sampling design among areas; and Plot ID (n = 1,282), to account for dependency among the observations in the fixed plots. Basal ice thickness, Rain and Snow_P were log-transformed (after adding one to avoid log of zero) in the analyses. Covariates were standardized in the models for comparison. We performed model selection based on Akaike's Information Criterion (AIC; Burnham and Anderson, 2002; supplementary material 4). For the LMM of basal ice thickness, model selection was performed on models fitted using maximum likelihood, while the parameter estimates for the selected models were obtained after refitting the models using restricted maximum likelihood (REML; Verbeke and Molenberghs, 2000). We also calculated estimates of R^2 following Nakagawa and Schielzeth (2013) and performed cross-validation of the models by excluding one year at a time (i.e., leave-one-out cross-validation) to evaluate robustness of parameter estimates and model predictions (supplementary material 5).

Spatial correlation

To analyze patterns of spatial correlation of annual fluctuations in winter rain and basal ice, we used a nonparametric covariance function that uses smoothing splines to analyze spatial covariance as a function of distance (Bjørnstad and Falck, 2001) implemented in the R-package *ncf* (Bjørnstad, 2016). This method estimates local and regional correlation based on pairwise correlations and distances among sample plots (or meteorological stations for winter rain). We set a criterion of at least five years of overlapping data within the available time-series to calculate pairwise correlations. This left us with 19 pairwise correlations of winter rain time-series from seven different meteorological stations covering distances of 14 - 410 km. For basal

ice, spatial correlation was first analyzed separately for the two study areas. For Central Spitsbergen, we obtained 8,035 pairwise correlations from 128 plots with distances ranging up to 22 km. For the NW coast, only data of fixed plots (i.e. following the hierarchical or random grid design) was used, leaving us with 1,676 pairwise correlations from 82 plots with distances up to 45 km (covering the period 2005-2017, except 2009). Thereafter, we combined data from both study areas (for the period 2010-2017) to analyze spatial correlation in basal ice up to 142 km in distance between sampling plots. To investigate the contribution of rain to spatial correlation in basal ice, we fitted log-linear models of basal ice thickness with Rain as a predictor for every plot (2010-2017), using weather data from Svalbard Airport and Ny-Ålesund for Central Spitsbergen and NW coast, respectively. We then analyzed spatial correlation in annual fluctuations of the residuals from these models. The maximum degrees of freedom for the smoothing spline was set to three and confidence intervals around the nonparametric curve were calculated by bootstrapping the analysis using 100 and 1,000 iterations for spatial correlation in basal ice and winter rain, respectively (Bjørnstad and Falck, 2001).

Regime shifts

Basal ice occurrence and thickness were estimated using historical weather data (since 1957 and 1969 for Svalbard Airport and Ny-Ålesund, respectively) after refitting the selected mixed-effects models using unstandardized covariates. For years when no rain events occurred, Snow_P was equivalent to the total amount of snowfall (November-March). We then tested for regime shifts (i.e. inter-decadal fluctuations in average climatic levels; Overland et al., 2006) in winter rain and modelled basal ice using the Binary Segmentation method in the *cpt.mean* function implemented in the R-package *changepoint* (Killick et al., 2016). Minimum segment

length was set to five years and the maximum number of change points was restricted based on the breakpoint in the curve of the change points' penalty values.

3. Snow depth – basal ice: regression parameters

Table S3: Parameter estimates (β) with standard errors (SE) from the linear regression model of average snow depth (cm; measured in April/early May) in relation to basal ice thickness (cm), study area (as a categorical variable) and cumulative snowfall (mm: November-March), which was standardized within each study area. The intercept is given for the NW coast study area.

Parameter	β	SE	*P*-value
Intercept (NW coast)	58.50	6.83	< 0.001
Study area (Central Spitsbergen)	-20.30	7.36	0.012
Basal ice thickness	-2.41	0.87	0.012
Snowfall	3.70	3.07	0.242

4. Model selection

Model selection for the analysis of basal ice thickness resulted in only one top-ranked model ($\Delta AIC > 2$ for all other models; table S4.1), whereas five candidate models were selected for the analysis of basal ice occurrence (table S4.2(a)). These models included either the climatic variables Rain in interaction with Snow_P, or Rain with an additive effect of Heat sum. However, when excluding data from 2017 from the analysis, models including an additive effect of Snow_P outperformed models including Heat sum (table S4.2(b)). Therefore, and because the interaction between Rain and Snow_P was also included in the selected model for basal ice thickness, historical basal ice occurrence was modelled using the estimates from the top ranked model based on the full data set (table S4.2(a); table 1 in the main text).

Table S4.1: Model selection based on Akaike's Information criterion (AIC) for the fixed effects on basal ice thickness (LMM), showing the top ten candidate models. All models included Year, Location and Plot ID as random effects on the intercept.

Model rank	Elevation	Slope	Rain	Snow_P	Heat sum	Rain : Elevation	Rain : Snow_P	Rain : Heat sum	*AIC*	*ΔAIC*	Log Likelihood
1	x	x	x	x		x	x		5583.00	0.00	-2780.50
2	x	x	x		x	x		x	5588.95	5.95	-2783.48
3	x	x	x		x	x			5598.05	15.05	-2789.03
4	x	x	x			x			5604.22	21.22	-2793.11
5	x	x	x	x		x			5605.95	22.95	-2792.98
6	x		x	x		x	x		5615.66	32.66	-2797.83
7	x	x	x	x			x		5621.86	38.86	-2800.93
8	x		x		x	x		x	5623.73	40.73	-2801.86
9	x		x		x	x			5632.88	49.88	-2807.44
10	x		x			x			5639.71	56.71	-2811.86

Table S4.2: Model selection based on Akaike's Information criterion (AIC) for the fixed effects on basal ice occurrence (binomial GLMM), showing the top ten candidate models for (a) the full data set, and (b) time-series excluding winter 2016/2017. All models included Year, Location and Plot ID as random effects on the intercept.

Model rank	Elevation	Slope	Rain	Snow_P	Heat sum	Rain : Elevation	Rain : Snow_P	Rain : Heat sum	*AIC*	*ΔAIC*	Log Likelihood
(a) full data set											
1	x	x	x	x			x		1953.10	0.00	-967.55
2	x	x	x	x		x	x		1953.70	0.60	-966.85
3	x	x	x		x	x			1954.69	1.59	-968.34
4	x	x	x		x				1954.96	1.86	-969.48
5	x		x	x			x		1954.96	1.86	-969.48
6	x		x	x		x	x		1955.67	2.57	-968.84
7	x		x		x	x			1956.09	2.99	-970.04
8	x		x		x				1956.26	3.16	-971.13
9	x	x	x		x	x		x	1956.65	3.55	-968.33
10	x	x	x	x		x			1956.80	3.70	-969.40
(b) excluding winter 2016/2017											
1	x	x	x	x		x			1736.62	0.00	-859.31
2	x		x	x		x			1738.03	1.41	-861.01
3	x	x	x	x		x	x		1738.62	2.00	-859.31
4	x		x	x		x	x		1740.01	3.39	-861.01
5	x	x	x	x					1740.63	4.01	-862.31
6	x		x	x					1741.91	5.29	-863.96
7	x	x	x	x			x		1742.19	5.57	-862.10
8	x		x	x			x		1743.35	6.73	-863.67
9	x	x	x			x			1744.76	8.14	-864.38
10	x		x			x			1746.15	9.53	-866.08

5. Cross-validation

We checked whether the parameter estimates for basal ice occurrence and thickness were sensitive to observed weather variables in certain years. This could indicate how, for example, a year with a very early rain event and hence low accumulated snowfall (Snow_P) can influence the overall interpretation of the results. Therefore, we performed cross-validation by excluding one year at a time from the analysis (i.e., leave-one-out cross-validation) to detect systematic deviations in parameter estimates. Confidence intervals of fixed effect estimates were approximated using Wald's method implemented in the *confint* function in the R-package *lme4* (Bates et al., 2015), which is computationally much faster than parametric bootstrapping. We also predicted basal ice occurrence/thickness for the year that was left out, and compared it with the observed mean and predicted response based on the full model.

Overall, cross-validation revealed few systematic deviations in parameter estimates and predictions among years (figures S5.1-4). Average observed basal ice thickness was strongly correlated (Pearson's r = 0.91) with predictions based on the full data set, and with cross-validated predictions (i.e. when basal ice was predicted for each year based on a model where this year was excluded; r = 0.84). Similarly, the correlation between average observed and predicted basal ice occurrence was 0.93 when modelling the full data set and 0.87 when based on cross-validated predictions. This indicates that our models were highly robust.

When excluding 2012 from the model for basal ice thickness, the interaction between rain and Snow_P and additive effect of Snow_P became considerably stronger (figure S5.1). This year was characterized by a record mid-winter warm spell and extreme rain event leading to the strongest observed basal ice occurrence and thickness in both study sites (figure 3 in main text; Hansen et al., 2014). However, the difference in predicted basal ice thickness with and without 2012 was small (figure S5.2). For the analysis of basal ice occurrence, cross-validation indicated that the interaction between rain and Snow_P was no longer significant

when excluding data from 2017 (figures S5.3-4). This year was characterized by very low Snow_P due to an early major rain event, and a very high cumulative heat sum (the mildest winter recorded at Svalbard Airport in that study period; figure 3 in main text). However, the prediction of basal ice occurrence was strongly overestimated for Svalbard Airport 2017 when this year was not included in the model (figure S5.4(b)). In addition, when excluding this year, the interaction effect between rain and Snow_P on basal ice occurrence became less important in the model selection (table S5.1). Therefore, while the interaction of rain with snow cover seems an overall important determinant for basal ice thickness, snow and rain have primarily additive effects on basal ice occurrence.

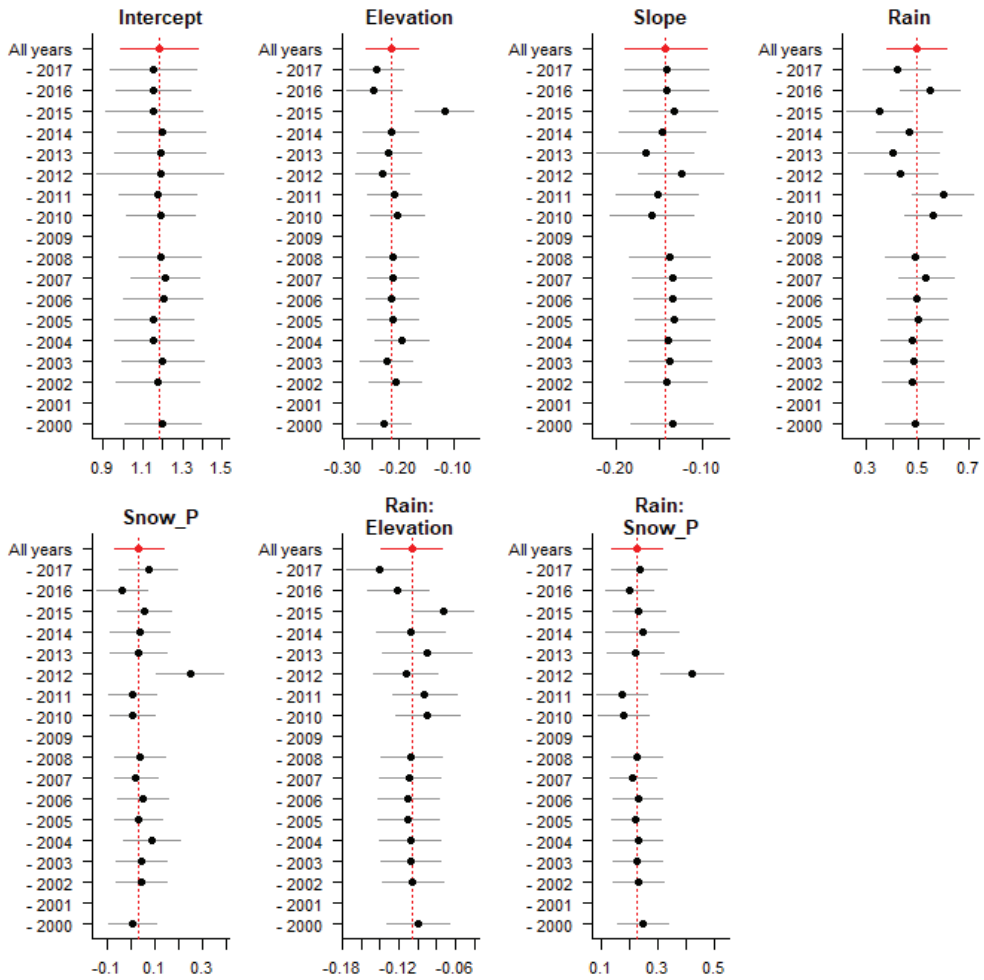

Figure S5.1: Cross-validation of basal ice thickness showing parameter estimates of fixed effect covariates when excluding one year at a time (indicated on the y-axis). Horizontal lines show 95% CIs. Estimates are shown for standardized variables. Red symbols indicate estimates of the model including all years.

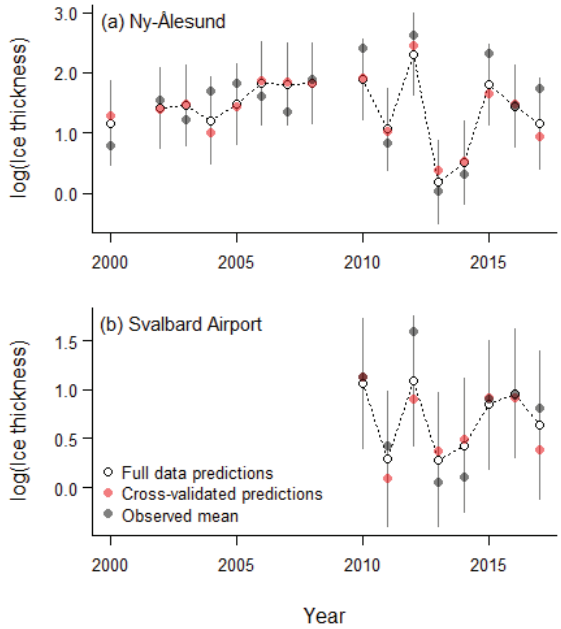

Figure S5.2: Observed and predicted (i.e. modelled) basal ice thickness (natural logarithmic scale) for meteorological stations in (a) Ny-Ålesund, NW coast, and at (b) Svalbard Airport, Central Spitsbergen. Red dots indicate predicted mean basal ice thickness for a given year based on a model where this year was excluded. Open dots and vertical lines indicate predicted values with 95% prediction intervals based on the top ranked model including all years. Grey dots indicate mean observed basal ice thickness.

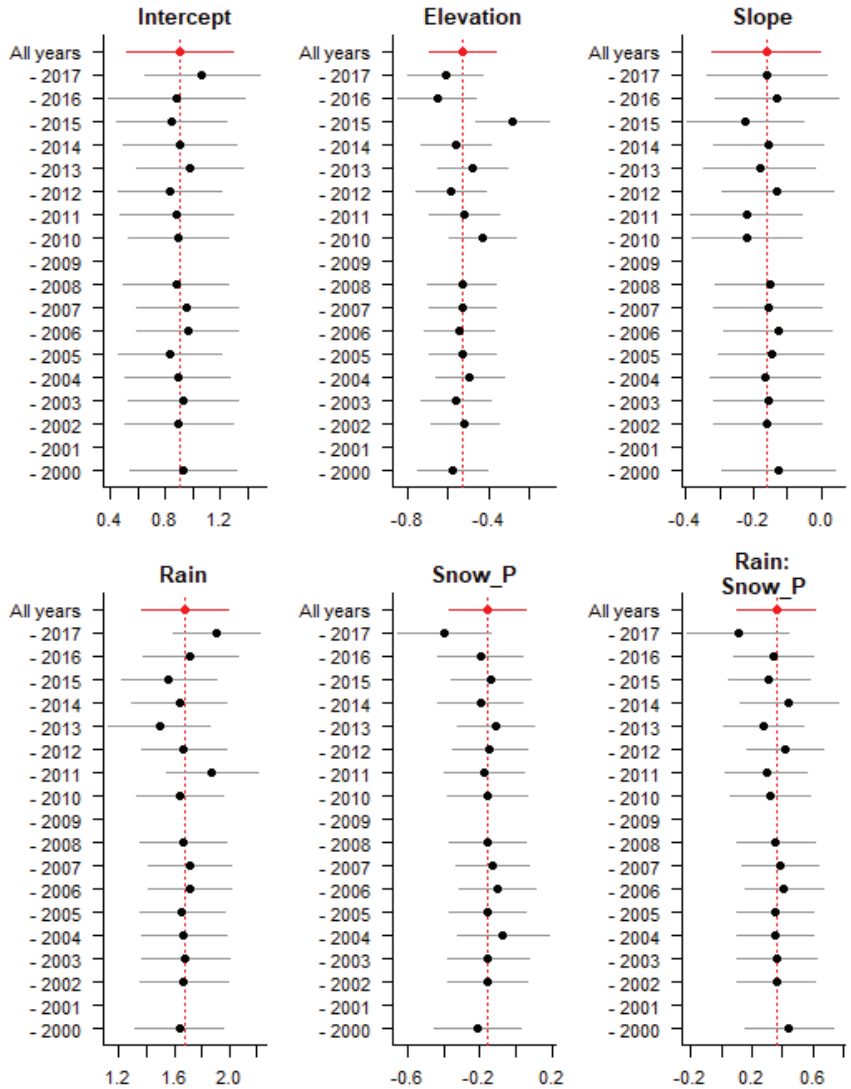

Figure S5.3: Cross-validation of basal ice occurrence showing parameter estimates of fixed effect covariates when excluding one year at a time (indicated on the y-axis). Horizontal lines show 95% CIs. Estimates are shown for standardized variables. Red symbols indicate estimates of the model including all years.

