

RESEARCH REVIEW

Climate change impacts on wildlife in a High Arctic archipelago – Svalbard, Norway

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Abstract

The Arctic is warming more rapidly than other region on the planet, and the northern Barents Sea, including the Svalbard Archipelago, is experiencing the fastest temperature increases within the circumpolar Arctic, along with the highest rate of sea ice loss. These physical changes are affecting a broad array of resident Arctic organisms as well as some migrants that occupy the region seasonally. Herein, evidence of climate change impacts on terrestrial and marine wildlife in Svalbard is reviewed, with a focus on bird and mammal species. In the terrestrial ecosystem, increased winter air temperatures and concomitant increases in the frequency of ‘rain-on-snow’ events are one of the most important facets of climate change with respect to impacts on flora and fauna. Winter rain creates ice that blocks access to food for herbivores and synchronizes the population dynamics of the herbivore–predator guild. In the marine ecosystem, increases in sea temperature and reductions in sea ice are influencing the entire food web. These changes are affecting the foraging and breeding ecology of most marine birds and mammals and are associated with an increase in abundance of several temperate fish, seabird and marine mammal species. Our review indicates that even though a few species are benefiting from a warming climate, most Arctic endemic species in Svalbard are experiencing negative consequences induced by the warming environment. Our review emphasizes the tight relationships between the marine and terrestrial ecosystems in this High Arctic archipelago. Detecting changes in trophic relationships within and between these ecosystems requires long-term (multidecadal) demographic, population- and ecosystem-based monitoring, the results of which are necessary to set appropriate conservation priorities in relation to climate warming.

Keywords: climate warming, marine ecosystem, rain-on-snow, sea ice, sea temperature, terrestrial ecosystem, trophic interactions

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Introduction

The Earth’s climate is changing; the atmosphere and ocean have warmed, sea level has risen, the amount of snow and ice has declined globally and the Arctic is a global ‘hot-spot’ that is warming more quickly than any other region on the planet (Intergovernmental Panel on Climate Change, 2013). One of the most visible and dramatic impacts of climate change in the Arctic has been the reduction in sea ice, which has declined markedly in recent decades in terms of overall extent, thickness, proportion of multiyear ice and seasonal duration. Although the physical models that predict sea ice extent still contain much variability, continued sea ice declines are expected and a seasonally ice-free Arctic is predicted to occur well before the end of this

century (Kwok *et al.*, 2009; Overland & Wang, 2010; Wang & Overland, 2009; see also Tietsche *et al.*, 2011 for an alternate view). This would be a first for Arctic marine systems during the last 5 + million years (see Polyak *et al.*, 2010 for historical sea ice patterns). A summer-time ice-free Arctic Ocean will have implications for ocean circulation and our global climate system (Kern *et al.*, 2010; White *et al.*, 2010), and it will also induce changes throughout Arctic food webs (ACIA, 2004; Piepenburg, 2005; Hunt *et al.*, 2008; Mueter & Lit-zow, 2008; Mueter *et al.*, 2009; Post *et al.*, 2013).

Arctic terrestrial ecosystems are also being impacted heavily by climate change, with the major changes in earth-surface phenomena being declines in glacier ice and snow, melting of permafrost, increases in vegetation productivity and climate-feedbacks induced by shrub encroachment, which are all expected to mediate changes in trophic interactions (Sturm *et al.*, 2001; Ims & Ehrich, 2013; Cooper, 2014). The strong warming

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predicted for the coming decades in the Arctic will result in average mid-winter temperatures approaching 0 °C (Hansen *et al.*, 2014), which will likely have far-reaching implications for terrestrial ecosystems in the region.

Climate change is rapid and unidirectional all over the Arctic, but still shows considerable amounts of spatial heterogeneity (e.g. Bhatt *et al.*, 2010). For example, during the period 1979–2013, the summer, open-water season has increased between five and ten weeks over most of the Arctic, while it has increased by more than 20 weeks in the northern parts of the Barents Sea (Laidre *et al.*, 2015). This dramatic regional change in sea ice is concomitant with higher local air and sea water temperatures (Kelly *et al.*, 2010; Pavlov *et al.*, 2013; Nordli *et al.*, 2014; Onarheim *et al.*, 2014). In a European context, the Svalbard Archipelago has experienced the fastest air temperature increases in recent decades (Nordli *et al.*, 2014) and downscaled projections from climate models for Svalbard indicate that the current warming trend will continue unabated through to the end of this century (Førland *et al.*, 2012).