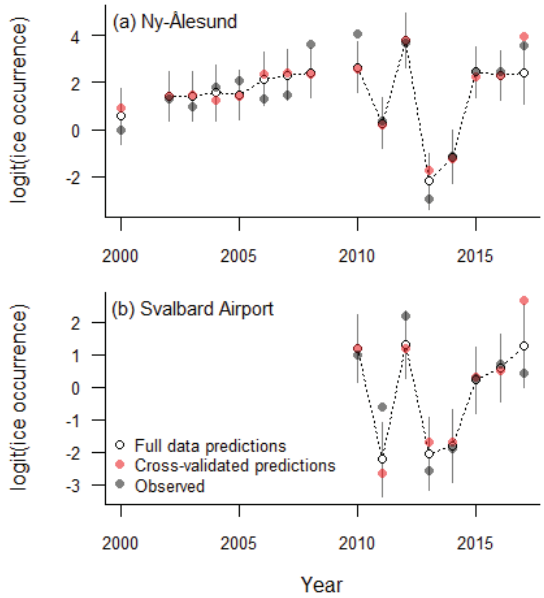

Figure S5.4: Observed and predicted (i.e. modelled) basal ice occurrence (on logit scale) for the meteorological stations in (a) Ny-Ålesund, NW coast, and at (b) Svalbard Airport, Central Spitsbergen. Red dots indicate predicted mean basal ice occurrence for a given year based on a model where this year was excluded. Open dots and vertical lines indicate predicted values with 95% prediction intervals based on the top ranked model including all years. Grey dots indicate mean observed basal ice occurrence.

6. Spatial correlation: total study area

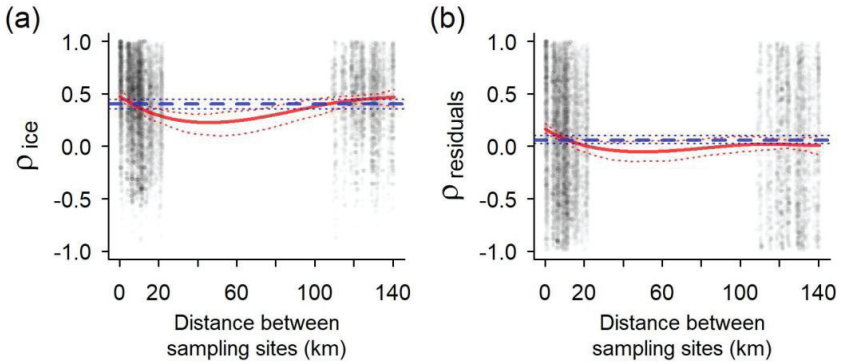

Figure S6: Spatial correlation across the total study area in annual fluctuations of (a) basal ice thickness and (b) residuals in basal ice thickness after accounting for the effect of winter rain. Dots indicate pairwise correlations between sampling sites. The dashed blue line shows the average spatial, i.e. "regional", correlation, while the solid red line shows the nonparametric covariance as a function of distance, both with 95% CI (dotted lines).

7. Within-snowpack ice thickness

Methods

During fieldwork in April/early May, the total thickness of ice layers within the snowpack was measured in Central Spitsbergen (*n* = 128; 2010-2017) and on the NW coast (*n* = 251 unique sites; 2005-2017, except 2009). Here, we provide an explorative analysis to support our interpretation of how within-snowpack ice formation varies with snow depth and the amount of winter rain. We ran a linear mixed model (LMM) for total within-snowpack ice thickness (cm; log-transformed after adding one unit to avoid log of zero). Similar to the analysis of basal ice occurrence and thickness, we included Year, Location and Plot ID as random effects on the intercept. Elevation and Slope were included to correct for topographic effects, and Rain and Snow_P (i.e., cumulative snowfall from 1 November until the peak rain event) as climatic variables. We also included two-way interactions between Rain and Snow_P, and Rain and Elevation. Also, a quadratic effect of Rain was included since rain is expected to percolate through the entire snowpack when substantial quantities of rain fall (Putkonen and Roe, 2003), thus creating more ice at the snow/ground interface than within the snowpack. Since the ice layer data only includes twelve years of data, the model is over-parametrized (four annual climatic variables) and estimates must therefore be interpreted with caution. However, this supplementary analysis is included for explorative reasons and we, therefore, chose to report estimates of the global model rather than performing full model selection.

Results and discussion

Firstly, total within-snowpack ice thickness, observed in April/early May, increased strongly with cumulative snowfall until the peak rain event (Snow_P), as within snowpack ice formation is inherently dependent on the snowpack thickness (table S7). However, this effect of Snow_P decreased with increasing amount of rain, and there was a strong negative quadratic effect of

Rain on within-snowpack ice thickness (table S7, figure S7). These observed patterns likely reflect the process of rain percolating through the entire snowpack during extreme rain events (Putkonen and Roe, 2003, Würzer et al., 2016), which is coherent with the observed positive effect of Rain and the positive interaction between Rain and Snow_P on basal ice thickness and occurrence (see table 1 and figure 5 in main paper). The positive interaction effect between Elevation and Rain (table S7) may again indicate that, during a warm spell with air temperatures above freezing at lower elevations, precipitation is more likely to fall as snow or wet snow at higher elevations.

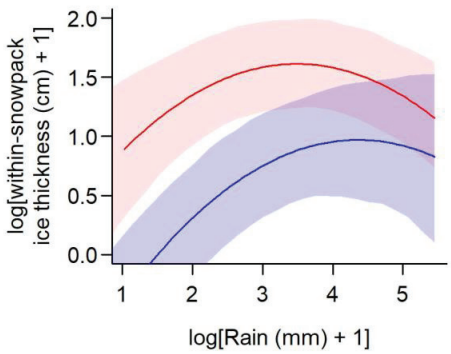

Figure S7: Total within-snowpack ice thickness (cm, on log scale) as a function of winter rain (mm, log scale). Red and blue lines are for, respectively, high and low (mean ± 1SD) accumulated snowfall until the peak rain event (Snow_P), with 95% CI indicated by shaded areas.

Table S7: Parameter estimates (β) and standard errors (SE) of standardized covariates from the mixed-effects model on total within-snowpack ice thickness. Rain, Snow_P (i.e. accumulated snowfall until the peak rain event) and within-snowpack ice thickness were log-transformed after adding one unit to avoid log of zero. Standard deviations (SD) and number of groups (*n*) are given for the random effects on the intercept. Marginal and conditional R^2 indicate variance explained by the fixed effects and by both fixed and random effects, respectively (Nakagawa and Schielzeth, 2013).

Fixed effects	$\beta \pm SE$	*P*-value	**Random effects**	SD	*n*
Intercept	1.308 ± 0.171	<0.001	Year	0.558	12
Elevation	-0.030 ± 0.036	0.400	Location	0.108	13
Slope	-0.071 ± 0.035	0.044	Plot ID	0.310	251
Rain	0.129 ± 0.082	0.117			
Snow_P	0.326 ± 0.074	<0.001			
$Rain^2$	-0.224 ± 0.044	<0.001			
Rain : Snow_P	-0.126 ± 0.078	0.109		Marginal	Conditional
Rain : Elevation	0.083 ± 0.020	<0.001	R^2	0.204	0.638

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Paper II

Spatial heterogeneity in climate change effects decouples the long-term dynamics of wild reindeer populations in the high Arctic

by

Brage B. Hansen[1]*, Åshild Ø. Pedersen[2], Bart Peeters[1], Mathilde Le Moullec[1], Steve D. Albon[3], Ivar Herfindal[1], Bernt-Erik Sæther[1], Vidar Grøtan[1], Ronny Aanes[1,2]

Affiliations:

[1]Centre for Biodiversity Dynamics (CBD), Dept. of Biology, Norwegian University of Science and Technology (NTNU), N-7491 Trondheim, Norway

[2]Norwegian Polar Institute (NPI), Fram Centre, N-9296 Tromsø, Norway

[3]James Hutton Institute, Aberdeen, UK

*Correspondence: Brage Bremset Hansen (email: brage.b.hansen@ntnu.no)

Abstract

The 'Moran effect' predicts that dynamics of populations of a species are synchronized over similar distances as their environmental drivers. Strong population synchrony reduces species viability, but spatial heterogeneity in density dependence, the environment, or its ecological responses may decouple dynamics in space, preventing extinctions. How such heterogeneity buffers impacts of global change on large-scale population dynamics is not well studied. Here, we show that spatially auto-correlated fluctuations in annual winter weather synchronize wild reindeer dynamics across high-Arctic Svalbard, while, paradoxically, spatial variation in winter climate trends contribute to diverging local population trajectories. Warmer summers have improved the carrying capacity and apparently led to increased total reindeer abundance. However, fluctuations in population size seem mainly driven by negative effects of stochastic winter rain-on-snow (ROS) events causing icing, with strongest effects at high densities. Count data for ten reindeer populations 8-324 km apart suggested that density-dependent ROS effects contributed to synchrony in population dynamics, mainly through spatially autocorrelated mortality. By comparing a coastal and 'continental' reindeer population over four decades, we show that locally contrasting abundance trends can arise from spatial differences in climate change and responses to weather. The coastal population experienced a larger increase in ROS, and a stronger density-dependent ROS effect on population growth rates, than the continental population. In contrast, the latter experienced stronger summer warming and showed the strongest positive response to summer temperatures. Accordingly, contrasting net effects of a recent climate regime shift – with increased ROS and harsher winters, yet higher summer temperatures and improved carrying capacity – led to negative and positive abundance trends in the coastal and continental population, respectively. Thus, synchronized population fluctuations by climatic drivers can be buffered by spatial heterogeneity in the same drivers, as well as in the ecological responses, averaging out climate change effects at larger spatial scales.

Introduction

Fluctuations in the abundance of wildlife populations are often strongly influenced by stochastic weather effects and, in the longer run, climate (Sæther, 1997). Because climate and weather patterns are typically auto-correlated in space (Koenig 1999), Moran (1953) suggested that fluctuations of spatially distinct populations should be synchronized similarly if their dynamics are driven by these weather patterns, and when assuming equal (loglinear) density dependence (i.e. the 'Moran effect', Royama, 1992). Spatial population synchrony has indeed been observed across large areas and in a wide range of taxa (e.g. Bjørnstad *et al.*, 1999, Koenig, 1999, Liebhold *et al.*, 2004, Sæther *et al.*, 2007, Walter *et al.*, 2017), yet it has often proved difficult to disentangle the synchronizing role of weather from those of dispersal and trophic interaction effects (Engen *et al.*, 2002, Engen *et al.*, 2005, Ims & Andreassen, 2000, Lande *et al.*, 1999, Liebhold *et al.*, 2004, Moran, 1953, Royama, 1992, Ydenberg, 1987). Nevertheless, several studies have now demonstrated that the Moran effect is often the main cause of spatial co-fluctuations in population abundances (e.g. in feral sheep *Ovies aries* (Grenfell et al. 1998); roe deer *Capreolus capreolus* (Grøtan *et al.*, 2005); caribou and reindeer *Rangifer tarandus* (Post & Forchhammer, 2004); passerine birds (Sæther *et al.*, 2007); plants (i.e. an analogue to the Moran effect; Defriez & Reuman, 2017, Koenig & Knops, 2013, Koenig & Knops, 1998); marine plankton (Defriez *et al.*, 2016)).

While fluctuations in asynchronous local populations will be cancelled out in large-scale population sizes, a high level of population synchrony may lead to mass extinctions, for instance under extreme events (Heino *et al.*, 1997). Thus, strong, weather-driven population synchrony is expected to increase extinction risk at the 'meta-population' or species level (Engen *et al.*, 2002, Heino *et al.*, 1997, Ranta *et al.*, 1995) under widespread environmental change, such as global warming (Post & Forchhammer, 2002). However, the observed strength and spatial scale of synchrony in population dynamics is usually much lower than that

of climate itself (Stenseth, 1999, Sæther *et al.*, 2003, Sæther *et al.*, 2007, Walter *et al.*, 2017). A multitude of other drivers, which vary spatially, may also act on population growth rates or the ecological carrying capacity, desynchronizing population dynamics (Engen & Sæther, 2005). Even the extent to which different populations respond to a specific weather driver often varies locally due, for instance, to habitat heterogeneity (Anders & Post, 2006, Engen & Sæther, 2005, Post *et al.*, 2009a, Sæther, 1997). This may lead to uncorrelated dynamics in space that could moderate the effects of common environmental drivers, such as weather and climate, at the level of meta-population or species (Hilborn *et al.*, 2003), thereby enhancing species persistence (Anders & Post, 2006). Accordingly, to understand climate change effects at large spatial scales we should assess how spatial heterogeneity in the environment or in the ecological responses averages out the effects of shared climate forcing acting across populations (Post *et al.*, 2009b, Sheppard *et al.*, 2016).

The relative contribution of weather fluctuations to animal population dynamics seems to be particularly large in marginal habitats, such as at high latitudes (Ims & Ehrich, 2013), so Arctic tundra food-webs tend to display relatively strong population synchrony within and across species (Hansen *et al.*, 2013, Ims & Fuglei, 2005, Post & Forchhammer, 2002, Post & Forchhammer, 2004). The climate is changing more rapidly in the Arctic than in any other biome on earth, especially during winter (AMAP, 2017, Bintanja & Andry, 2017). As a consequence, the frequency of extreme warm spells and associated heavy rain-on-snow (ROS) events in winter is increasing, causing dramatic changes to the snow-pack characteristics (Hansen *et al.*, 2014, Kohler & Aanes, 2004, Peeters *et al.*, 2019, Putkonen & Roe, 2003) and, hence, the feeding conditions for over-wintering herbivores. Especially in permafrost conditions, heavy ROS percolating through the snow may lead to the formation of basal ice (‘ground-ice’), encapsulating the vegetation. Such ice-locked tundra has potentially ecosystem-wide consequences (Hansen *et al.*, 2013). For instance, icing events can cause over-winter body mass loss, reduced skeleton growth, and reduced survival and fecundity in muskox

(*Ovibos moschatus*) and reindeer (Albon *et al.*, 2017, Berger *et al.*, 2018, Stien *et al.*, 2012). These effects of fluctuations in ROS, which can interact with density-dependent mechanisms (Hansen *et al.*, 2019), may result in large annual fluctuations in animal densities (Forbes *et al.*, 2016, Forchhammer & Boertmann, 1993, Hansen *et al.*, 2011, Hansen *et al.*, 2011, Kohler & Aanes, 2004, Miller & Gunn, 2003). However, such negative influence of warmer and wetter winters may – at least locally – be counteracted by the positive impacts of a shorter winter and a longer and warmer plant growth season (Albon *et al.*, 2017, Tews *et al.*, 2007), causing an increase in ecological carrying capacity due to increased primary production (Van der Wal & Stien, 2014) and 'Arctic greening' (Jia *et al.*, 2003, Vickers *et al.*, 2016).

Disentangling such contrasting climate change effects on population dynamics is difficult, regardless of spatial scale (for a simulation study of caribou, see Tews *et al.*, 2007). Arctic ungulate populations are typically influenced by a variety of other factors, such as hunting, insect harassment, infrastructure development, and predators, and these impacts often vary spatially (Gunn *et al.*, 2009). Poor data quality and discontinuous time-series also characterize many monitored populations. Few long-term, continuous time-series have therefore been available with sufficient spatial replication to investigate spatial population synchrony (but see Post & Forchhammer, 2004, based on harvest records), and the buffering role of spatial heterogeneity, either in the environment or ecological responses. Here, we take advantage of such a rare, spatially replicated dataset, to analyze spatiotemporal patterns of population dynamics in wild Svalbard reindeer (*R. t. platyrhynchus*) in the high Arctic, a hot-spot of climate change. We ask: what is the role of the Moran effect in the large-scale net outcome of recent climate change for this northernmost *Rangifer* sub-species? We assess this by examining (1) local and total population size trends for ten reindeer populations; (2) how annual fluctuations in weather (i.e. ROS), and their pattern of spatial autocorrelation, synchronize reindeer dynamics in space (Moran 1953); and (3) how the effects of this synchronization are moderated by spatial heterogeneity in climate, climate trends (i.e. long-

term changes in weather), and density-dependent climate responses. In particular, we account for local variation in strength of density dependence and how it may interact with ROS effects on fecundity, mortality and population growth rates (Hansen *et al.*, 2019).

Materials and methods

Study system

The climate in Svalbard is mild for the latitude (74-81°N, 10-35 °E), with mean annual, summer (July-August) and winter (November-April) temperatures at Svalbard Airport of -6.7, 5.3 and -13.9 °C, respectively. Conditions are generally oceanic, yet dry (mean annual precipitation = 190 mm), and become increasingly dry with distance from the coastline (Van Pelt *et al.*, 2016). Furthermore, weather patterns differ considerably between western parts, which are strongly influenced by the warm Gulf Stream, and the east, which is more influenced by the Arctic Ocean and sea-ice cover (Johansen *et al.*, 2012, Sakshaug *et al.*, 2009).

The Svalbard tundra is characterized by a simple food web, with few species. The wild Svalbard reindeer is the only mammalian herbivore, besides a small local population of sibling voles *Microtus levis* (Ims & Ehrich, 2013). The reindeer are largely solitary and virtually free from predation, although rare attacks by polar bears (*Ursus maritimus*) on sick or weak reindeer have been observed (Derocher *et al.*, 2000). Thus, direct density dependence and large annual variations in weather conditions – notably the amount of ROS, but also the length and warmth of the summer – shape the reindeer's body condition and vital rates (Albon *et al.*, 2017, Solberg *et al.*, 2001, Stien *et al.*, 2012). This, in turn, causes large fluctuations in population abundances from year to year (Albon *et al.*, 2017, Hansen *et al.*, 2011, Hansen *et al.*, 2013, Kohler & Aanes, 2004, Solberg *et al.*, 2001). There is some evidence of spatial population synchrony (Aanes *et al.*, 2003), most likely explained by spatially auto-correlated fluctuations in weather rather than dispersal, which is strongly restricted by natural barriers

such as open sea, glaciers and steep mountains. Genetic analyses also indicate significant population differentiation across very small distances (Côté *et al.*, 2002), largely confirming the observation that Svalbard reindeer are resident within annual home ranges of only a few km^2 (Tyler & Øritsland, 1989). Overall, individuals do not move between neighboring populations, except under special circumstances, such as following overgrazing or extreme ROS events (Hansen *et al.*, 2010, Loe *et al.*, 2016). Combined with the strong climatic signals observed in vital rates (Albon *et al.*, 2017), the characteristics of this study system provide a rare opportunity to investigate the impacts of climate-induced environmental change on the population dynamics and trends of a high-Arctic ungulate, both locally and at a meta-population scale.

Data

We obtained daily time series of mean temperature and total precipitation data from five manned weather stations 14-410 km apart (Figure 1). Data from Barentsburg were downloaded from Tutiempo Network, S.L. (https://en.tutiempo.net/climate/ws-201070.html), while data from Hornsund were provided by the Institute of Geophysics of the Polish Academy of Sciences. For the three remaining weather stations (i.e. Svalbard Airport, Ny-Ålesund, and Hopen), we downloaded data from the Norwegian Meteorological Institute (http://eklima.met.no).

Reindeer population monitoring data were obtained using multiple census methods across 10 reindeer populations. Total counts of live reindeer, calves, and carcasses (easily visible as patches of white fur in the terrain) were carried out annually by helicopter in early August 1997-2015 across six populations (Figure 1). Five of these six populations are hunted in the fall with a fairly constant annual offtake corresponding to < 5% of the local population size. In addition, total population counts were performed annually on foot in late June/early July 1979-2015 in Adventdalen (Hansen *et al.*, 2013, Tyler *et al.*, 2008) and included the

number of calves and carcasses. Finally, following the re-introduction of 12 reindeer to Ny-Ålesund, Brøggerhalvøya, in 1978 and the subsequent population irruption and spatial expansion southwards (Aanes *et al.*, 2000), three semi-isolated populations in this northwestern area have been monitored by annual total ground counts (including number of calves). Counts were conducted by snowmobile in early spring (i.e. late March-April 1978-2015 on Brøggerhalvøya) and on foot in summer (i.e. July; Brøggerhalvøya 1999-2015; Sarsøyra 2000-2015, except 2011; Kaffiøyra 2002-2015, except 2011-2012) (Hansen *et al.*, 2011, Le Moullec *et al.*, 2017). The two seasonal measures of population size on Brøggerhalvøya were highly correlated ($r = 0.92$, Figure S1). For Brøggerhalvøya, we used (1) the summer count time-series in the analysis of Svalbard-scale population dynamics and patterns of population synchrony (see below), to maximize methodological consistency, and (2) the spring count time-series for the comparison of population dynamics with Adventdalen, to maximize time-series length.

Svalbard-scale reindeer parameters

Based on all ten reindeer populations, we estimated overall annual abundances and vital rates, and their temporal trends. For consistency, and because most population time-series were established in 1997, we restricted the study period to 1997-2015. Note that, because of missing years in some populations, simple averaging or adding of population sizes was not possible. For each population, we obtained annual proxies of ‘fecundity’ by dividing number of calves by total number of reindeer, and ‘mortality’ by dividing number of carcasses by total number of reindeer the previous year (see Peeters *et al.*, 2017). Note that carcass counts are likely to give underestimates of mortality rates, although presumably consistent between years. Annual estimates of the ‘across Svalbard-scale’ fecundity and mortality (i.e. across all populations) were then obtained through linear mixed effects regression models of the local fecundity or mortality estimates (on a logit scale) as a function of year (as a fixed factor) and population

(random intercept effect). These regressions were weighted by the population-specific mean population size (over each time-series) to allow larger populations to contribute more to the across Svalbard proxies than smaller ones. Estimates of across Svalbard-scale proxies of relative abundance ('population size' $N_{Svalbard}$) and, thereby, population growth rates ($R_{Svalbard,t} = \ln(N_{Svalbard,t+1}/N_{Svalbard,t})$), were also obtained using a similar linear mixed effects regression model of local population sizes N.

Estimating the contribution of Svalbard-scale climate to spatial synchrony

We analyzed spatial synchrony in fecundity, mortality and population growth rates R_t between the ten local populations by implementing a nonparametric covariance function, which uses smoothing splines to estimate spatial covariance as a function of distance (Bjørnstad & Falck, 2001). This method estimates spatial synchrony based on pairwise correlations and distances among populations. We set the maximum degrees of freedom for the smoothing spline to four (two for mortality due to low sample size), and confidence intervals around the nonparametric curve were based on bootstrapping with 1000 iterations. We used ≥ five years of data overlap as a criterion to calculate pairwise correlations, and the available population time-series resulted in 45 (8-324 km), 15 (8-64 km), and 45 (8-324 km) pairwise correlations for reindeer fecundity, mortality (data lacking for Brøggerhalvøya, Sarsøyra, Kaffiøyra, Svenskøya; Table S2), and population growth rates, respectively.

ROS and population density are clearly the main drivers of annual fluctuations in vital rates and abundance (Albon *et al.*, 2017, Hansen *et al.*, 2011, Hansen *et al.*, 2013, Hansen *et al.*, 2019, Kohler & Aanes, 2004, Solberg *et al.*, 2001, Stien *et al.*, 2012), and ROS and density effects may also interact (Hansen *et al.*, 2019; see also Coulson *et al.*, 2001). More specifically, the ROS effect diminishes at very low population densities because available ice-free patches per capita will anyways be sufficient, while at high densities, 'all' reindeer will suffer from a multiplicative effect of ROS on resource competition (Hansen *et al.*, 2019). We therefore tested

to what extent density-dependent ROS effects contributed to the synchrony in fecundity, mortality and population growth rates by also estimating the correlations between populations *after* accounting for this climate-density interaction effect, i.e. the correlations in model residuals. ROS_t was calculated as the annual amount of rain in winter ($November_t$ – $April_{t+1}$), i.e. ln(mm precipitation + 1, to avoid log of zero) falling at temperatures ≥1 °C. For each local population we fitted generalized linear regression models of fecundity and mortality (quasi-binomial family, logit link), and linear regression models of population growth rates, as functions of ROS_t in interaction with detrended ln population size. As nearby weather station data were not available for most populations (Figure 1), we used a common 'across Svalbard-scale' ROS_t estimate obtained from a linear mixed effects regression model of ROS_t at the five weather stations as a function of year (as fixed factor), and with weather station as random intercept effect. The residuals from the population-specific models of fecundity, mortality and population growth rates were then analyzed for pairwise correlations and spatial synchrony across the range of distances. The contribution of density-dependent ROS effects to the observed synchrony in fecundity, mortality and population growth was estimated based on the difference in nonparametric bootstrapped replicates of average synchrony (n = 1000) before and after accounting for the density-dependent ROS effect.

Although any (temporal variation in) spatially correlated monitoring efforts could 'artificially' increase the measured synchrony, the different monitoring methods between populations reduce this risk. For the counts performed on the ground, the accuracy seems relatively high (i.e. less biased and more precise; Le Moullec *et al.*, 2017, Tyler *et al.*, 2008). For instance, the correlation between early spring and summer population size on Brøggerhalvøya, counted on snow mobiles and on foot, respectively, was very high (r = 0.92). Likewise, the correlation in population size between our Adventdalen count data and independent counts performed by Tyler and colleagues (2008) in the same valley in 2001-07 was also very high (r = 0.97), indicating high precision of the counts.

In-depth analysis of climate effects on the dynamics of two focal populations

To obtain a more detailed understanding of local population dynamics and trends, and the causes and consequences of spatial heterogeneity, we analyzed the population dynamics of the two longer reindeer abundance time-series from Adventdalen (1979-2015) and Brøggerhalvøya (1978-2015). These two populations are each near a manned weather station (Figure 1), enabling the inclusion of local weather conditions in the analyses. We first looked for linear trends and sudden break points in the mean (i.e. 'regime shifts') weather conditions, by implementing the *binseg* function (with segment length restricted to minimum five years) in the *changepoint* package (Killick *et al.*, 2016) for *R* (R Core Team 2018).

For the 'continental' population in Adventdalen, central Spitsbergen (Figure 1), we fitted a linear regression model of population growth rates against the following local-scale predictors: density N_t, ROS_t, the interaction N_t x ROS_t, annual amount of snow $fall_t$ (in mm, calculated as total precipitation (mm) falling at temperatures <1 °C) (Solberg *et al.*, 2001), mean summer $temperature_t$ (July-August, Hansen *et al.*, 2013), and winter $length_t$ (see also Albon *et al.*, 2017). Winter length was estimated as the number of days between the time when the ten-day running mean of daily temperature in the $fall_t$ fell *below* freezing (0 °C) and stayed below for a minimum of ten consecutive days, and the time in $spring_{t+1}$ when the ten-day running mean of daily temperature was *above* freezing and stayed above for a minimum of ten consecutive days (Le Moullec *et al.*, 2019).

For comparison of climate effects between the two populations, a similar model was then applied to the coastal Brøggerhalvøya population, adding a two-level factor 'period' (irruptive phase and post-irruptive phase, see Results) in the N_t x ROS_t interaction (i.e. a three-way interaction, period x N_t x ROS_t) to account for a possible change in density dependence in this irruptive population from the crash year in 1994 and onwards (Kohler & Aanes, 2004). All analyses were performed in *R* (R Core Team 2018), implementing the packages *lme4* for

mixed-effects models (Bates *et al.*, 2015) and *ncf* for the nonparametric covariance function (Bjørnstad, 2016).

Results

Spatiotemporal patterns in weather and reindeer dynamics across Svalbard

During 1997-2015, data from weather stations across Svalbard showed an overall positive trend in both ROS (Figure 2a,f) and summer temperature (Figure S2). This indicates worsening winter feeding conditions due to more frequent icing (shown through in situ ice measurements, Figure S3a), yet, at the same time, improved food abundance and carrying capacity due to higher plant productivity in the warmer summers (inferred by the Normalized Difference Vegetation Index, NDVI, Figure S3b). Although reindeer population size trajectories (Figure 2d) showed locally contrasting linear trends, varying from negative to positive (Figure 2g), there was evidence of a statistically significant increase over time of the 'across Svalbard-scale' reindeer abundance index (Figure 2g), weighted for local mean population sizes. Fecundity, mortality and population growth rates were all characterized by large annual fluctuations (Figure 2b,c,e), resulting in saw-shaped patterns indicating direct density dependence. For instance, population growth rates R_t were particularly small in 2005, 2007 and 2009 – i.e. years with fairly high levels of ROS at most weather stations, as well as high estimated mortality and low fecundity. Conversely, population growth rates were relatively large in 2006, 2008 and 2010. Thus, at the Svalbard-scale, correlations with annual ROS_t were negative for fecundity (Pearson's $r = -0.63$, $P < 0.01$), positive for mortality ($r = 0.56$, $P < 0.05$), and negative for population growth rates ($r = -0.44$, $P = 0.07$) (Figure 3). Linear regression models accounting for potential density dependence in this ROS effect confirmed the overall presence of direct density dependence but also indicated inconsistent patterns of climate-density interactions across populations (Table S1).

ROS showed a high mean pairwise correlation between weather stations (ρ_{ROS} = 0.62 [95% confidence interval = 0.48, 0.76], and the correlation decreased with distance (Figure S4). Similarly, pairwise correlations between the reindeer populations in annual fecundity (mean pairwise correlation $\rho_{Fecundity}$ = 0.52 [0.39, 0.67]), mortality ($\rho_{Mortality}$ = 0.83 [0.77, 0.89]; note the shorter extent of distances) and population growth rates (ρ_R = 0.23 [0.02, 0.43]) were generally positive and decreased with increasing distance between populations (Figure 4a-c, Table S2). When accounting for only an additive effect of ROS_t in population-specific linear models, the average pairwise population correlations (in residuals) remained similar for mortality (ρ_{resid} = 0.83 [0.76, 0.91]) and population growth rates (ρ_{resid} = 0.21 [0.01, 0.39]), but were lower for fecundity (ρ_{resid} = 0.44 [0.28, 0.62]). However, when accounting for a density-dependent ROS effect (N_t x ROS_t, Table S1), correlations between populations were lower for population growth rates (ρ_{resid} = 0.15 [-0.18, 0.48]) and, in particular, mortality (ρ_{resid} = 0.67 [0.49, 0.88]), while less so for fecundity (ρ_{resid} = 0.47 [0.26, 0.64]) (Figure 4d-f). Thus, based on whether the lower 5% percentile (i.e. an *a priori* expected change, 'one-tailed') of the change in pairwise correlation obtained from bootstrapping was above or below zero (Figure 4g-i), this change in correlation due to the N_t x ROS_t effect was far from 'significant' for fecundity (mean difference = 0.06 [-0.12, 0.26]), significant for mortality (0.44 [0.17, 0.79]), and marginally non-significant for population growth rates (0.12 [-0.02, 0.25]). Note that synchrony models with other weather variables (analyses not presented) or with only density N_t included as covariate caused relatively little or no reduction in average regional synchrony (fecundity: ρ_{resid} = 0.52 [0.31, 0.71]; mortality: ρ_{resid} = 0.73 [0.60, 0.89]; population growth rates: ρ_{resid} = 0.23 [0.01, 0.47]). Thus, we conclude that density-dependent ROS effects were the main detected contributor to the observed synchrony in population dynamics, yet marginally non-significant, and mainly operating through synchronization of mortality.

Causes and consequences of spatial heterogeneity

Can the same climate or weather parameters cause synchronous annual population dynamics while simultaneously causing diverging long-term trends? Population growth rates were indeed positively correlated ($r = 0.46$, Table S2) between our two focal reindeer populations (i.e. Adventdalen ['continental'] and Brøggerhalvøya [coastal], 126 km apart, Figure 1), from which we had both local weather data and long-term, ground-based count data. However, some small yet important differences in climate trends between these two populations have become evident since the 1990s (Figure 5a,b). Firstly, the linear regressions indicated a significant increase in annual amount of ROS (on natural log-scale) during 1978-2015 at the weather station on Brøggerhalvøya (i.e. Ny-Ålesund; $\beta = 0.055$, $t = 2.44$, $P < 0.05$), but not at the station in Adventdalen (i.e. Svalbard Airport; $\beta = 0.030$, $t = 1.63$, $P = 0.11$). A regime shift with overall higher annual ROS since around year 2000 was detected in Ny-Ålesund (Figure 5a), but not at Svalbard Airport (see Peeters *et al.*, 2019 for a longer time-span). Secondly, while linear regression models indicated a summer temperature increase over time for both Ny-Ålesund ($\beta = 0.028$, $t = 3.09$, $P < 0.01$) and Svalbard Airport ($\beta = 0.053$, $t = 4.85$, $P < 0.001$), the slope was twice as steep at the latter station. Thus, a sudden regime shift with elevated summer temperature levels from around 1998 was detected at both weather stations, but in this case the increase was greater at Svalbard Airport (ca. 1.3 °C) than in Ny-Ålesund (ca. 0.9 °C, Figure 5b). We found no evidence for other differences between Adventdalen and Brøggerhalvøya in temporal trends of potential drivers of reindeer population growth (Figure S2), i.e. winter length (equally strong linear decrease in both areas) and total snow fall (no strong trends).

The differences in the relative magnitude of temporal change in ROS and summer temperature between populations contributed to the long-term reindeer population trajectories in these two focal populations. Overall, the effects of local weather variables on population growth rates were broadly similar (i.e. similar signs, but with different strengths) in Adventdalen and on Brøggerhalvøya (Figure 6). Thus, linear regression models (for a cross-

validation procedure, see Figure S5), which were run separately for each population due to the period/irruption factor on Brøggerhalvøya, suggested an overall negative ROS effect on population growth rates. The ROS effect was stronger at high reindeer densities, and, importantly, this interaction effect between ROS and density was stronger on Brøggerhalvøya than in Adventdalen (Figure 6). In contrast, the positive effect of summer temperature was stronger in Adventdalen than on Brøggerhalvøya. Snowfall amount tended to have an overall negative effect, while there was no evidence of an influence of winter length in either population.

As expected from the slightly different effects of local weather on population growth and the local differences in climate trends, we found contrasting abundance trends between the two populations. More specifically, the population size trend was strongly positive in Adventdalen (irrespective of trend starting year; Figure 5d) where the local weather station data indicated no significant increase in ROS (Figure 5a) but a strong regime shift in summer temperatures from the late 1990s (Figure 5b). In contrast, the trend slopes for the post-irruptive Brøggerhalvøya population – which experienced weaker summer warming but stronger ROS increase – tended to be negative when the trend starting year was before ~2001 (Figure 5d). Since around that time, the population size first declined for then to stabilize around relatively low densities (Figure 5c). Accordingly, there was a consistent difference in estimated trends of abundance between the two focal populations (i.e. generally no overlap between confidence intervals and the mean estimate for the other population), irrespective of choice of trend starting year (Figure 5e).

Discussion

This study has demonstrated that, although weather fluctuations tend to synchronize short-term (i.e. annual) dynamics, the longer-term dynamics of wild reindeer populations can be decoupled by spatially heterogeneous climate change effects. Annual fluctuations in amount of ROS during winter contributed to synchronized mortality rates and, thereby, population dynamics across large distances in Svalbard (Figure 4), while paradoxically, the very same environmental driver contributed to opposite trends in local reindeer abundances (Figures 2g, 5d). We document how such diverging population trends can occur due to local variation in both the relative strength of winter versus summer climate change trends (Figure 5) and the density-dependent responses to warming (Figure 6). However, the net outcome of improved carrying capacity versus worsening winter-feeding conditions appears to be a growing total population of Svalbard reindeer (Figure 2d,g), in contrast to the recent patterns of decline observed in some other *Rangifer* populations (Mallory & Boyce, 2017, Vors & Boyce, 2009).

Post and colleagues (2009b) pointed out that spatial environmental heterogeneity and scale-dependent ecological responses are key to understanding and predicting net implications of the various climate change effects reported in Arctic tundra study sites. In caribou and reindeer, some observed population declines have indeed been linked to global environmental change, but the proposed drivers seem to differ locally and include habitat fragmentation (Festa-Bianchet *et al.*, 2011), Arctic 'shrubification' (Fauchald *et al.*, 2017), increased insect harassment (Mallory & Boyce, 2017), and worsening winter-feeding conditions (Forbes *et al.*, 2016, Hansen *et al.*, 2011). Also, the drivers of change may vary in time. For instance, the early population size trajectories on Brøggerhalvøya since the reindeer reintroduction in 1978 followed irruption-like dynamics (Aanes *et al.*, 2000), with habitat degradation in the early 1990s (Hansen *et al.*, 2007) that may have contributed to the 1994 population crash and, thereby, our trend estimates. The more recent negative trends, which appear to be a

consequence of negative net effects of climate change, were in sharp contrast to the Adventdalen population increase during the same period. Accordingly, because of the spatial and temporal diversity of factors influencing *Rangifer* population growth rates and ecological carrying capacity, Gunn and colleagues (2009) warned against generalizing observed local abundance trends and impacts of climate change. The concern that there is a 'global' decline in *Rangifer* abundance due to increased anthropogenic impact (Vors & Boyce, 2009) also lacks quantitative support. Most Eurasian reindeer populations show no sign of decline, but rather the opposite (Uboni *et al.*, 2016), which also appears to be the case for Svalbard reindeer. Importantly, however, the substantial local variation in abundance trends calls for great caution when extrapolating results from single-population studies of long-term climate change effects, even on such small spatial scales (in a *Rangifer* context).