These climatic changes are already causing major impacts on the biota of the region, both in terrestrial and marine ecosystems (Table 1). Herein, the effects of climate warming on resident and migratory birds and mammals in the Svalbard Archipelago (Fig. 1) are reviewed. Both terrestrial and marine ecosystems, as well as their interactions, are considered. Finally, future priorities for research in Svalbard and the broader Arctic are identified.

Climate change and the Svalbard terrestrial ecosystem

Winter air temperature, precipitation and 'rain-on-snow' events

Climate projections focused on the Svalbard Region indicate a future warming rate up to year 2100 that is three times stronger than that observed during the last 100 years (Førland *et al.*, 2012). Winters are getting warmer (Førland *et al.*, 2012; Hansen *et al.*, 2014; Nordli *et al.*, 2014), which is having significant impacts on the biodiversity, structure and functioning of Arctic terrestrial ecosystems (Ims & Fuglei, 2005; Hansen *et al.*, 2013; Cooper, 2014).

The average mid-winter air temperature in the Longyearbyen area (West Spitsbergen, 78°15'N, 15°30'E) at the end of this century is projected to be around 10 °C higher than at present (Førland *et al.*, 2012; Hansen *et al.*, 2014); air temperature data from other weather stations in Svalbard show a similar rate of warming (Fig. 2). Projections for precipitation

indicate a continued increase up to the year 2100 (Førland *et al.*, 2012). However, data on precipitation are not very reliable due to the difficulties in measuring solid forms of precipitation (Førland & Hanssen-Bauer, 2000). In general, there has been a decrease throughout the Arctic in the maximum winter snow water equivalent depth and the snow cover duration (Liston & Hiemstra, 2011). Data on snowfall in Svalbard are relatively sparse, but the longest time series available suggests that snow cover duration and spring snow depth have significantly decreased in recent decades (Fig. 3). Snow measurements are influenced by many factors (Cooper, 2014) that vary across spatial scales, and the decrease in the seasonal duration of snow cover and snow depth observed in the Longyearbyen area (Fig. 3) may not necessarily represent other areas in Svalbard.

Winter in Svalbard has recently become less variable in terms of temperature, because of fewer very cold days (Ims *et al.*, 2014). 'Rain-on-snow' events (hereafter ROS events) have always occurred in Svalbard due to the strong oceanic influence on the weather systems within the archipelago (Svendsen *et al.*, 2002), but such events are increasing in frequency due to winter warming (Førland *et al.*, 2012). ROS events have a significant impact on the entire terrestrial ecosystem by changing snowpack properties and sub-snowpack soil temperatures (Putkonen & Roe, 2003; Rennert *et al.*, 2009). Winter rain results in encapsulation of vegetation in ice, which blocks access to food resources for herbivores (Hansen *et al.*, 2013). ROS events have synchronized the population dynamics of the Svalbard reindeer *Rangifer tarandus platyrhynchus*, the Svalbard rock ptarmigan *Lagopus muta hyperborea*, the sibling vole *Microtus levis* and with a time delay also their principal predator/scavenger, the Arctic fox *Vulpes lagopus* (Stien *et al.*, 2012; Hansen *et al.*, 2013). Changes in winter climate and the frequency of occurrence of ROS events have also affected Svalbard reindeer behaviour (i.e. habitat use and diet, Hansen *et al.*, 2010; Stien *et al.*, 2010) and population sex ratios (Peeters, 2014). ROS events likely represent one of the most important facets of ongoing climate change for Arctic terrestrial ecosystems (Thompson *et al.*, 2013).

Primary productivity and changes in herbivory pressure

During summer (June to August), air temperatures have increased since the 1990s in Svalbard, but similar to winter conditions, there has been no clear trend in precipitation (Førland *et al.*, 2012; Ims *et al.*, 2014). The extent of the growth season (expressed as the degree-days above 5 °C) has increased significantly from 1975 to 2015 with some regional variability; it has more than doubled in Longyearbyen and Hopen and nearly

Table 1 Key published evidence showing the measured impacts of climate warming on wildlife species breeding in Svalbard. The 'timescale' column represents the duration of the studies