The extinction risk of a meta-population or (sub-)species depends in part on the degree of population synchrony, and thereby the strength of climate as a synchronizing agent (Engen *et al.*, 2002, Heino *et al.*, 1997, Ranta *et al.*, 1995). The estimated regional level of synchrony of Svalbard reindeer dynamics was high for single vital rates, but this was less apparent in the population growth rates, which are more strongly influenced by sampling error. However, as expected based on the observed pattern of autocorrelation in ROS (Fig. S4), synchrony declined with distance for all these population parameters. Uboni *et al.* (2016) found no such pattern of spatial scaling in their pairwise population correlations in population growth rates across large distances (up to ~7000 km) in Eurasian reindeer, but for our range of distances (up to ~324 km) their average regional synchrony (ca. 0.24) was very similar to ours ($\rho_R = 0.23$). Their lack of evidence for climate effects on population dynamics and synchrony could, at least in part, be a result of not accounting for local variation in density dependence and climate-density interactions, which importance has been clearly demonstrated here. Thus, even in 'simple' trophic systems such as Svalbard, where the influence of human presence is low and where few external factors other than weather fluctuations are expected to influence annual

reindeer population fluctuations (Tyler *et al.*, 2008, Ims & Ehrich, 2013), it has proven crucial to account for density dependence in population-dynamic studies (Aanes *et al.*, 2000, Albon *et al.*, 2017, Hansen *et al.*, 2011, Tyler *et al.*, 2008). In this study, direct density dependence was generally present across populations and population parameters, but there was little evidence of a consistent pattern of ROS-density interaction effects (as found in Hansen *et al.*, 2019) across the ten populations. The contribution of this interaction effect to population synchrony was therefore not huge; its synchronizing effect was significant for mortality, yet negligible for fecundity (which seemed better explained by an additive ROS effect), and, thereby, only close to significant for population growth rates. This lack of significance, and the local variation across Svalbard in estimated effects of ROS, and its interaction with density, could in part also be due to the slightly 'noisy' and short datasets used for this analysis. Furthermore, the Svalbard-scale ROS variable probably reflected local conditions better for some populations (close to one or more weather stations) than others, e.g. the remote Svenskøya population in eastern Svalbard (Figure 1). Nevertheless, the in-depth analysis of the two high-quality datasets confirmed that important local differences in density regulation indeed occur. Accordingly, when density dependence and its potential interaction with climate effects differ locally, the assumption of the Moran effect that there is a similar (log-linear) density dependence among populations does not hold. Contrasting density dependence de-synchronizes population dynamics (Engen *et al.*, 2005) and should clearly be accounted for in the analysis of climate effects on population synchrony.

One major reason for the overall poor understanding of density-dependent and -independent drivers of Arctic ungulate population dynamics, and how they vary in space, is that monitoring time-series are notoriously discontinuous (Mallory *et al.*, 2018, Uboni *et al.*, 2016, Vors & Boyce, 2009). This complicates any attempt to quantify how climate change shapes the dynamics and trends at the level of population/herd, meta-population, and sub-species, as well as patterns of spatial population synchrony. The accuracy of 'total population

count' data are also rarely assessed, but aerial counts are often assumed to be uncertain and underestimates of the actual population sizes (Poole *et al.*, 2013). We have no reason to believe that the helicopter counts used here differ in that sense, however, ground counts appear highly accurate (Le Moullec *et al.*, 2017). Uncertain aerial counts contribute to noise in the dataset, reducing the measured level of population synchrony and the ability to detect effects of climate on population growth rates and their spatial synchrony. However, because of the solitary, non-migratory behaviour of Svalbard reindeer, and the rather small, well-defined study areas in open tundra landscapes, we believe that these helicopter counts generally captured major changes occurring from year to year, as well as the long-term trends. This is especially the case for the vital rates, which were highly correlated across relatively nearby populations, as also indicated in other sub-species of *Rangifer* (Hegel *et al.*, 2012).

Climate projections suggest that the rapid regime shifts observed in winter (Peeters *et al.*, 2019) and summer climate in Svalbard represent a bellwether for future changes in other parts of the Arctic (IPCC, 2013). Based on our results (see also Albon *et al.*, 2017), it seems likely that continued warming leads to a changing relative importance of seasons for reindeer population dynamics, locally and at the meta-population level. ROS events and the phenomenon of ice-locked pastures are anticipated to increase further in frequency, magnitude and spatial extent, and not only in Svalbard (Bintanja & Andry, 2017, Rennert *et al.*, 2009). Because the local impact of such events may depend on the population state, often with a multiplicative effect at high density due to the strong resource competition, a change in event frequency will influence population stability and local extinction probability in *Rangifer* (Hansen *et al.*, 2019). Given the local variation in density-climate interactions found here, altered patterns of large-scale population dynamics and synchrony can therefore also be expected.

Other snow pack changes than basal ice formation, notably snow depth (Tyler, 2010), may modify the effects of ROS events on winter-feeding conditions (Peeters *et al.*, 2019), and

snow fall amount *per se* was also found to have a negative effect on both the Adventdalen and Brøggerhalvøya populations. Furthermore, a progressively longer snow-free season (Albon *et al.*, 2017) and improved carrying capacity due to summer warming and 'greening' (which is likely highly auto-correlated in space; Milner *et al.*, 2018) can have positive effects on population growth, both in the short and long run, as observed in Adventdalen (but see Fauchald *et al.*, 2017 for the low Arctic). As demonstrated in this study, the net effect of changes in environmental drivers linked with summer or winter warming could be expected to vary spatially due to local variation in climate trends and density-dependent responses, decoupling *Rangifer* population dynamics in space and, potentially, reducing extinction risk (e.g. Heino *et al.*, 1997).

The results from this study have ecological implications far beyond the levels of population, meta-population and sub-species. Like many other deer species (Côté *et al.*, 2004), Svalbard reindeer play a key role in the ecosystem through top-down and bottom-up effects of trophic interactions. Impacts of grazing, trampling and high nutrient turnover rates resulting from increased reindeer densities may cause vegetation state transitions from lichen- to moss- and graminoid-dominated vegetation (Hansen *et al.*, 2007, Van der Wal, 2006). Thus, similar or contrasting long-term trends in abundance between reindeer populations, distributed across large areas, may influence the spatial autocorrelation in vegetation structure, with implications for other herbivores and ecosystem components (Ims & Ehrich, 2013). Importantly, reindeer carcasses represent a major food source for the Svalbard population of Arctic fox (*Vulpes lagopus*), and stochastic ROS events therefore cause lagged synchrony in the two species' population growth rates (Hansen *et al.*, 2013). The Arctic fox does not kill reindeer but is the most important predator of the other over-wintering herbivore, the Svalbard rock ptarmigan (*Lagopus muta hyperborea*), as well as migratory birds. This key ecosystem role of *Rangifer* through trophic interaction effects is not unique to Svalbard (Ims & Ehrich, 2013, Legagneux *et al.*, 2014). Thus, how future climate change affects the level and spatial scaling of

abundance synchrony in caribou and reindeer and, in turn, their food plants and consumers, are likely to impact spatiotemporal ecological dynamics occurring at the entire tundra community level.

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Figures

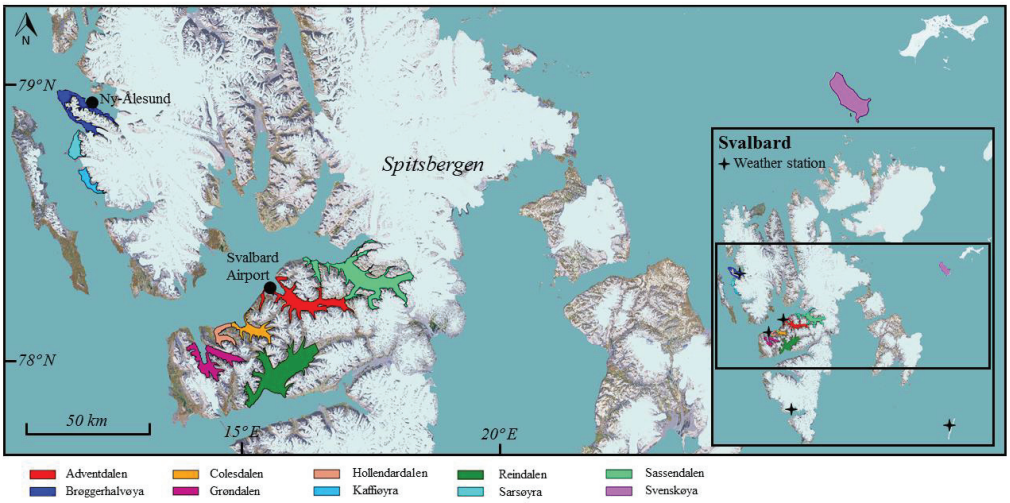

Figure 1. Map of Svalbard (inset) and the study area. Crosses show the locations of weather stations, colored polygons delineate the monitored reindeer populations (see also Figure 2), and black dots show the position of the Ny-Ålesund (Brøggerhalvøya) and Svalbard Airport (Adventdalen) weather stations.

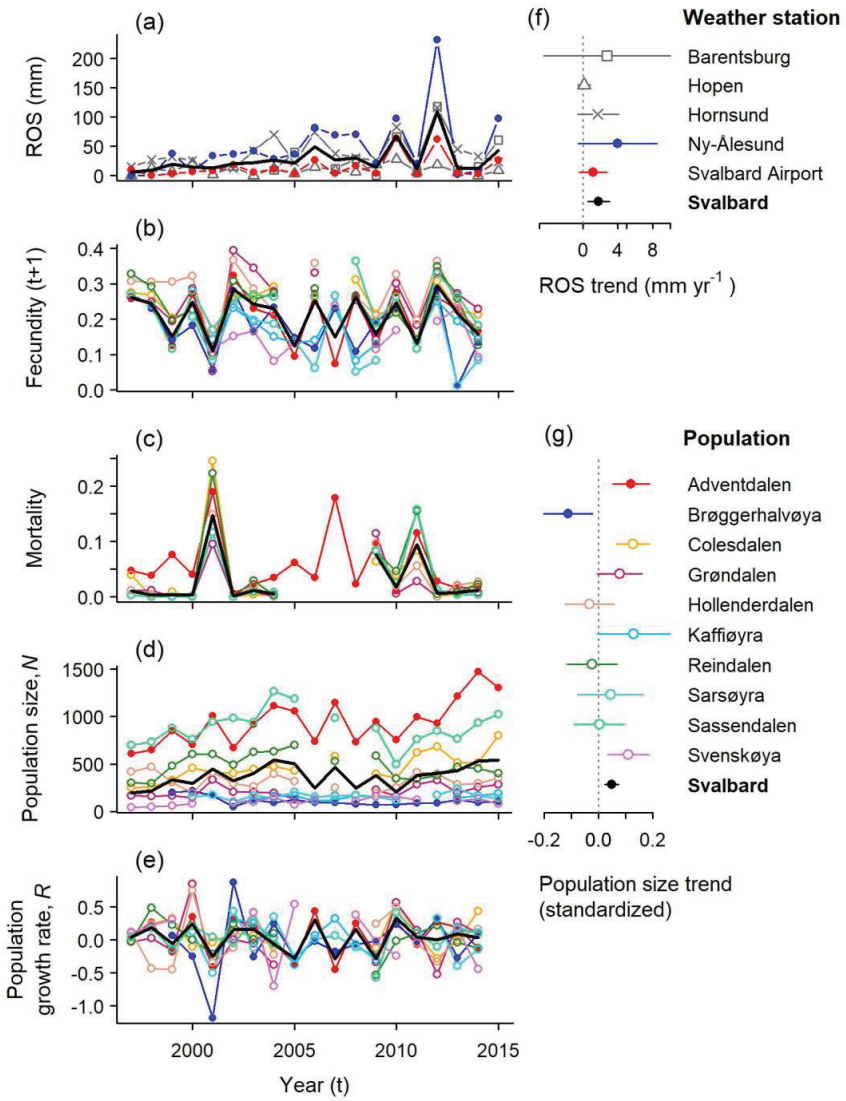

Figure 2. Time-series data and trend estimates. Annual fluctuations and temporal trends in rain-on-snow (ROS) and reindeer population parameters in Svalbard are shown for the period used for population synchrony analyses (1997-2015). (a) Annual ROS (mm) recorded at five weather stations. (b-e) Annual reindeer fecundity (proxy), mortality (proxy), population sizes and growth rates based on summer ground and helicopter counts. (f-g) Linear trend estimates of ROS and reindeer population sizes over the study period. Whiskers indicate 95% confidence interval. In (a-e), solid black lines show 'across Svalbard-scale' estimates from linear mixed regression models.

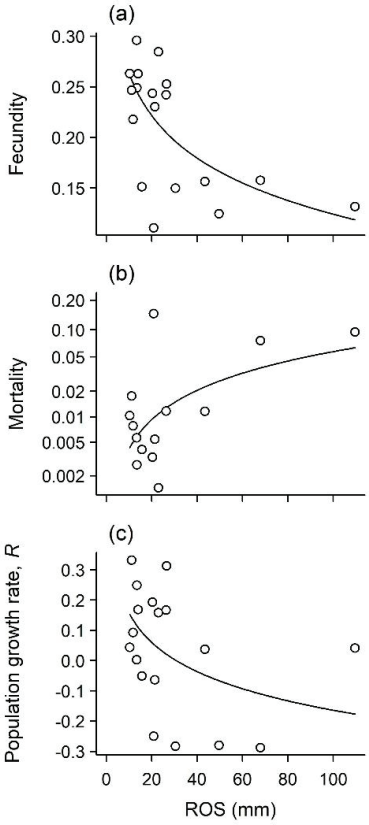

Figure 3. Rain-on-snow (ROS) effects on Svalbard reindeer. Annual (a) fecundity (proxy), (b) mortality (proxy) and (c) population growth rates of the 'across Svalbard-scale' reindeer population during 1997-2015 as a function of rain-on-snow. Note that the y-axis in (b) is on natural log-scale.

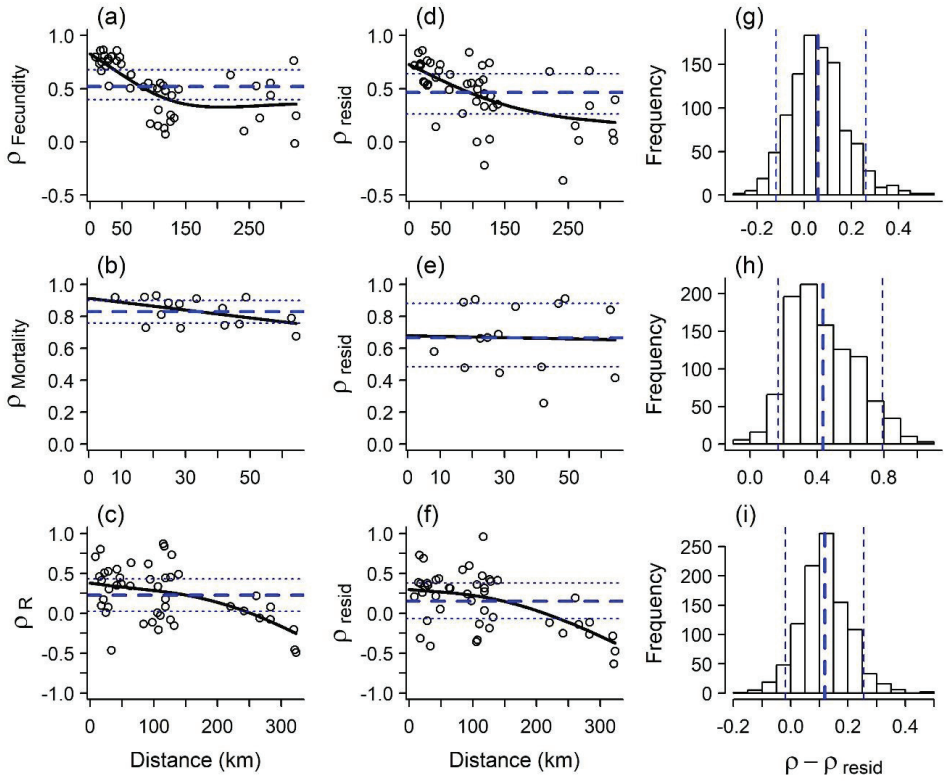

Figure 4. Spatial synchrony in reindeer population parameters across Svalbard, and the impact of rain-on-snow (ROS). (a-c) Pairwise correlations between populations in (a) fecundity (proxy), (b) mortality (proxy), and (c) population growth rates during 1997-2015, as function of distance (see also Table S2). Note the different axes scales for the different population parameters. The thick solid line represents the smoothed spline function, while the average regional synchrony (i.e. mean correlation) and bootstrapped 90% confidence intervals are shown with dashed and dotted blue lines, respectively. (d-f) Pairwise correlations between populations of residuals (when accounting for density-dependent ROS effects; Table S1) of (d) fecundity, (e) mortality and (f) population growth rates, as functions of distance. (g-i) The contributions of the density-dependent ROS effect to synchrony in (g) fecundity, (h) mortality, and (i) population growth rates, shown as histograms of the difference in nonparametric bootstrap replicates of average synchrony (n = 1000) before and after accounting for the density-dependent ROS effect. Thick (50%) and thin (5% and 95%) blue dashed lines illustrate the percentiles.

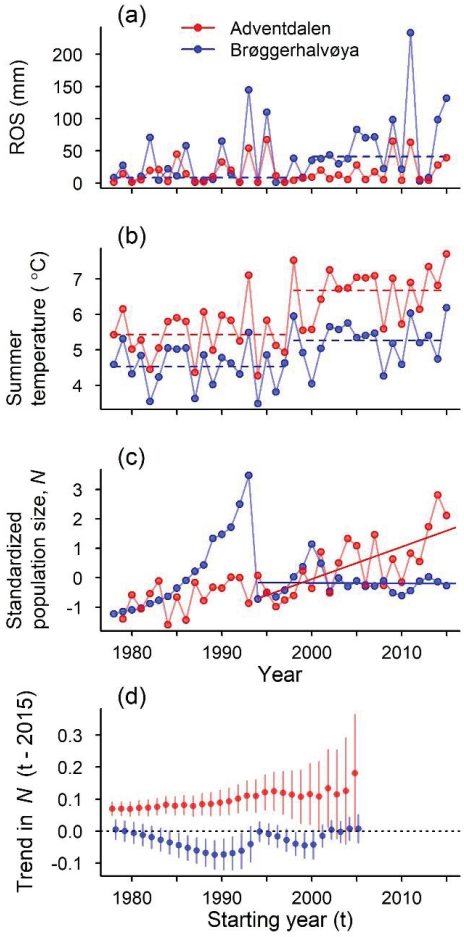

Figure 5. Time-series data and population trends in two focal reindeer populations. Annual fluctuations in (a) rain-on-snow (ROS), (b) summer temperatures and (c) standardized reindeer population sizes, and the estimates of (d) population size trends (with varying trend starting year; whiskers showing 95% CI) over the period 1978-2015 in Brøggerhalvøya (blue; Ny-Ålesund weather station) and Adventdalen (red; Svalbard Airport weather station). Horizontal dashed lines in (a-b) denote detected 'regime shifts', i.e. change points in mean. Population size trends in (c) are shown as solid lines, for the period after the irruptive phase in Brøggerhalvøya.

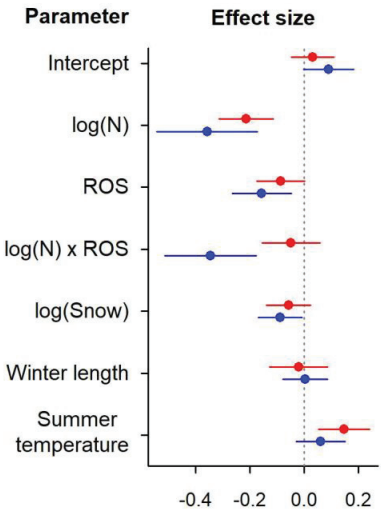

Figure 6. Climate-density effects on two focal reindeer populations. Standardized parameter estimates are shown for effects of weather and population size (*N*) on reindeer population growth rates on Brøggerhalvøya (blue; estimates from the post-irruptive phase are shown) and in Adventdalen (red). Whiskers show 95% confidence intervals.

Supplementary material for:

Spatial heterogeneity in climate change effects decouples the long-term dynamics of wild reindeer populations in the high Arctic

by

Brage B. Hansen, Åshild Ø. Pedersen, Bart Peeters, Mathilde Le Moullec, Steve D. Albon, Ivar Herfindal, Bernt-Erik Sæther, Vidar Grøtan, Ronny Aanes

Figure S1. Time-series of the Brøggerhalvøya reindeer population counts in summer versus early spring.

Figure S2. Time-series and linear trend estimates of summer temperature, total snow fall and winter length across Svalbard.

Figure S3. The relationships between ground ice and rain-on-snow (ROS), and between Normalized Difference Vegetation Index (NDVI) and summer temperature.

Figure S4. Spatial synchrony in annual rain-on-snow (ROS) against distance across Svalbard.

Figure S5. Cross-validation of linear regression models of reindeer population growth rates on Brøggerhalvøya and in Adventdalen.

Table S1. Estimates of density-dependent ROS effects on reindeer population growth rates and vital rates across Svalbard.

Table S2. Pairwise correlations in annual fecundity, mortality and population growth rates in the ten monitored reindeer populations.

Figure S1. Time-series of reindeer population size *N* in Brøggerhalvøya obtained from total counts in early spring (pre-breeding census, black circles) and summer (post-breeding census, red circles).

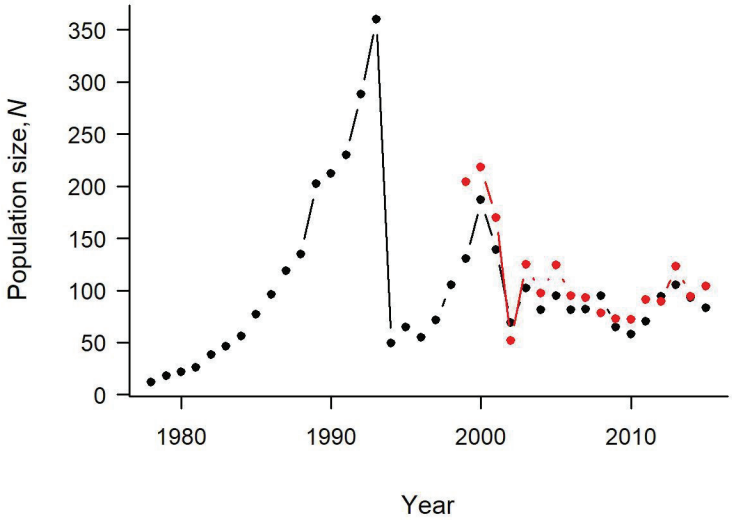

Figure S2. Time-series and linear trend estimates of summer temperature, total snow fall and winter length in weather stations across Svalbard, and for the 'across Svalbard-scale' (see Materials and Methods).

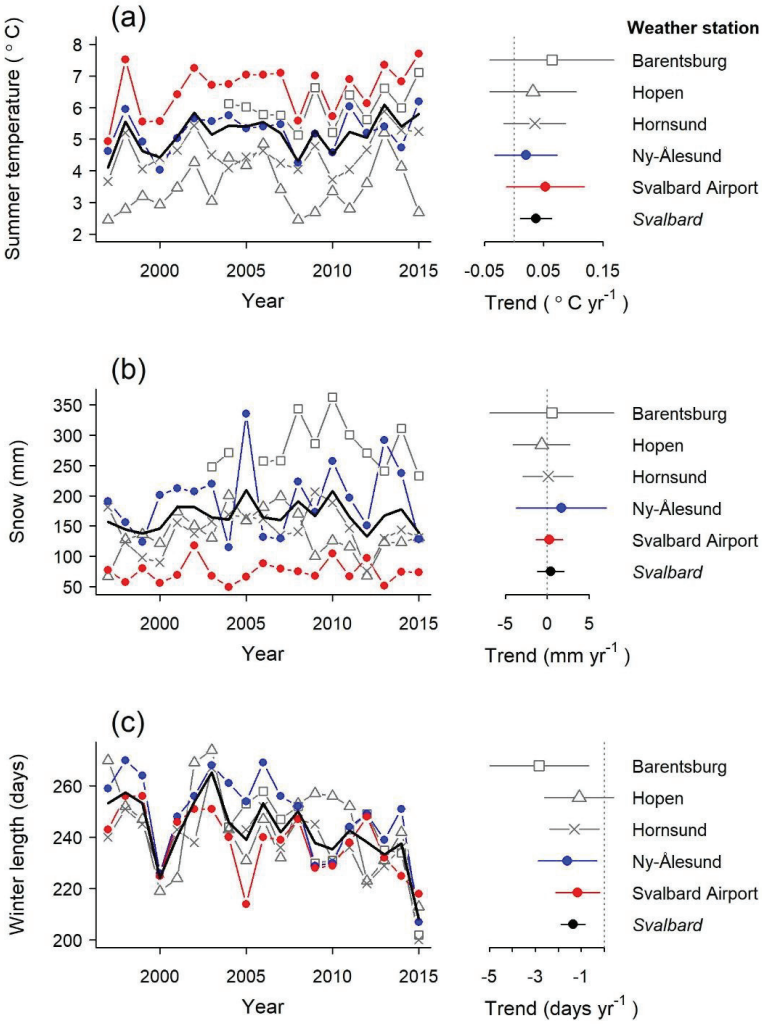

Figure S3. While increased rain-on-snow (ROS) causes icier and harsher winter feeding conditions, higher summer temperatures increase the primary productivity and vegetation greenness, and thereby also the carrying capacity for reindeer. (a) Ground ice ('basal ice') thickness plotted against annual ROS (November-April) in Ny-Ålesund. Ground ice data were collected *in situ* in snow pits in late winter (April/early May) nearby Ny-Ålesund (Peeters et al. 2018). In 2005-2008 and 2010-2012, snow pits were dug at fixed sites along a random grid placed at < 200m elevation in Brøggerhalvøya (n = 14-28 plots), Sarsøyra (n = 22-33) and Kaffiøyra (n = 13-18). In 2013-2016, data were collected on Brøggerhalvøya at (other) fixed sites (n = 40), which followed a spatially hierarchical block design covering two vegetation types (ridge and sub-ridge) and two altitudes ('low' [mean = 34 m a.s.l.] and 'high' [179 m a.s.l.]). For more details on ground ice methodology and sampling design, see Hansen et al. (2011) and Peeters et al. (2018). (b) Annual (1986-2015) maximum Normalized Difference Vegetation Index (NDVI) averaged across Nordenskiöld Land, central Spitsbergen, plotted against mean summer (July-August) temperature at Svalbard Airport. The NDVI time-series is obtained from Vickers et al. (2016), using NOAA AVHRR data.

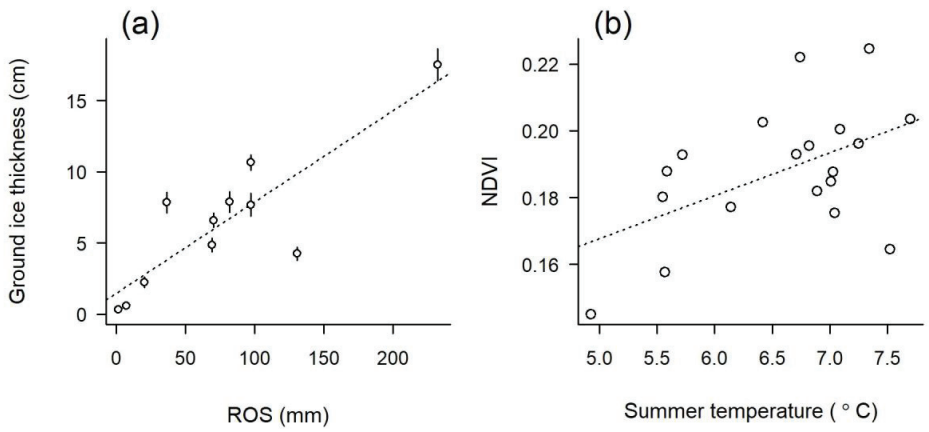

Figure S4. Spatial synchrony in annual amount of rain-on-snow (ROS) across seven Svalbard weather stations, as a function of distance between them (for details on weather data, see Peeters *et al.*, 2019). Dots are pairwise correlations between weather stations. The thick solid line represents the smoothed spline function (four df), while the estimated bootstrap mean (i.e. average synchrony ρ_{ROS}) and 90% confidence interval are shown with dashed and dotted blue lines, respectively.

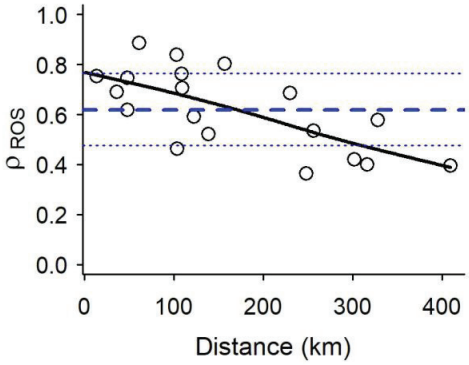

Figure S5. Leave-One-Out Cross-Validation (LOOCV) of population-dynamic models for the Svalbard reindeer populations in Adventdalen and Brøggerhalvøya. LOOCV-predictions are based on models where the predicted year was excluded, one at a time, from the data. Population counts ('observed') and full model predictions ('predicted') are shown for comparison.

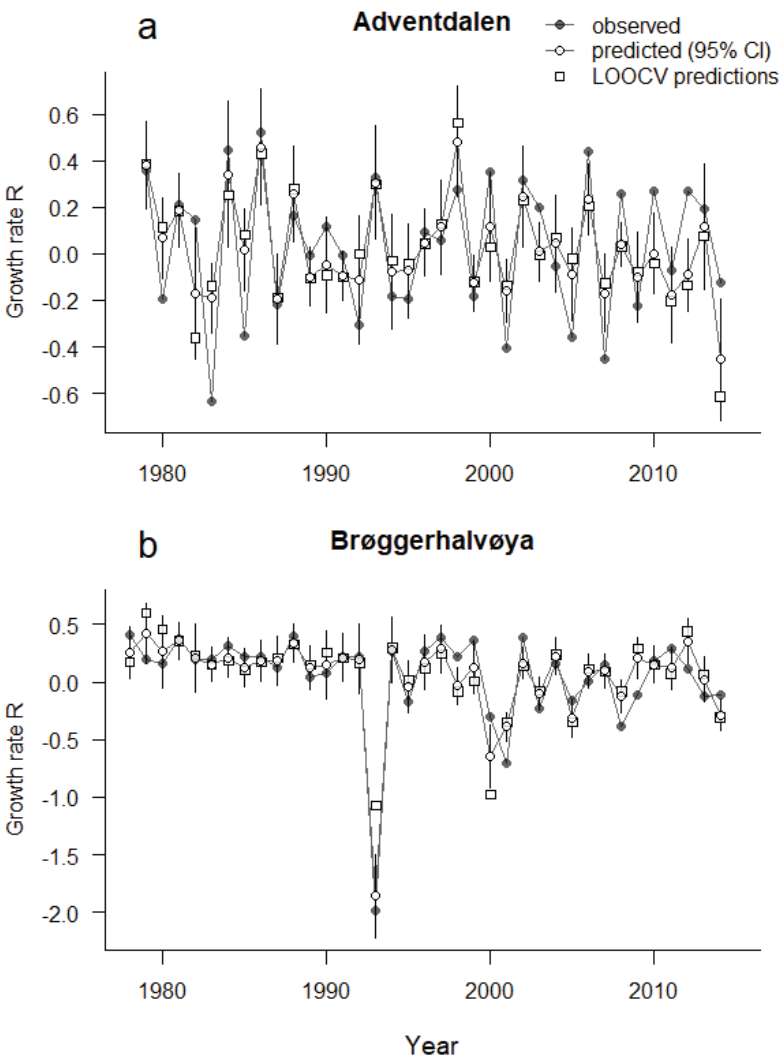

Table S1. Model estimates ($\beta \pm SE$) and adjusted R^2 of density-dependent rain-on-snow (ROS) effects on population growth rates and vital rates in the ten Svalbard reindeer populations used in the synchrony analysis (see Figure 3), as well as in the 'across Svalbard' reindeer population (see Figure 2). Data span the period 1997-2015. At the population level, fecundity and mortality were analyzed using GLM with quasibinomial family and logit link (from which adjusted R^2 cannot be calculated). At the 'across Svalbard' level, fecundity and mortality were first estimated using linear mixed models with population as random effect on the intercept, weighted for population size. Number of calves and carcasses were then back calculated by multiplying the estimated 'across Svalbard' $N_{Svalbard}$ with the estimated fecundity and mortality, respectively, before fitting the GLM. Note that because mortality rates for 2005-2008 were only available for Adventdalen, this period was not included in the mortality analysis for 'across Svalbard'.

Population	Intercept	N_t	ROS_t	N_t x ROS_t	Adj. R^2	*n* (years)
Population growth rate R_t						
Adventdalen	0.048 ± 0.046	-0.199 ± 0.047	-0.097 ± 0.050	-0.070 ± 0.069	0.587	18
Brøggerhalvøya	-0.066 ± 0.091	-0.303 ± 0.106	-0.066 ± 0.095	-0.058 ± 0.158	0.315	16
Colesdalen	0.068 ± 0.052	-0.114 ± 0.057	0.027 ± 0.054	0.076 ± 0.054	0.330	14
Grøndalen	-0.080 ± 0.080	-0.116 ± 0.100	-0.105 ± 0.080	0.314 ± 0.119	0.649	14
Hollenderdalen	0.022 ± 0.069	-0.260 ± 0.066	-0.011 ± 0.070	0.078 ± 0.059	0.515	14
Kaffiøyra	0.096 ± 0.051	-0.159 ± 0.054	-0.055 ± 0.077	-0.139 ± 0.096	0.592	10
Reindalen	0.022 ± 0.050	-0.133 ± 0.052	-0.121 ± 0.057	-0.134 ± 0.056	0.421	14
Sarsøyra	0.019 ± 0.052	-0.227 ± 0.059	-0.185 ± 0.076	0.122 ± 0.082	0.608	13
Sassen-Diabas	0.024 ± 0.064	-0.118 ± 0.096	-0.076 ± 0.084	-0.033 ± 0.124	0.094	14
Svenskøya	0.087 ± 0.108	-0.230 ± 0.121	0.045 ± 0.123	0.008 ± 0.127	0.091	12
Across Svalbard	0.098 ± 0.072	-0.311 ± 0.079	-0.146 ± 0.075	-0.189 ± 0.104	0.564	18
Fecundity$_{t+1}$						
Adventdalen	-1.352 ± 0.074	-0.256 ± 0.079	-0.214 ± 0.084	-0.089 ± 0.111	-	18
Brøggerhalvøya	-1.584 ± 0.128	-0.257 ± 0.130	-0.088 ± 0.138	-0.018 ± 0.224	-	17
Colesdalen	-1.237 ± 0.083	-0.026 ± 0.091	-0.161 ± 0.084	-0.085 ± 0.086	-	16
Grøndalen	-0.983 ± 0.165	-0.324 ± 0.213	-0.022 ± 0.159	-0.222 ± 0.229	-	16
Hollenderdalen	-1.070 ± 0.106	-0.064 ± 0.098	-0.222 ± 0.108	0.018 ± 0.092	-	16

Kaffiøyra	-1.627 ± 0.103	-0-263 ± 0.114	-0.008 ± 0.147	0.086 ± 0.199	-	12
Reindalen	-1.224 ± 0.109	-0.064 ± 0.116	-0.197 ± 0.138	0.078 ± 0.141	-	16
Sarsøyra	-1.707 ± 0.179	-0.320 ± 0.193	-0.434 ± 0.310	0.695 ± 0.374	-	14
Sassen-Diabas	-1.267 ± 0.088	0.122 ± 0.131	-0.211 ± 0.126	0.131 ± 0.178	-	16
Svenskøya	-1.674 ± 0.087	-0.186 ± 0.100	-0.295 ± 0.092	0.137 ± 0.099	-	11
Across Svalbard	-1.299 ± 0.071	-0.151 ± 0.084	-0.221 ± 0.080	-0.128 ± 0.114	-	18
Mortality,						
Adventdalen	-2.861 ± 0.240	0.403 ± 0.236	0.270 ± 0.202	-0.487 ± 0.320	-	18
Colesdalen	-3.341 ± 0.616	0.058 ± 0.659	0.394 ± 0.483	0.138 ± 0.554	-	14
Grøndalen	-4.380 ± 0.810	0.616 ± 0.479	1.146 ± 0.837	-0.867 ± 0.942	-	14
Hollenderdalen	-3.687 ± 0.586	0.316 ± 0.617	0.662 ± 0.499	-0.343 ± 0.461	-	14
Reindalen	-3.381 ± 0.678	0.567 ± 0.808	0.622 ± 0.496	-0.328 ± 0.547	-	14
Sassen-Diabas	-3.742 ± 0.548	-0.214 ± 0.676	0.716 ± 0.614	-0.277 ± 0.869	-	14
Across Svalbard	-3.422 ± 0.538	0.277 ± 0.652	0.485 ± 0.420	-0.717 ± 1.254	-	14

Table S2. Population-pairwise correlation (Pearson's *r*) matrix for annual (a) fecundity, (b) mortality and (c) population growth rates in ten monitored populations of Svalbard reindeer (for data, see Figure 2). Pairwise distances (km) between populations are shown in the above-diagonal in (a). Only the first three letters of population names are shown (see Figures 1 and 2 for reference).