Species	Environmental variable	Effect	Timescale	Reference
Polar bear	Decrease in sea ice around denning areas in autumn	Fewer pregnant bears reaching traditional denning areas	2009–2012, 1994–2008	Aars (2013), Derocher <i>et al.</i> (2011)
	Annual variation in Arctic Oscillation Index	Mild spring weather leads to decreased reproduction the following year *	1988–2002	Derocher (2005)
Brünnich's guillemot	Increase in sea temperature, weakening of the subpolar gyre (winter grounds)	Decrease in population size	1988–2010	Descamps <i>et al.</i> (2013)
	Increase in winter air temperature (summer grounds)	Higher tick prevalence	2007–2012	Descamps (2013)
Little auk	Increase in sea temperature (summer grounds)	Lower survival	2006–2013	Hovinen <i>et al.</i> (2014a)
		Lower fledging success	2008–2010	Hovinen <i>et al.</i> (2014b)
	Increase in air temperature (summer grounds)	Earlier breeding	1963–2008	Moe <i>et al.</i> (2009)
Black-legged kittiwake	Increase in sea temperature (summer grounds)	Earlier breeding	1970–2008	Moe <i>et al.</i> (2009)
Common eider	Reduced spring sea ice concentration	Higher number of breeding pairs	1981–2011	Hanssen <i>et al.</i> (2013)
	Increase in air temperature	Lower energetic costs of incubation	2012–2014	Hilde <i>et al.</i> (2016)
	Advanced onset of spring †	Increase in reproductive success	1981–2011	Jensen <i>et al.</i> (2014)
Pink-footed goose	Reduction in spring snow cover	Shift from density-dependent to density-independent reproduction	1981–2011	Jensen <i>et al.</i> (2014)
		Earlier breeding	2003–2006	Madsen <i>et al.</i> (2007)
		Higher number of breeding pairs	2003–2006, 2003–2014 ‡	Madsen <i>et al.</i> (2007), Anderson <i>et al.</i> (2015)
		Increase in reproductive success	2003–2006, 2000–2011	Madsen <i>et al.</i> (2007), Jensen <i>et al.</i> (2014)
			1997–2010	Hansen <i>et al.</i> (2013)
Svalbard rock ptarmigan	'Rain-on-snow'	Short-term decrease in population growth rate	1997–2010	Hansen <i>et al.</i> (2013)
Svalbard reindeer	'Rain-on-snow'	Short-term decrease in population growth rate	1999–2010, 1991–2010	Hansen <i>et al.</i> (2011, 2013)
		Decrease in recruitment rate	1995–2011	Stien <i>et al.</i> (2012)
		Range displacement	1994–1998	Stien <i>et al.</i> (2010)
	Increase in winter precipitation	Increase in mortality	1978–1998, 1979–1999	Aanes <i>et al.</i> (2000, 2003), Solberg <i>et al.</i> (2001)
		Decrease in recruitment rate	1979–1999	Solberg <i>et al.</i> (2001)
	Increase in Arctic Oscillation (i.e. milder winter)	Decrease in population growth rate	1978–1999	Aanes <i>et al.</i> (2002)
	Increase in summer temperature	Increase in population growth rate	1991–2010	Hansen <i>et al.</i> (2013)
Ablation in winter	Increase in population growth rate	1979–2007	Tyler <i>et al.</i> (2008)	
Sibling vole	'Rain-on-snow'	Decrease in population size	1996–2007	Stien <i>et al.</i> (2012)
Arctic fox	'Rain-on-snow'	Decrease in population growth rate (1-year lagged)	1997–2011	Hansen <i>et al.</i> (2013)
Ringed seal	Decrease in sea ice extent	Increase in foraging effort	2002–2012 §	Hamilton <i>et al.</i> (2015, 2016)

*The effect could be local, as only parts of the Barents Sea area are surveyed, and it is possible that bears den in colder areas in the Russian Arctic when sea ice is scarce in the Svalbard area.

†Measured as the number of days in May with average daily mean temperature >0 °C.

‡No data in 2008 and 2009.

§Data from 2002–2003 and 2010–2012.