(a) Pairwise distances (above-diag.) and correlations in fecundity (below-diag.)

Population	ADV	BRØ	COL	GRØ	HOL	KAF	REIN	SAR	SAS	SVE
ADV	-	126	25	42	41	107	28	118	22	242
BRØ	0.26	-	118	118	110	30	139	16	132	321
COL	0.71	0.48	-	18	17	94	21	107	47	266
GRØ	0.86	0.48	0.75	-	8	92	28	105	64	283
HOL	0.76	0.56	0.67	0.80	-	84	33	98	63	283
KAF	0.15	0.53	0.17	0.56	0.52	-	115	15	116	320
REIN	0.79	0.50	0.87	0.76	0.80	0.53	-	128	49	261
SAR	0.07	0.86	0.30	0.50	0.51	0.74	0.44	-	126	324
SAS	0.81	0.23	0.80	0.63	0.51	0.13	0.73	0.20	-	220
SVE	0.11	-0.01	0.23	0.44	0.56	0.77	0.53	0.25	0.63	-

(b) Pairwise correlations in mortality

Population	ADV	BRØ	COL	GRØ	HOL	KAF	REIN	SAR	SAS	SVE
ADV	-	-	-	-	-	-	-	-	-	-
BRØ	-	-	-	-	-	-	-	-	-	-
COL	0.89	-	-	-	-	-	-	-	-	-
GRØ	0.75	-	0.73	-	-	-	-	-	-	-
HOL	0.85	-	0.92	0.92	-	-	-	-	-	-
KAF	-	-	-	-	-	-	-	-	-	-

REIN	0.88	-	0.93	0.73	0.91	-	-	-	-	-
SAR	-	-	-	-	-	-	-	-	-	-
SAS	0.81	-	0.75	0.68	0.79	-	0.92	-	-	-
SVE	-	-	-	-	-	-	-	-	-	-

(c) Pairwise correlations in population growth rates

Population	ADV	BRØ	COL	GRØ	HOL	KAF	REIN	SAR	SAS	SVE
ADV	-	-	-	-	-	-	-	-	-	-
BRØ	0.46	-	-	-	-	-	-	-	-	-
COL	0.01	0.18	-	-	-	-	-	-	-	-
GRØ	0.56	0.08	0.42	-	-	-	-	-	-	-
HOL	0.35	-0.03	0.10	0.71	-	-	-	-	-	-
KAF	0.34	0.31	0.43	0.62	-0.13	-	-	-	-	-
REIN	0.53	0.49	0.17	0.08	-0.46	0.88	-	-	-	-
SAR	0.44	0.81	-0.21	0.01	-0.11	0.46	0.74	-	-	-
SAS	0.51	-0.15	0.45	0.64	0.35	0.84	0.37	-0.08	-	-
SVE	0.03	-0.45	-0.06	0.08	-0.07	-0.20	0.22	-0.49	0.09	-

Paper III

This article is awaiting publication and is not included in NTNU Open

Paper IV

Doctoral theses in Biology
Norwegian University of Science and Technology
Department of Biology

Year	Name	Degree	Title
1974	Tor-Henning Iversen	Dr. philos Botany	The roles of statholiths, auxin transport, and auxin metabolism in root gravitropism
1978	Tore Slagsvold	Dr. philos Zoology	Breeding events of birds in relation to spring temperature and environmental phenology
1978	Egil Sakshaug	Dr. philos Botany	The influence of environmental factors on the chemical composition of cultivated and natural populations of marine phytoplankton
1980	Arnfinn Langeland	Dr. philos Zoology	Interaction between fish and zooplankton populations and their effects on the material utilization in a freshwater lake
1980	Helge Reinertsen	Dr. philos Botany	The effect of lake fertilization on the dynamics and stability of a limnetic ecosystem with special reference to the phytoplankton
1982	Gunn Mari Olsen	Dr. scient Botany	Gravitropism in roots of *Pisum sativum* and *Arabidopsis thaliana*
1982	Dag Dolmen	Dr. philos Zoology	Life aspects of two sympartic species of newts (*Triturus, Amphibia*) in Norway, with special emphasis on their ecological niche segregation
1984	Eivin Røskaft	Dr. philos Zoology	Sociobiological studies of the rook *Corvus frugilegus*
1984	Anne Margrethe Cameron	Dr. scient Botany	Effects of alcohol inhalation on levels of circulating testosterone, follicle stimulating hormone and luteinzing hormone in male mature rats
1984	Asbjørn Magne Nilsen	Dr. scient Botany	Alveolar macrophages from expectorates – Biological monitoring of workers exposed to occupational air pollution. An evaluation of the AM-test
1985	Jarle Mork	Dr. philos Zoology	Biochemical genetic studies in fish
1985	John Solem	Dr. philos Zoology	Taxonomy, distribution and ecology of caddisflies (*Trichoptera*) in the Dovrefjell mountains
1985	Randi E. Reinertsen	Dr. philos Zoology	Energy strategies in the cold: Metabolic and thermoregulatory adaptations in small northern birds
1986	Bernt-Erik Sæther	Dr. philos Zoology	Ecological and evolutionary basis for variation in reproductive traits of some vertebrates: A comparative approach
1986	Torleif Holthe	Dr. philos Zoology	Evolution, systematics, nomenclature, and zoogeography in the polychaete orders *Oweniimorpha* and *Terebellomorpha*, with special reference to the Arctic and Scandinavian fauna
1987	Helene Lampe	Dr. scient Zoology	The function of bird song in mate attraction and territorial defence, and the importance of song repertoires
1987	Olav Hogstad	Dr. philos Zoology	Winter survival strategies of the Willow tit *Parus montanus*
1987	Jarle Inge Holten	Dr. philos Botany	Autecological investigations along a coust-inland transect at Nord-Møre, Central Norway

1987	Rita Kumar	Dr. scient Botany	Somaclonal variation in plants regenerated from cell cultures of *Nicotiana sanderae* and *Chrysanthemum morifolium*
1987	Bjørn Åge Tømmerås	Dr. scient Zoology	Olfaction in bark beetle communities: Interspecific interactions in regulation of colonization density, predator - prey relationship and host attraction
1988	Hans Christian Pedersen	Dr. philos Zoology	Reproductive behaviour in willow ptarmigan with special emphasis on territoriality and parental care
1988	Tor G. Heggberget	Dr. philos Zoology	Reproduction in Atlantic Salmon (*Salmo salar*): Aspects of spawning, incubation, early life history and population structure
1988	Marianne V. Nielsen	Dr. scient Zoology	The effects of selected environmental factors on carbon allocation/growth of larval and juvenile mussels (*Mytilus edulis*)
1988	Ole Kristian Berg	Dr. scient Zoology	The formation of landlocked Atlantic salmon (*Salmo salar* L.)
1989	John W. Jensen	Dr. philos Zoology	Crustacean plankton and fish during the first decade of the manmade Nesjø reservoir, with special emphasis on the effects of gill nets and salmonid growth
1989	Helga J. Vivås	Dr. scient Zoology	Theoretical models of activity pattern and optimal foraging: Predictions for the Moose *Alces alces*
1989	Reidar Andersen	Dr. scient Zoology	Interactions between a generalist herbivore, the moose *Alces alces*, and its winter food resources: a study of behavioural variation
1989	Kurt Ingar Draget	Dr. scient Botany	Alginate gel media for plant tissue culture
1990	Bengt Finstad	Dr. scient Zoology	Osmotic and ionic regulation in Atlantic salmon, rainbow trout and Arctic charr: Effect of temperature, salinity and season
1990	Hege Johannesen	Dr. scient Zoology	Respiration and temperature regulation in birds with special emphasis on the oxygen extraction by the lung
1990	Åse Krøkje	Dr. scient Botany	The mutagenic load from air pollution at two work-places with PAH-exposure measured with Ames Salmonella/microsome test
1990	Arne Johan Jensen	Dr. philos Zoology	Effects of water temperature on early life history, juvenile growth and prespawning migrations of Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*): A summary of studies in Norwegian streams
1990	Tor Jørgen Almaas	Dr. scient Zoology	Pheromone reception in moths: Response characteristics of olfactory receptor neurons to intra- and interspecific chemical cues
1990	Magne Husby	Dr. scient Zoology	Breeding strategies in birds: Experiments with the Magpie *Pica pica*
1991	Tor Kvam	Dr. scient Zoology	Population biology of the European lynx (*Lynx lynx*) in Norway
1991	Jan Henning L'Abêe Lund	Dr. philos Zoology	Reproductive biology in freshwater fish, brown trout *Salmo trutta* and roach *Rutilus rutilus* in particular
1991	Asbjørn Moen	Dr. philos Botany	The plant cover of the boreal uplands of Central Norway. I. Vegetation ecology of Sølendet nature reserve; haymaking fens and birch woodlands
1991	Else Marie Løbersli	Dr. scient Botany	Soil acidification and metal uptake in plants
1991	Trond Nordtug	Dr. scient Zoology	Reflectometric studies of photomechanical adaptation in superposition eyes of arthropods
1991	Thyra Solem	Dr. scient Botany	Age, origin and development of blanket mires in Central Norway

1991	Odd Terje Sandlund	Dr. philos Zoology	The dynamics of habitat use in the salmonid genera *Coregonus* and *Salvelinus*: Ontogenic niche shifts and polymorphism
1991	Nina Jonsson	Dr. philos Zoology	Aspects of migration and spawning in salmonids
1991	Atle Bones	Dr. scient Botany	Compartmentation and molecular properties of thioglucoside glucohydrolase (myrosinase)
1992	Torgrim Breiehagen	Dr. scient Zoology	Mating behaviour and evolutionary aspects of the breeding system of two bird species: the Temminck's stint and the Pied flycatcher
1992	Anne Kjersti Bakken	Dr. scient Botany	The influence of photoperiod on nitrate assimilation and nitrogen status in timothy (*Phleum pratense* L.)
1992	Tycho Anker-Nilssen	Dr. scient Zoology	Food supply as a determinant of reproduction and population development in Norwegian Puffins *Fratercula arctica*
1992	Bjørn Munro Jenssen	Dr. philos Zoology	Thermoregulation in aquatic birds in air and water: With special emphasis on the effects of crude oil, chemically treated oil and cleaning on the thermal balance of ducks
1992	Arne Vollan Aarset	Dr. philos Zoology	The ecophysiology of under-ice fauna: Osmotic regulation, low temperature tolerance and metabolism in polar crustaceans.
1993	Geir Slupphaug	Dr. scient Botany	Regulation and expression of uracil-DNA glycosylase and O^6-methylguanine-DNA methyltransferase in mammalian cells
1993	Tor Fredrik Næsje	Dr. scient Zoology	Habitat shifts in coregonids.
1993	Yngvar Asbjørn Olsen	Dr. scient Zoology	Cortisol dynamics in Atlantic salmon, *Salmo salar* L.: Basal and stressor-induced variations in plasma levels and some secondary effects.
1993	Bård Pedersen	Dr. scient Botany	Theoretical studies of life history evolution in modular and clonal organisms
1993	Ole Petter Thangstad	Dr. scient Botany	Molecular studies of myrosinase in Brassicaceae
1993	Thrine L. M. Heggberget	Dr. scient Zoology	Reproductive strategy and feeding ecology of the Eurasian otter *Lutra lutra*.
1993	Kjetil Bevanger	Dr. scient Zoology	Avian interactions with utility structures, a biological approach.
1993	Kåre Haugan	Dr. scient Botany	Mutations in the replication control gene trfA of the broad host-range plasmid RK2
1994	Peder Fiske	Dr. scient Zoology	Sexual selection in the lekking great snipe (*Gallinago media*): Male mating success and female behaviour at the lek
1994	Kjell Inge Reitan	Dr. scient Botany	Nutritional effects of algae in first-feeding of marine fish larvae
1994	Nils Røv	Dr. scient Zoology	Breeding distribution, population status and regulation of breeding numbers in the northeast-Atlantic Great Cormorant *Phalacrocorax carbo carbo*
1994	Annette-Susanne Hoepfner	Dr. scient Botany	Tissue culture techniques in propagation and breeding of Red Raspberry (*Rubus idaeus* L.)
1994	Inga Elise Bruteig	Dr. scient Botany	Distribution, ecology and biomonitoring studies of epiphytic lichens on conifers
1994	Geir Johnsen	Dr. scient Botany	Light harvesting and utilization in marine phytoplankton: Species-specific and photoadaptive responses

1994	Morten Bakken	Dr. scient Zoology	Infanticidal behaviour and reproductive performance in relation to competition capacity among farmed silver fox vixens, *Vulpes vulpes*
1994	Arne Moksnes	Dr. philos Zoology	Host adaptations towards brood parasitism by the Cockoo
1994	Solveig Bakken	Dr. scient Botany	Growth and nitrogen status in the moss *Dicranum majus* Sm. as influenced by nitrogen supply
1994	Torbjørn Forseth	Dr. scient Zoology	Bioenergetics in ecological and life history studies of fishes.
1995	Olav Vadstein	Dr. philos Botany	The role of heterotrophic planktonic bacteria in the cycling of phosphorus in lakes: Phosphorus requirement, competitive ability and food web interactions
1995	Hanne Christensen	Dr. scient Zoology	Determinants of Otter *Lutra lutra* distribution in Norway: Effects of harvest, polychlorinated biphenyls (PCBs), human population density and competition with mink *Mustela vision*
1995	Svein Håkon Lorentsen	Dr. scient Zoology	Reproductive effort in the Antarctic Petrel *Thalassoica antarctica*; the effect of parental body size and condition
1995	Chris Jørgen Jensen	Dr. scient Zoology	The surface electromyographic (EMG) amplitude as an estimate of upper trapezius muscle activity
1995	Martha Kold Bakkevig	Dr. scient Zoology	The impact of clothing textiles and construction in a clothing system on thermoregulatory responses, sweat accumulation and heat transport
1995	Vidar Moen	Dr. scient Zoology	Distribution patterns and adaptations to light in newly introduced populations of *Mysis relicta* and constraints on Cladoceran and Char populations
1995	Hans Haavardsholm Blom	Dr. philos Botany	A revision of the *Schistidium apocarpum* complex in Norway and Sweden
1996	Jorun Skjærmo	Dr. scient Botany	Microbial ecology of early stages of cultivated marine fish; inpact fish-bacterial interactions on growth and survival of larvae
1996	Ola Ugedal	Dr. scient Zoology	Radiocesium turnover in freshwater fishes
1996	Ingibjørg Einarsdottir	Dr. scient Zoology	Production of Atlantic salmon (*Salmo salar*) and Arctic charr (*Salvelinus alpinus*): A study of some physiological and immunological responses to rearing routines
1996	Christina M. S. Pereira	Dr. scient Zoology	Glucose metabolism in salmonids: Dietary effects and hormonal regulation
1996	Jan Fredrik Børseth	Dr. scient Zoology	The sodium energy gradients in muscle cells of *Mytilus edulis* and the effects of organic xenobiotics
1996	Gunnar Henriksen	Dr. scient Zoology	Status of Grey seal *Halichoerus grypus* and Harbour seal *Phoca vitulina* in the Barents sea region
1997	Gunvor Øie	Dr. scient Botany	Eevalution of rotifer *Brachionus plicatilis* quality in early first feeding of turbot *Scophtalmus maximus* L. larvae
1997	Håkon Holien	Dr. scient Botany	Studies of lichens in spruce forest of Central Norway. Diversity, old growth species and the relationship to site and stand parameters
1997	Ole Reitan	Dr. scient Zoology	Responses of birds to habitat disturbance due to damming
1997	Jon Arne Grøttum	Dr. scient Zoology	Physiological effects of reduced water quality on fish in aquaculture