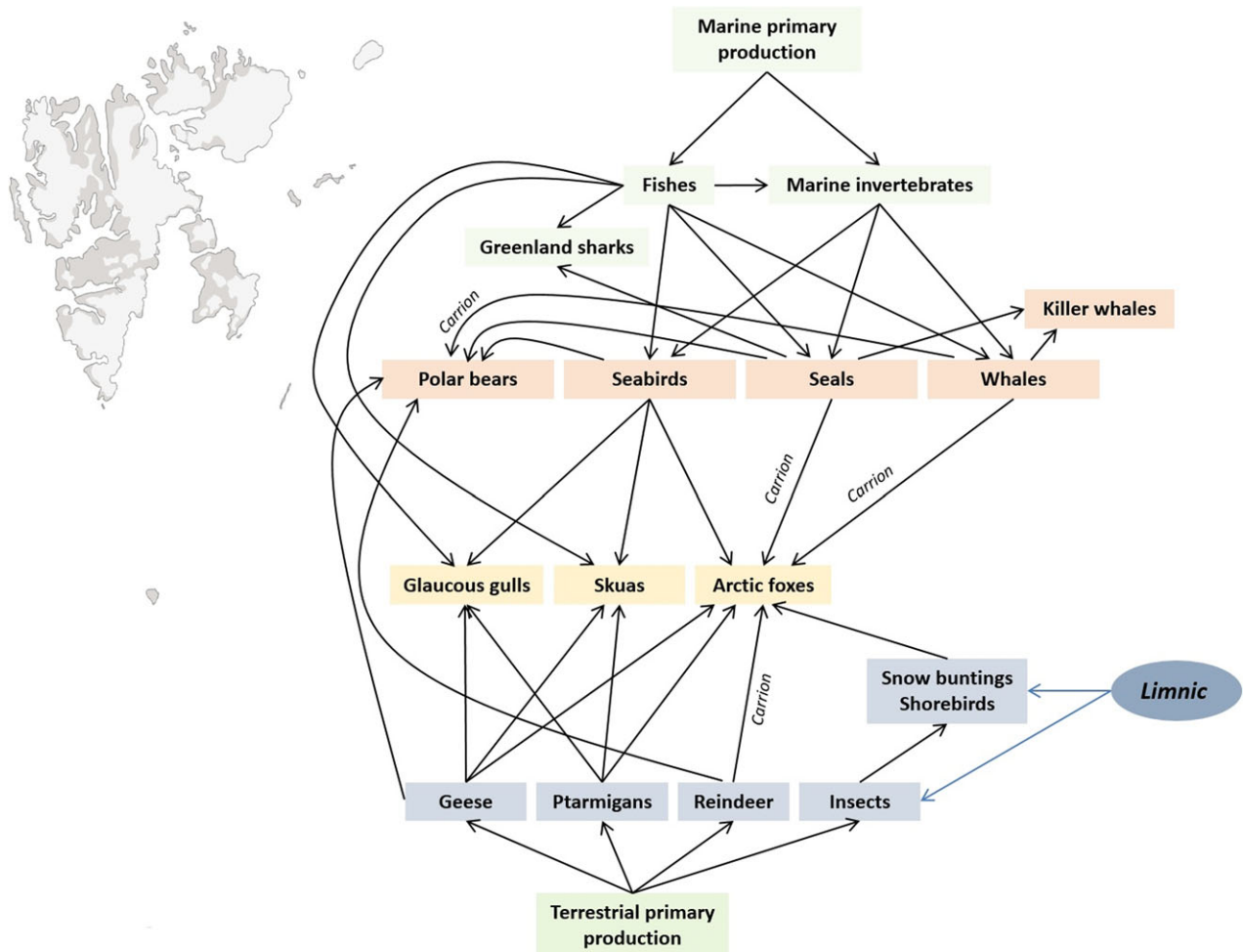


Fig. 1 Key components (species/functional groups) and trophic flows (arrows) in the Svalbard food web (adapted from Ims *et al.*, 2013). Terrestrial ecosystem: The tundra food web is characterized by primary producers comprised of low-statured plants with various growth forms, two endemic herbivore species (Svalbard reindeer and Svalbard rock ptarmigan) and three species of migratory geese (the abundant pink-footed and barnacle geese and the less abundant light-bellied Brent goose), three main predators (Arctic fox, glaucous gull and skua spp.), which to a large degree also feed from the marine food web. A spatially restricted, introduced vole population is present in Svalbard, but the Svalbard terrestrial ecosystem lacks the key stone lemmings, important to many Arctic ecosystems and specialist predators. Marine ecosystem: The marine ecosystem is rich in species diversity, and Svalbard is the region with the greatest species richness in the High Arctic in terms of the number of marine mammal species. But, similar to other Arctic systems, it is still a simple food web with only a few levels. Polar bears, killer whales and Greenland sharks are top predators that feed on various other trophic levels. All three Arctic endemic whale species (bowhead, narwhal and white whales) and all three circumpolar pinnipeds (ringed seals, bearded seals and walruses) are resident in Svalbard; harbour seals also reside on the west coast of Spitsbergen (the largest island of the Svalbard archipelago), due to the presence of the West Spitsbergen Current and its warm, Atlantic water, while harp and hooded seals are seasonal residents along with many migratory cetaceans. The seabird community is dominated by gulls and auks. Polar cod and Arctic calanoid copepods are among the most important prey species for top trophic animals.

doubled in Ny Ålesund (Fig. 4). However, this has not resulted in statistically significant trends in productivity based on remote sensing data (Karlsen *et al.*, 2013). Nevertheless, the warming of Svalbard has already had strong impacts on herbivores. It explains part of the rapid increase in the population of pink-footed geese *Anser brachyrhynchus* (Kery *et al.*, 2006; Madsen *et al.*, 2007; Jensen *et al.*, 2014) from 15000 [1965] to 76000 individuals [2014] (Madsen & Williams, 2012; Johnson

et al., 2014). The increase in this population has been caused by a combination of conservation efforts (including a reduction in hunting), changes in agricultural practices in Europe (wintering grounds), but also a warming climate (Jensen *et al.*, 2008, 2014). The relative importance of each factor on the pink-footed goose population size remains unknown, but clearly, climate changes on the breeding grounds have played a role. Indeed, nesting success of pink-footed geese almost

doubled between 2003 and 2014 in Svalbard (Anderson *et al.*, 2015). Snow cover has a profound cascading effect on pink-footed geese reproduction (Table 1) and lower spring snow cover was associated with earlier nesting, increased number of breeding pairs and higher breeding success (e.g. Madsen *et al.*, 2007; Anderson

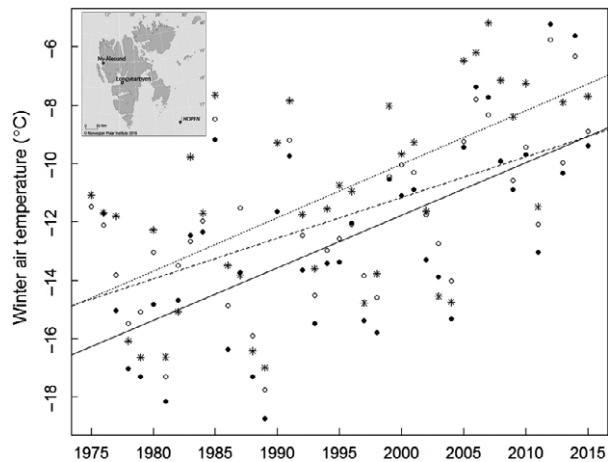


Fig. 2 Annual mean winter air temperature (December–March) in Svalbard between 1975 and 2015 at three sites; Longyearbyen (78°14'N 15°30'E; filled circles), Ny Ålesund (78°55'N 11°55'E; open circles) and Hopen (76°30'N 25°030'E; stars). Long-term trends indicate an increase of 0.18 °C yr⁻¹ (±0.04 SE, $t = 5.0$, $p < 0.001$) in Longyearbyen (solid line), of 0.14 °C yr⁻¹ (±0.03 SE, $t = 4.8$, $p < 0.001$) at Ny Ålesund (dashed line) and of 0.18 °C yr⁻¹ (±0.04 SE, $t = 4.8$, $p < 0.001$) at Hopen (dotted line). There was no interaction between trend and location ($p = 0.74$). Data are available at <http://www.eklima.met.no>.

et al., 2015). The current snow cover decline, observed in some geese breeding areas in Svalbard (Fig. 3), will likely further benefit the pink-footed goose population.

Clearly, the pink-footed goose is already benefiting from warming in Svalbard, and their abundance increase and corresponding expected range expansion (Jensen *et al.*, 2008) and shift from density-dependent to density-independent reproduction (Jensen *et al.*, 2014) represent one of the most significant changes in the terrestrial ecosystem in the archipelago (Ims *et al.*, 2014). Such an extreme increase in a herbivore population has the potential to affect the state of Svalbard's vegetation substantially (Van Der Wal, 2006; Gornall *et al.*, 2009; Sjøgersten *et al.*, 2010; Speed *et al.*, 2010; Pedersen *et al.*, 2013), with possible cascading consequences for other herbivorous species and their associated predators, as has been described from other Arctic regions (see Jefferies *et al.*, 2006, for a summary of a classical example from the coast of Hudson Bay).