1997	Per Gustav Thingstad	Dr. scient Zoology	Birds as indicators for studying natural and human-induced variations in the environment, with special emphasis on the suitability of the Pied Flycatcher
1997	Torgeir Nygård	Dr. scient Zoology	Temporal and spatial trends of pollutants in birds in Norway: Birds of prey and Willow Grouse used as
1997	Signe Nybø	Dr. scient Zoology	Impacts of long-range transported air pollution on birds with particular reference to the dipper *Cinclus cinclus* in southern Norway
1997	Atle Wibe	Dr. scient Zoology	Identification of conifer volatiles detected by receptor neurons in the pine weevil (*Hylobius abietis*), analysed by gas chromatography linked to electrophysiology and to mass spectrometry
1997	Rolv Lundheim	Dr. scient Zoology	Adaptive and incidental biological ice nucleators
1997	Arild Magne Landa	Dr. scient Zoology	Wolverines in Scandinavia: ecology, sheep depredation and conservation
1997	Kåre Magne Nielsen	Dr. scient Botany	An evolution of possible horizontal gene transfer from plants to sail bacteria by studies of natural transformation in *Acinetobacter calcoacetius*
1997	Jarle Tufto	Dr. scient Zoology	Gene flow and genetic drift in geographically structured populations: Ecological, population genetic, and statistical models
1997	Trygve Hesthagen	Dr. philos Zoology	Population responses of Arctic charr (*Salvelinus alpinus* (L.)) and brown trout (*Salmo trutta* L.) to acidification in Norwegian inland waters
1997	Trygve Sigholt	Dr. philos Zoology	Control of Parr-smolt transformation and seawater tolerance in farmed Atlantic Salmon (*Salmo salar*) Effects of photoperiod, temperature, gradual seawater acclimation, NaCl and betaine in the diet
1997	Jan Østnes	Dr. scient Zoology	Cold sensation in adult and neonate birds
1998	Seethaledsumy Visvalingam	Dr. scient Botany	Influence of environmental factors on myrosinases and myrosinase-binding proteins
1998	Thor Harald Ringsby	Dr. scient Zoology	Variation in space and time: The biology of a House sparrow metapopulation
1998	Erling Johan Solberg	Dr. scient Zoology	Variation in population dynamics and life history in a Norwegian moose (*Alces alces*) population: consequences of harvesting in a variable environment
1998	Sigurd Mjøen Saastad	Dr. scient Botany	Species delimitation and phylogenetic relationships between the Sphagnum recurvum complex (Bryophyta): genetic variation and phenotypic plasticity
1998	Bjarte Mortensen	Dr. scient Botany	Metabolism of volatile organic chemicals (VOCs) in a head liver S9 vial equilibration system in vitro
1998	Gunnar Austrheim	Dr. scient Botany	Plant biodiversity and land use in subalpine grasslands. – A conservation biological approach
1998	Bente Gunnveig Berg	Dr. scient Zoology	Encoding of pheromone information in two related moth species
1999	Kristian Overskaug	Dr. scient Zoology	Behavioural and morphological characteristics in Northern Tawny Owls *Strix aluco*: An intra- and interspecific comparative approach
1999	Hans Kristen Stenøien	Dr. scient Botany	Genetic studies of evolutionary processes in various populations of nonvascular plants (mosses, liverworts and hornworts)
1999	Trond Arnesen	Dr. scient Botany	Vegetation dynamics following trampling and burning in the outlying haylands at Sølendet, Central Norway

1999	Ingvar Stenberg	Dr. scient Zoology	Habitat selection, reproduction and survival in the White-backed Woodpecker *Dendrocopos leucotos*
1999	Stein Olle Johansen	Dr. scient Botany	A study of driftwood dispersal to the Nordic Seas by dendrochronology and wood anatomical analysis
1999	Trina Falck Galloway	Dr. scient Zoology	Muscle development and growth in early life stages of the Atlantic cod (*Gadus morhua* L.) and Halibut (*Hippoglossus hippoglossus* L.)
1999	Marianne Giæver	Dr. scient Zoology	Population genetic studies in three gadoid species: blue whiting (*Micromisistius poutassou*), haddock (*Melanogrammus aeglefinus*) and cod (*Gadus morhua*) in the North-East Atlantic
1999	Hans Martin Hanslin	Dr. scient Botany	The impact of environmental conditions of density dependent performance in the boreal forest bryophytes *Dicranum majus*, *Hylocomium splendens*, *Plagiochila asplenigides*, *Ptilium crista-castrensis* and *Rhytidiadelphus lokeus*
1999	Ingrid Bysveen Mjølnerød	Dr. scient Zoology	Aspects of population genetics, behaviour and performance of wild and farmed Atlantic salmon (*Salmo salar*) revealed by molecular genetic techniques
1999	Else Berit Skagen	Dr. scient Botany	The early regeneration process in protoplasts from *Brassica napus* hypocotyls cultivated under various g-forces
1999	Stein-Are Sæther	Dr. philos Zoology	Mate choice, competition for mates, and conflicts of interest in the Lekking Great Snipe
1999	Katrine Wangen Rustad	Dr. scient Zoology	Modulation of glutamatergic neurotransmission related to cognitive dysfunctions and Alzheimer's disease
1999	Per Terje Smiseth	Dr. scient Zoology	Social evolution in monogamous families:
1999	Gunnbjørn Bremset	Dr. scient Zoology	Young Atlantic salmon (*Salmo salar* L.) and Brown trout (*Salmo trutta* L.) inhabiting the deep pool habitat, with special reference to their habitat use, habitat preferences and competitive interactions
1999	Frode Ødegaard	Dr. scient Zoology	Host specificity as a parameter in estimates of arthropod species richness
1999	Sonja Andersen	Dr. scient Zoology	Expressional and functional analyses of human, secretory phospholipase A2
2000	Ingrid Salvesen	Dr. scient Botany	Microbial ecology in early stages of marine fish: Development and evaluation of methods for microbial management in intensive larviculture
2000	Ingar Jostein Øien	Dr. scient Zoology	The Cuckoo (*Cuculus canorus*) and its host: adaptions and counteradaptions in a coevolutionary arms race
2000	Pavlos Makridis	Dr. scient Botany	Methods for the microbial control of live food used for the rearing of marine fish larvae
2000	Sigbjørn Stokke	Dr. scient Zoology	Sexual segregation in the African elephant (*Loxodonta africana*)
2000	Odd A. Gulseth	Dr. philos Zoology	Seawater tolerance, migratory behaviour and growth of Charr, (*Salvelinus alpinus*), with emphasis on the high Arctic Dieset charr on Spitsbergen, Svalbard
2000	Pål A. Olsvik	Dr. scient Zoology	Biochemical impacts of Cd, Cu and Zn on brown trout (*Salmo trutta*) in two mining-contaminated rivers in Central Norway
2000	Sigurd Einum	Dr. scient Zoology	Maternal effects in fish: Implications for the evolution of breeding time and egg size
2001	Jan Ove Evjemo	Dr. scient Zoology	Production and nutritional adaptation of the brine shrimp *Artemia* sp. as live food organism for larvae of marine cold water fish species

2001	Olga Hilmo	Dr. scient Botany	Lichen response to environmental changes in the managed boreal forest systems
2001	Ingebrigt Uglem	Dr. scient Zoology	Male dimorphism and reproductive biology in corkwing wrasse (*Symphodus melops* L.)
2001	Bård Gunnar Stokke	Dr. scient Zoology	Coevolutionary adaptations in avian brood parasites and their hosts
2002	Ronny Aanes	Dr. scient Zoology	Spatio-temporal dynamics in Svalbard reindeer (*Rangifer tarandus platyrhynchus*)
2002	Mariann Sandsund	Dr. scient Zoology	Exercise- and cold-induced asthma. Respiratory and thermoregulatory responses
2002	Dag-Inge Øien	Dr. scient Botany	Dynamics of plant communities and populations in boreal vegetation influenced by scything at Sølendet, Central Norway
2002	Frank Rosell	Dr. scient Zoology	The function of scent marking in beaver (*Castor fiber*)
2002	Janne Østvang	Dr. scient Botany	The Role and Regulation of Phospholipase A_2 in Monocytes During Atherosclerosis Development
2002	Terje Thun	Dr. philos Biology	Dendrochronological constructions of Norwegian conifer chronologies providing dating of historical material
2002	Birgit Hafjeld Borgen	Dr. scient Biology	Functional analysis of plant idioblasts (Myrosin cells) and their role in defense, development and growth
2002	Bård Øyvind Solberg	Dr. scient Biology	Effects of climatic change on the growth of dominating tree species along major environmental gradients
2002	Per Winge	Dr. scient Biology	The evolution of small GTP binding proteins in cellular organisms. Studies of RAC GTPases in *Arabidopsis thaliana* and the Ral GTPase from *Drosophila melanogaster*
2002	Henrik Jensen	Dr. scient Biology	Causes and consequences of individual variation in fitness-related traits in house sparrows
2003	Jens Rohloff	Dr. philos Biology	Cultivation of herbs and medicinal plants in Norway – Essential oil production and quality control
2003	Åsa Maria O. Espmark Wibe	Dr. scient Biology	Behavioural effects of environmental pollution in threespine stickleback *Gasterosteus aculeatur* L.
2003	Dagmar Hagen	Dr. scient Biology	Assisted recovery of disturbed arctic and alpine vegetation – an integrated approach
2003	Bjørn Dahle	Dr. scient Biology	Reproductive strategies in Scandinavian brown bears
2003	Cyril Lebogang Taolo	Dr. scient Biology	Population ecology, seasonal movement and habitat use of the African buffalo (*Syncerus caffer*) in Chobe National Park, Botswana
2003	Marit Stranden	Dr. scient Biology	Olfactory receptor neurones specified for the same odorants in three related Heliothine species (*Helicoverpa armigera, Helicoverpa assulta* and *Heliothis virescens*)
2003	Kristian Hassel	Dr. scient Biology	Life history characteristics and genetic variation in an expanding species, *Pogonatum dentatum*
2003	David Alexander Rae	Dr. scient Biology	Plant- and invertebrate-community responses to species interaction and microclimatic gradients in alpine and Artic environments
2003	Åsa A Borg	Dr. scient Biology	Sex roles and reproductive behaviour in gobies and guppies: a female perspective
2003	Eldar Åsgard Bendiksen	Dr. scient Biology	Environmental effects on lipid nutrition of farmed Atlantic salmon (*Salmo salar* L.) parr and smolt
2004	Torkild Bakken	Dr. scient Biology	A revision of Nereidinae (Polychaeta, Nereididae)

2004	Ingar Pareliussen	Dr. scient Biology	Natural and Experimental Tree Establishment in a Fragmented Forest, Ambohitantely Forest Reserve, Madagascar
2004	Tore Brembu	Dr. scient Biology	Genetic, molecular and functional studies of RAC GTPases and the WAVE-like regulatory protein complex in *Arabidopsis thaliana*
2004	Liv S. Nilsen	Dr. scient Biology	Coastal heath vegetation on central Norway; recent past, present state and future possibilities
2004	Hanne T. Skiri	Dr. scient Biology	Olfactory coding and olfactory learning of plant odours in heliothine moths. An anatomical, physiological and behavioural study of three related species (*Heliothis virescens, Helicoverpa armigera* and *Helicoverpa assulta*)
2004	Lene Østby	Dr. scient Biology	Cytochrome P4501A (CYP1A) induction and DNA adducts as biomarkers for organic pollution in the natural environment
2004	Emmanuel J. Gerreta	Dr. philos Biology	The Importance of Water Quality and Quantity in the Tropical Ecosystems, Tanzania
2004	Linda Dalen	Dr. scient Biology	Dynamics of Mountain Birch Treelines in the Scandes Mountain Chain, and Effects of Climate Warming
2004	Lisbeth Mehli	Dr. scient Biology	Polygalacturonase-inhibiting protein (PGIP) in cultivated strawberry (*Fragaria* x *ananassa*): characterisation and induction of the gene following fruit infection by *Botrytis cinerea*
2004	Børge Moe	Dr. scient Biology	Energy-Allocation in Avian Nestlings Facing Short-Term Food Shortage
2005	Matilde Skogen Chauton	Dr. scient Biology	Metabolic profiling and species discrimination from High-Resolution Magic Angle Spinning NMR analysis of whole-cell samples
2005	Sten Karlsson	Dr. scient Biology	Dynamics of Genetic Polymorphisms
2005	Terje Bongard	Dr. scient Biology	Life History strategies, mate choice, and parental investment among Norwegians over a 300-year period
2005	Tonette Røstelien	PhD Biology	Functional characterisation of olfactory receptor neurone types in heliothine moths
2005	Erlend Kristiansen	Dr. scient Biology	Studies on antifreeze proteins
2005	Eugen G. Sørmo	Dr. scient Biology	Organochlorine pollutants in grey seal (*Halichoerus grypus*) pups and their impact on plasma thyroid hormone and vitamin A concentrations
2005	Christian Westad	Dr. scient Biology	Motor control of the upper trapezius
2005	Lasse Mork Olsen	PhD Biology	Interactions between marine osmo- and phagotrophs in different physicochemical environments
2005	Åslaug Viken	PhD Biology	Implications of mate choice for the management of small populations
2005	Ariaya Hymete Sahle Dingle	PhD Biology	Investigation of the biological activities and chemical constituents of selected *Echinops* spp. growing in Ethiopia
2005	Anders Gravbrøt Finstad	PhD Biology	Salmonid fishes in a changing climate: The winter challenge
2005	Shimane Washington Makabu	PhD Biology	Interactions between woody plants, elephants and other browsers in the Chobe Riverfront, Botswana
2005	Kjartan Østbye	Dr. scient Biology	The European whitefish *Coregonus lavaretus* (L.) species complex: historical contingency and adaptive radiation

2006	Kari Mette Murvoll	PhD Biology	Levels and effects of persistent organic pollutans (POPs) in seabirds, Retinoids and α-tocopherol – potential biomakers of POPs in birds?
2006	Ivar Herfindal	Dr. scient Biology	Life history consequences of environmental variation along ecological gradients in northern ungulates
2006	Nils Egil Tokle	PhD Biology	Are the ubiquitous marine copepods limited by food or predation? Experimental and field-based studies with main focus on *Calanus finmarchicus*
2006	Jan Ove Gjershaug	Dr. philos Biology	Taxonomy and conservation status of some booted eagles in south-east Asia
2006	Jon Kristian Skei	Dr. scient Biology	Conservation biology and acidification problems in the breeding habitat of amphibians in Norway
2006	Johanna Järnegren	PhD Biology	*Acesta oophaga* and *Acesta excavata* – a study of hidden biodiversity
2006	Bjørn Henrik Hansen	PhD Biology	Metal-mediated oxidative stress responses in brown trout (*Salmo trutta*) from mining contaminated rivers in Central Norway
2006	Vidar Grøtan	PhD Biology	Temporal and spatial effects of climate fluctuations on population dynamics of vertebrates
2006	Jafari R Kideghesho	PhD Biology	Wildlife conservation and local land use conflicts in Western Serengeti Corridor, Tanzania
2006	Anna Maria Billing	PhD Biology	Reproductive decisions in the sex role reversed pipefish *Syngnathus typhle*: when and how to invest in reproduction
2006	Henrik Pärn	PhD Biology	Female ornaments and reproductive biology in the bluethroat
2006	Anders J. Fjellheim	PhD Biology	Selection and administration of probiotic bacteria to marine fish larvae
2006	P. Andreas Svensson	PhD Biology	Female coloration, egg carotenoids and reproductive success: gobies as a model system
2007	Sindre A. Pedersen	PhD Biology	Metal binding proteins and antifreeze proteins in the beetle *Tenebrio molitor* - a study on possible competition for the semi-essential amino acid cysteine
2007	Kasper Hancke	PhD Biology	Photosynthetic responses as a function of light and temperature: Field and laboratory studies on marine microalgae
2007	Tomas Holmern	PhD Biology	Bushmeat hunting in the western Serengeti: Implications for community-based conservation
2007	Kari Jørgensen	PhD Biology	Functional tracing of gustatory receptor neurons in the CNS and chemosensory learning in the moth *Heliothis virescens*
2007	Stig Ulland	PhD Biology	Functional Characterisation of Olfactory Receptor Neurons in the Cabbage Moth, (*Mamestra brassicae* L.) (Lepidoptera, Noctuidae). Gas Chromatography Linked to Single Cell Recordings and Mass Spectrometry
2007	Snorre Henriksen	PhD Biology	Spatial and temporal variation in herbivore resources at northern latitudes
2007	Roelof Frans May	PhD Biology	Spatial Ecology of Wolverines in Scandinavia
2007	Vedasto Gabriel Ndibalema	PhD Biology	Demographic variation, distribution and habitat use between wildebeest sub-populations in the Serengeti National Park, Tanzania
2007	Julius William Nyahongo	PhD Biology	Depredation of Livestock by wild Carnivores and Illegal Utilization of Natural Resources by Humans in the Western Serengeti, Tanzania

2007	Shombe Ntaraluka Hassan	PhD Biology	Effects of fire on large herbivores and their forage resources in Serengeti, Tanzania
2007	Per-Arvid Wold	PhD Biology	Functional development and response to dietary treatment in larval Atlantic cod *(Gadus morhua* L.) Focus on formulated diets and early weaning
2007	Anne Skjetne Mortensen	PhD Biology	Toxicogenomics of Aryl Hydrocarbon- and Estrogen Receptor Interactions in Fish: Mechanisms and Profiling of Gene Expression Patterns in Chemical Mixture Exposure Scenarios
2008	Brage Bremset Hansen	PhD Biology	The Svalbard reindeer (*Rangifer tarandus platyrhynchus*) and its food base: plant-herbivore interactions in a high-arctic ecosystem
2008	Jiska van Dijk	PhD Biology	Wolverine foraging strategies in a multiple-use landscape
2008	Flora John Magige	PhD Biology	The ecology and behaviour of the Masai Ostrich (*Struthio camelus massaicus*) in the Serengeti Ecosystem, Tanzania
2008	Bernt Rønning	PhD Biology	Sources of inter- and intra-individual variation in basal metabolic rate in the zebra finch, *Taeniopygia guttata*
2008	Sølvi Wehn	PhD Biology	Biodiversity dynamics in semi-natural mountain landscapes - A study of consequences of changed agricultural practices in Eastern Jotunheimen
2008	Trond Moxness Kortner	PhD Biology	The Role of Androgens on previtellogenic oocyte growth in Atlantic cod (*Gadus morhua*): Identification and patterns of differentially expressed genes in relation to Stereological Evaluations
2008	Katarina Mariann Jørgensen	Dr. scient Biology	The role of platelet activating factor in activation of growth arrested keratinocytes and re-epithelialisation
2008	Tommy Jørstad	PhD Biology	Statistical Modelling of Gene Expression Data
2008	Anna Kusnierczyk	PhD Biology	*Arabidopsis thaliana* Responses to Aphid Infestation
2008	Jussi Evertsen	PhD Biology	Herbivore sacoglossans with photosynthetic chloroplasts
2008	John Eilif Hermansen	PhD Biology	Mediating ecological interests between locals and globals by means of indicators. A study attributed to the asymmetry between stakeholders of tropical forest at Mt. Kilimanjaro, Tanzania
2008	Ragnhild Lyngved	PhD Biology	Somatic embryogenesis in *Cyclamen persicum.* Biological investigations and educational aspects of cloning
2008	Line Elisabeth Sundt-Hansen	PhD Biology	Cost of rapid growth in salmonid fishes
2008	Line Johansen	PhD Biology	Exploring factors underlying fluctuations in white clover populations – clonal growth, population structure and spatial distribution
2009	Astrid Jullumstrø Feuerherm	PhD Biology	Elucidation of molecular mechanisms for pro-inflammatory phospholipase A2 in chronic disease
2009	Pål Kvello	PhD Biology	Neurons forming the network involved in gustatory coding and learning in the moth *Heliothis virescens:* Physiological and morphological characterisation, and integration into a standard brain atlas
2009	Trygve Devold Kjellsen	PhD Biology	Extreme Frost Tolerance in Boreal Conifers
2009	Johan Reinert Vikan	PhD Biology	Coevolutionary interactions between common cuckoos *Cuculus canorus* and *Fringilla* finches