Climate change and the Svalbard marine ecosystem

Svalbard marine environments: from Arctic to temperate conditions

Svalbard is strongly influenced by two main currents, the West Spitsbergen Current (WSC) that is characterized by relatively warm, salty Atlantic Water and the East Spitsbergen Current (ESC) that is characterized by colder and fresher Arctic Water (Svendsen *et al.*, 2002). The relative strengths of these currents, and thus the inflows of cold or warm waters, on the western coast of

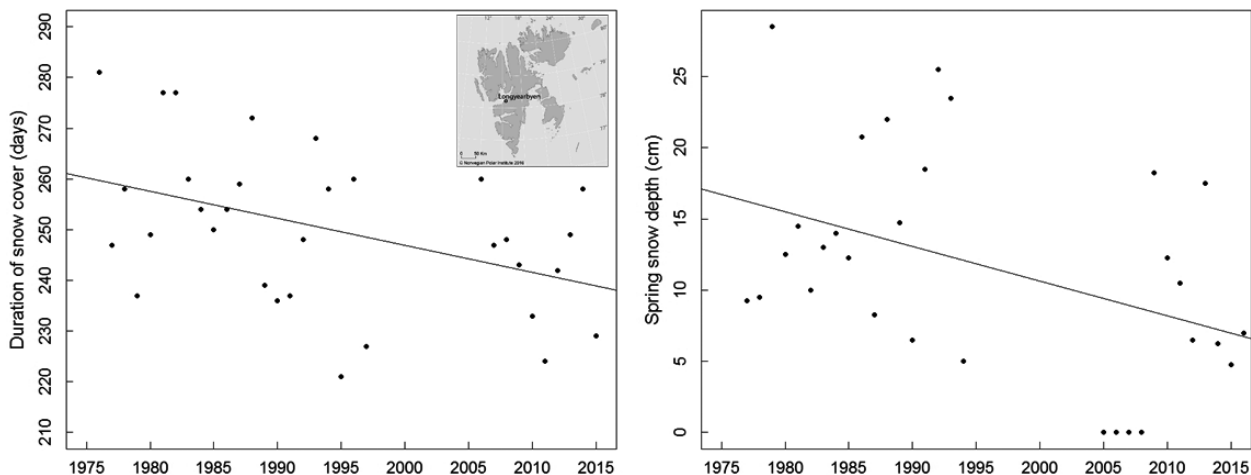


Fig. 3 Duration of snow cover (left panel) and spring snow depth (right panel) in Longyearbyen, Svalbard (78°14'N 15°30'E). The long-term trends (solid lines) indicate a decline of 0.5 day yr⁻¹ (±0.2 SE, $t = -2.6$, $p = 0.01$) in the snow cover duration and a decline of 0.24 cm yr⁻¹ (±0.01 SE, $t = -2.5$, $p = 0.02$) in the spring snow depth since the first measurements were made in 1976 and 1977, respectively. Data are available at <http://www.mosj.no/> (snow cover) and <http://www.eklima.met.no> (snow depth). Data from other Svalbard weather stations were too sparse to conduct similar analyses.

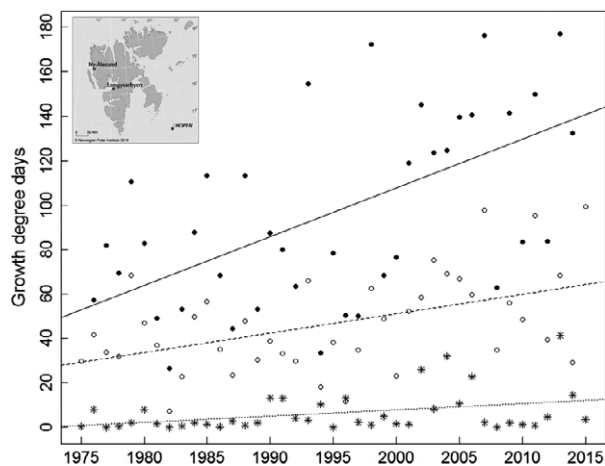


Fig. 4 Summer growth degree-days in Svalbard in the period 1975–2015. Symbols represent the sum of degree-days above 5 °C in summer (June–August) in Longyearbyen (78°14'N 15°30'E; filled circles), Ny Ålesund (78°55'N 11°55'E; open circles) and Hopen (76°30'N 25°30'E; stars). Long-term trends indicate a significant increase of 0.7 day yr⁻¹ (± 0.2 SE, $t = 4.4$, $p < 0.001$) in Longyearbyen (solid line), of 0.3 °C yr⁻¹ (± 0.09 SE, $t = 3.4$, $p = 0.002$) at Ny Ålesund (dashed line) and of 0.09 °C yr⁻¹ (± 0.04 SE, $t = 2.8$, $p = 0.02$) at Hopen (dotted line). Data are available at <http://www.eklima.met.no>.

Svalbard vary from year to year, but with a clear, increasing trend in warm Atlantic water in recent years (Moline *et al.*, 2008; Pavlov *et al.*, 2013). This warming of the sea (Fig. 5) is one of the main causes of the observed declines in sea ice extent around Svalbard (Onarheim *et al.*, 2014; Pavlova *et al.*, 2014; Fig. 6). Sea ice is a key habitat for all of the endemic marine mammals as well as for some species of invertebrates and some age groups of several fish species (the most important being polar cod *Boreogadus saida*), which are key prey for several Arctic bird and mammal species.

The changes in sea temperature and the changing nature of the sea ice (i.e. less multiyear ice, less seasonal coverage) have already affected the marine food web. For example, blue mussels *Mytilus edulis* have reappeared in Svalbard after an absence of 1000 years (Berge *et al.*, 2005), Atlantic cod *Gadus morhua*, Atlantic snake pipefish *Entolurus aequoreus* and haddock *Melanogrammus aeglefinus* have shifted their distributions poleward into Svalbard waters (Fleischer *et al.*, 2007; Renaud *et al.*, 2012), polar cod *Boreogadus saida* distribution and abundance are declining in the Barents Sea Region (Hop & Gjosaeter, 2013), and Atlantic mackerel *Scomber scombrus* have been recorded as novel fauna in coastal waters of Svalbard as of 2013 (Berge *et al.*, 2015). The changes in the marine environment are having consequences for upper trophic levels as well. For example, it has resulted in capelin replacing polar cod in the diet of breeding kittiwakes *Rissa tridactyla*

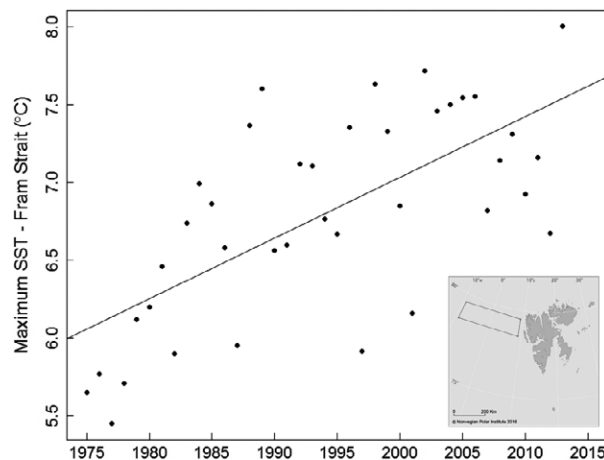


Fig. 5 Maximum annual sea surface temperature (SST) in the Fram Strait (transect between 78.5°N and 79.5°N,) in period 1975–2013. Long-term trends indicate a significant increase of 0.04 °C yr⁻¹ (± 0.007 SE, $t = 5.5$, $p < 0.001$). Data are available at <http://www.mosj.no/>.

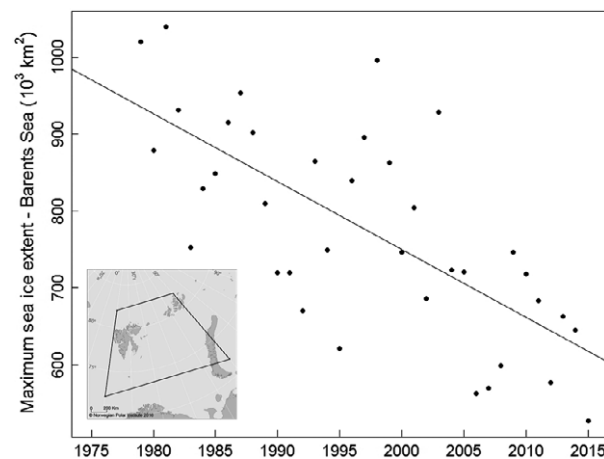


Fig. 6 Maximum sea ice extent in the Barents Sea. Symbols represent the annual sea ice extent in April in the area 72–82°N and 10–60°E. The long-term trend (solid line) indicates a significant decline of 8.8.10³ km² yr⁻¹ (± 1.5 SE) since the first measurements in 1979 ($t = -5.8$, $p < 0.001$). Data are available at <http://www.mosj.no/>.

(Gasbjerg, 2010). This particular dietary shift does not seem to be affecting the breeding success of this species (Gasbjerg, 2010), but the lower lipid contents of 'temperate' prey might affect some Arctic marine predators (Kovacs *et al.*, 2011).