2009	Zsolt Volent	PhD Biology	Remote sensing of marine environment: Applied surveillance with focus on optical properties of phytoplankton, coloured organic matter and suspended matter
2009	Lester Rocha	PhD Biology	Functional responses of perennial grasses to simulated grazing and resource availability
2009	Dennis Ikanda	PhD Biology	Dimensions of a Human-lion conflict: Ecology of human predation and persecution of African lions (*Panthera leo*) in Tanzania
2010	Huy Quang Nguyen	PhD Biology	Egg characteristics and development of larval digestive function of cobia (*Rachycentron canadum*) in response to dietary treatments - Focus on formulated diets
2010	Eli Kvingedal	PhD Biology	Intraspecific competition in stream salmonids: the impact of environment and phenotype
2010	Sverre Lundemo	PhD Biology	Molecular studies of genetic structuring and demography in *Arabidopsis* from Northern Europe
2010	Iddi Mihijai Mfunda	PhD Biology	Wildlife Conservation and People's livelihoods: Lessons Learnt and Considerations for Improvements. The Case of Serengeti Ecosystem, Tanzania
2010	Anton Tinchov Antonov	PhD Biology	Why do cuckoos lay strong-shelled eggs? Tests of the puncture resistance hypothesis
2010	Anders Lyngstad	PhD Biology	Population Ecology of *Eriophorum latifolium*, a Clonal Species in Rich Fen Vegetation
2010	Hilde Færevik	PhD Biology	Impact of protective clothing on thermal and cognitive responses
2010	Ingerid Brænne Arbo	PhD Medical technology	Nutritional lifestyle changes – effects of dietary carbohydrate restriction in healthy obese and overweight humans
2010	Yngvild Vindenes	PhD Biology	Stochastic modeling of finite populations with individual heterogeneity in vital parameters
2010	Hans-Richard Brattbakk	PhD Medical technology	The effect of macronutrient composition, insulin stimulation, and genetic variation on leukocyte gene expression and possible health benefits
2011	Geir Hysing Bolstad	PhD Biology	Evolution of Signals: Genetic Architecture, Natural Selection and Adaptive Accuracy
2011	Karen de Jong	PhD Biology	Operational sex ratio and reproductive behaviour in the two-spotted goby (*Gobiusculus flavescens*)
2011	Ann-Iren Kittang	PhD Biology	*Arabidopsis thaliana* L. adaptation mechanisms to microgravity through the EMCS MULTIGEN-2 experiment on the ISS: The science of space experiment integration and adaptation to simulated microgravity
2011	Aline Magdalena Lee	PhD Biology	Stochastic modeling of mating systems and their effect on population dynamics and genetics
2011	Christopher Gravningen Sørmo	PhD Biology	Rho GTPases in Plants: Structural analysis of ROP GTPases; genetic and functional studies of MIRO GTPases in Arabidopsis thaliana
2011	Grethe Robertsen	PhD Biology	Relative performance of salmonid phenotypes across environments and competitive intensities
2011	Line-Kristin Larsen	PhD Biology	Life-history trait dynamics in experimental populations of guppy (*Poecilia reticulata*): the role of breeding regime and captive environment
2011	Maxim A. K. Teichert	PhD Biology	Regulation in Atlantic salmon (*Salmo salar*): The interaction between habitat and density

2011	Torunn Beate Hancke	PhD Biology	Use of Pulse Amplitude Modulated (PAM) Fluorescence and Bio-optics for Assessing Microalgal Photosynthesis and Physiology
2011	Sajeda Begum	PhD Biology	Brood Parasitism in Asian Cuckoos: Different Aspects of Interactions between Cuckoos and their Hosts in Bangladesh
2011	Kari J. K. Attramadal	PhD Biology	Water treatment as an approach to increase microbial control in the culture of cold water marine larvae
2011	Camilla Kalvatn Egset	PhD Biology	The Evolvability of Static Allometry: A Case Study
2011	AHM Raihan Sarker	PhD Biology	Conflict over the conservation of the Asian elephant (*Elephas maximus*) in Bangladesh
2011	Gro Dehli Villanger	PhD Biology	Effects of complex organohalogen contaminant mixtures on thyroid hormone homeostasis in selected arctic marine mammals
2011	Kari Bjørneraas	PhD Biology	Spatiotemporal variation in resource utilisation by a large herbivore, the moose
2011	John Odden	PhD Biology	The ecology of a conflict: Eurasian lynx depredation on domestic sheep
2011	Simen Pedersen	PhD Biology	Effects of native and introduced cervids on small mammals and birds
2011	Mohsen Falahati-Anbaran	PhD Biology	Evolutionary consequences of seed banks and seed dispersal in *Arabidopsis*
2012	Jakob Hønborg Hansen	PhD Biology	Shift work in the offshore vessel fleet: circadian rhythms and cognitive performance
2012	Elin Noreen	PhD Biology	Consequences of diet quality and age on life-history traits in a small passerine bird
2012	Irja Ida Ratikainen	PhD Biology	Foraging in a variable world: adaptations to stochasticity
2012	Aleksander Handå	PhD Biology	Cultivation of mussels (*Mytilus edulis):* Feed requirements, storage and integration with salmon (*Salmo salar*) farming
2012	Morten Kraabøl	PhD Biology	Reproductive and migratory challenges inflicted on migrant brown trout (*Salmo trutta* L.) in a heavily modified river
2012	Jisca Huisman	PhD Biology	Gene flow and natural selection in Atlantic salmon
2012	Maria Bergvik	PhD Biology	Lipid and astaxanthin contents and biochemical post-harvest stability in *Calanus finmarchicus*
2012	Bjarte Bye Løfaldli	PhD Biology	Functional and morphological characterization of central olfactory neurons in the model insect *Heliothis virescens*.
2012	Karen Marie Hammer	PhD Biology	Acid-base regulation and metabolite responses in shallow- and deep-living marine invertebrates during environmental hypercapnia
2012	Øystein Nordrum Wiggen	PhD Biology	Optimal performance in the cold
2012	Robert Dominikus Fyumagwa	Dr. Philos Biology	Anthropogenic and natural influence on disease prevalence at the human –livestock-wildlife interface in the Serengeti ecosystem, Tanzania
2012	Jenny Bytingsvik	PhD Biology	Organohalogenated contaminants (OHCs) in polar bear mother-cub pairs from Svalbard, Norway. Maternal transfer, exposure assessment and thyroid hormone disruptive effects in polar bear cubs
2012	Christer Moe Rolandsen	PhD Biology	The ecological significance of space use and movement patterns of moose in a variable environment

2012	Erlend Kjeldsberg Hovland	PhD Biology	Bio-optics and Ecology in *Emiliania huxleyi* Blooms: Field and Remote Sensing Studies in Norwegian Waters
2012	Lise Cats Myhre	PhD Biology	Effects of the social and physical environment on mating behaviour in a marine fish
2012	Tonje Aronsen	PhD Biology	Demographic, environmental and evolutionary aspects of sexual selection
2012	Bin Liu	PhD Biology	Molecular genetic investigation of cell separation and cell death regulation in *Arabidopsis thaliana*
2013	Jørgen Rosvold	PhD Biology	Ungulates in a dynamic and increasingly human dominated landscape – A millennia-scale perspective
2013	Pankaj Barah	PhD Biology	Integrated Systems Approaches to Study Plant Stress Responses
2013	Marit Linnerud	PhD Biology	Patterns in spatial and temporal variation in population abundances of vertebrates
2013	Xinxin Wang	PhD Biology	Integrated multi-trophic aquaculture driven by nutrient wastes released from Atlantic salmon (*Salmo salar*) farming
2013	Ingrid Ertshus Mathisen	PhD Biology	Structure, dynamics, and regeneration capacity at the sub-arctic forest-tundra ecotone of northern Norway and Kola Peninsula, NW Russia
2013	Anders Foldvik	PhD Biology	Spatial distributions and productivity in salmonid populations
2013	Anna Marie Holand	PhD Biology	Statistical methods for estimating intra- and inter-population variation in genetic diversity
2013	Anna Solvang Båtnes	PhD Biology	Light in the dark – the role of irradiance in the high Arctic marine ecosystem during polar night
2013	Sebastian Wacker	PhD Biology	The dynamics of sexual selection: effects of OSR, density and resource competition in a fish
2013	Cecilie Miljeteig	PhD Biology	Phototaxis in *Calanus finmarchicus* – light sensitivity and the influence of energy reserves and oil exposure
2013	Ane Kjersti Vie	PhD Biology	Molecular and functional characterisation of the IDA family of signalling peptides in *Arabidopsis thaliana*
2013	Marianne Nymark	PhD Biology	Light responses in the marine diatom *Phaeodactylum tricornutum*
2014	Jannik Schultner	PhD Biology	Resource Allocation under Stress - Mechanisms and Strategies in a Long-Lived Bird
2014	Craig Ryan Jackson	PhD Biology	Factors influencing African wild dog *(Lycaon pictus*) habitat selection and ranging behaviour: conservation and management implications
2014	Aravind Venkatesan	PhD Biology	Application of Semantic Web Technology to establish knowledge management and discovery in the Life Sciences
2014	Kristin Collier Valle	PhD Biology	Photoacclimation mechanisms and light responses in marine micro- and macroalgae
2014	Michael Puffer	PhD Biology	Effects of rapidly fluctuating water levels on juvenile Atlantic salmon (*Salmo salar* L.)
2014	Gundula S. Bartzke	PhD Biology	Effects of power lines on moose *(Alces alces)* habitat selection, movements and feeding activity
2014	Eirin Marie Bjørkvoll	PhD Biology	Life-history variation and stochastic population dynamics in vertebrates
2014	Håkon Holand	PhD Biology	The parasite *Syngamus trachea* in a metapopulation of house sparrows
2014	Randi Magnus Sommerfelt	PhD Biology	Molecular mechanisms of inflammation – a central role for cytosolic phospholiphase A2

2014	Espen Lie Dahl	PhD Biology	Population demographics in white-tailed eagle at an on-shore wind farm area in coastal Norway
2014	Anders Øverby	PhD Biology	Functional analysis of the action of plant isothiocyanates: cellular mechanisms and in vivo role in plants, and anticancer activity
2014	Kamal Prasad Acharya	PhD Biology	Invasive species: Genetics, characteristics and trait variation along a latitudinal gradient.
2014	Ida Beathe Øverjordet	PhD Biology	Element accumulation and oxidative stress variables in Arctic pelagic food chains: *Calanus*, little auks (*Alle alle*) and black-legged kittiwakes (*Rissa tridactyla*)
2014	Kristin Møller Gabrielsen	PhD Biology	Target tissue toxicity of the thyroid hormone system in two species of arctic mammals carrying high loads of organohalogen contaminants
2015	Gine Roll Skjervø	Dr. philos Biology	Testing behavioral ecology models with historical individual-based human demographic data from Norway
2015	Nils Erik Gustaf Forsberg	PhD Biology	Spatial and Temporal Genetic Structure in Landrace Cereals
2015	Leila Alipanah	PhD Biology	Integrated analyses of nitrogen and phosphorus deprivation in the diatoms *Phaeodactylum tricornutum* and *Seminavis robusta*
2015	Javad Najafi	PhD Biology	Molecular investigation of signaling components in sugar sensing and defense in *Arabidopsis thaliana*
2015	Bjørnar Sporsheim	PhD Biology	Quantitative confocal laser scanning microscopy: optimization of in vivo and in vitro analysis of intracellular transport
2015	Magni Olsen Kyrkjeeide	PhD Biology	Genetic variation and structure in peatmosses (*Sphagnum*)
2015	Keshuai Li	PhD Biology	Phospholipids in Atlantic cod (*Gadus morhua* L.) larvae rearing: Incorporation of DHA in live feed and larval phospholipids and the metabolic capabilities of larvae for the de novo synthesis
2015	Ingvild Fladvad Størdal	PhD Biology	The role of the copepod *Calanus finmarchicus* in affecting the fate of marine oil spills
2016	Thomas Kvalnes	PhD Biology	Evolution by natural selection in age-structured populations in fluctuating environments
2016	Øystein Leiknes	PhD Biology	The effect of nutrition on important life-history traits in the marine copepod *Calanus finmarchicus*
2016	Johan Henrik Hårdensson Berntsen	PhD Biology	Individual variation in survival: The effect of incubation temperature on the rate of physiological ageing in a small passerine bird
2016	Marianne Opsahl Olufsen	PhD Biology	Multiple environmental stressors: Biological interactions between parameters of climate change and perfluorinated alkyl substances in fish
2016	Rebekka Varne	PhD Biology	Tracing the fate of escaped cod (*Gadus morhua* L.) in a Norwegian fjord system
2016	Anette Antonsen Fenstad	PhD Biology	Pollutant Levels, Antioxidants and Potential Genotoxic Effects in Incubating Female Common Eiders (*Somateria mollissima*)
2016	Wilfred Njama Marealle	PhD Biology	Ecology, Behaviour and Conservation Status of Masai Giraffe (*Giraffa camelopardalis tippelskirchi*) in Tanzania
2016	Ingunn Nilssen	PhD Biology	Integrated Enviromental Mapping and Monitoring: A Methodological approach for end users.
2017	Konika Chawla	PhD Biology	Discovering, analysing and taking care of knowledge.

2017	Øystein Hjorthol Opedal	PhD Biology	The Evolution of Herkogamy: Pollinator Reliability, Natural Selection, and Trait Evolvability.
2017	Ane Marlene Myhre	PhD Biology	Effective size of density dependent populations in fluctuating environments
2017	Emmanuel Hosiana Masenga	PhD Biology	Behavioural Ecology of Free-ranging and Reintroduced African Wild Dog (*Lycaon pictus*) Packs in the Serengeti Ecosystem, Tanzania
2017	Xiaolong Lin	PhD Biology	Systematics and evolutionary history of *Tanytarsus* van der Wulp, 1874 (Diptera: Chironomidae)
2017	Emmanuel Clamsen Mmassy	PhD Biology	Ecology and Conservation Challenges of the Kori bustard in the Serengeti National Park
2017	Richard Daniel Lyamuya	PhD Biology	Depredation of Livestock by Wild Carnivores in the Eastern Serengeti Ecosystem, Tanzania
2017	Katrin Hoydal	PhD Biology	Levels and endocrine disruptive effects of legacy POPs and their metabolites in long-finned pilot whales of the Faroe Islands
2017	Berit Glomstad	PhD Biology	Adsorption of phenanthrene to carbon nanotubes and its influence on phenanthrene bioavailability/toxicity in aquatic organism
2017	Øystein Nordeide Kielland	PhD Biology	Sources of variation in metabolism of an aquatic ectotherm
2017	Narjes Yousefi	PhD Biology	Genetic divergence and speciation in northern peatmosses (*Sphagnum*)
2018	Signe Christensen-Dalgaard	PhD Biology	Drivers of seabird spatial ecology - implications for development of offshore wind-power in Norway
2018	Janos Urbancsok	PhD Biology	Endogenous biological effects induced by externally supplemented glucosinolate hydrolysis products (GHPs) on *Arabidopsis thaliana*
2018	Alice Mühlroth	PhD Biology	The influence of phosphate depletion on lipid metabolism of microalgae
2018	Franco Peniel Mbise	PhD Biology	Human-Carnivore Coexistence and Conflict in the Eastern Serengeti, Tanzania
2018	Stine Svalheim Markussen	PhD Biology	Causes and consequences of intersexual life history variation in a harvested herbivore population
2018	Mia Vedel Sørensen	PhD Biology	Carbon budget consequences of deciduous shrub expansion in alpine tundra ecosystems
2018	Hanna Maria Kauko	PhD Biology	Light response and acclimation of microalgae in a changing Arctic
2018	Erlend I. F. Fossen	PhD Biology	Trait evolvability: effects of thermal plasticity and genetic correlations among traits
2019	Peter Sjolte Ranke	PhD Biology	Demographic and genetic and consequences of dispersal in house sparrows
2019	Mathilde Le Moullec	PhD Biology	Spatiotemporal variation in abundance of key tundra species: from local heterogeneity to large-scale synchrony
2019	Endre Grüner Ofstad	PhD Biology	Causes and consequences of variation in resource use and social structure in ungulates
2019	Yang Jin	PhD Biology	Development of lipid metabolism in early life stage of Atlantic salmon (*Salmo salar*)
2019	Elena Albertsen	PhD Biology	Evolution of floral traits: from ecological contex to functional integration
2019	Mominul Islam Nahid	PhD Biology	Interaction between two Asian cuckoos and their hosts in Bangladesh

2019	Knut Jørgen Egelie	Phd Biology	Management of intellectual property in university-industry collaborations – public access to and control of knowledge
2019	Thomas Ray Haaland	Phd Biology	Adaptive responses to enviromental stochasticity on different evolutionary time-scales
2019	Kwaslema Malle Hariohay	Phd Biology	Human wildlife interactions in the Ruaha-Rungwa Ecosystem, Central Tanzania
2019	Mari Engvig Løseth	Phd Biology	Exposure and effects of emerging and legacy organic pollutants in white-tailed eagle (*Haliaeetis albicilla*) nestlings
2019	Joseph Mbyati Mukeka	Phd Biology	Human-Wildlife Conflicts and Compensation for Losses in Kenya: Dynamics, Characteristics and Correlates
2019	Helene Løvstrand Svarva	Phd Biology	Dendroclimatology in southern Norway: tree rings, demography and climate
2019	Nathalie Briels	Phd Biology	Exposure and effects of legacy and emerging organic pollutants in developing birds – Laboratory and field studies