Temperate marine species residing in Svalbard will likely benefit from the ongoing warming of sea temperatures. There is little published evidence thus far, but the following predictions describe likely future changes. For Svalbard's isolated harbour seal *Phoca vitulina* population (Andersen *et al.*, 2011), a warmer

climate with reduced sea ice is likely to result in a broader distribution and increasing population size. Currently, harbour seals in Svalbard avoid areas with dense ice concentrations (Blanchet *et al.*, 2014) and mainly occupy the west coast of Svalbard where warm Atlantic water dominates (Blanchet *et al.*, 2014, 2015). It is expected that these harbour seals will increase their distributional area including expanding their pupping range in the coming years, a development that satellite telemetry tracking data suggests is already ongoing (Hamilton *et al.*, 2014). The diet of this seal species in Svalbard has shifted from being dominated by Arctic cod to being dominated by Atlantic cod over the period of a decade, the latter being more normal for this species in more southerly parts of its distribution (Colominas, 2013). Other temperate species, such as the great skua *Stercorarius skua* and northern gannet *Morus bassanus*, are also likely to benefit from warming of the sea around Svalbard. These bird species were first observed breeding in Svalbard in 1970 and 2011, respectively, and since that time, their population numbers have been growing rapidly (Strøm, 2006; Strøm, unpubl. data). All of these findings are in accordance with a general 'borealization' (i.e. increase in abundance of temperate 'boreal' species, replacing the Arctic ones) of the northern Barents Sea fish community that has been well documented (Fossheim *et al.*, 2015).

Changes in sea ice and consequences on bird and mammal breeding ecology

Warming of the Arctic seas and associated declines in sea ice will affect some Arctic wildlife through more direct mechanisms than changes in food webs and prey availability. This prediction is based on observed effects of sea ice loss on the reproduction of some marine species and on the tight relationships that exist between the breeding ecology of these animals and their sea ice habitats. Indeed, sea ice is a breeding platform for most Arctic seals, including the ringed seal *Pusa hispida* and bearded seal *Erignathus barbatus* as well as the walrus *Odobenus rosmarus*. Arctic ringed seals in particular are obligate sea ice breeders (Lydersen & Kovacs, 1999). In Svalbard, the sea ice in the fjords has to be formed early enough in the season to accumulate sufficient snow to enable construction of ringed seal lairs (Lydersen & Gjertz, 1986; Lydersen, 1998). Lairs are used for protection against harsh winter weather and also protection from the many predators that prey on ringed seal young, including polar bears *Ursus maritimus*, Arctic foxes and even avian predators such as glaucous gulls *Larus hyperboreus* (Gjertz & Lydersen, 1986; Lydersen & Smith, 1989). In most recent years (since 2006), sea ice has formed very late in the season if it has formed at all

and there has been little or no snow cover on the ice. As a result, there have been unnaturally high densities of ringed seals in the small areas that have land-fast ice during the pupping period, and females have given birth directly on the ice in areas with insufficient snow, leaving pups without the protection afforded by the snow lair. Pup mortality rates are extraordinarily high under such conditions (Lydersen & Smith, 1989; Smith & Lydersen, 1991, Kovacs and Lydersen, pers. obs).

For polar bears, sea ice provides a corridor that allows for movement between hunting, mating and denning areas (Hansen *et al.*, 2010; Derocher *et al.*, 2011). In Svalbard, some of the remote islands such as Kongsøya, Svenskøya and Hopen, have traditionally been very important polar bear denning areas because their rough topography allows snow to accumulate in sufficient amounts on the leeward sides of mountains and other topographical structures, for the purposes of denning (Andersen *et al.*, 2012). But, in recent years, sea ice has formed late and few females have reached Hopen and Kongsøya for denning (Derocher *et al.*, 2011; Aars, 2013).

Changes in sea ice and consequences on bird and mammal foraging ecology

The spring phytoplankton bloom is tightly associated with sea ice edges (Perrette *et al.*, 2011), which attract high densities of seals, whales and seabirds (Hunt *et al.*, 1996). Several species of seabirds remain tightly associated with sea ice for their entire annual cycle (e.g. ivory gull *Pagophila eburnea*) while other species spend somewhat less of their annual cycle (e.g. little auk *Alle alle* or Brünnich's guillemot *Uria lomvia*) in tight association with sea ice, feeding along ice edges (Bakken, 1990; Isaksen & Bakken, 1995; Mehlum, 1997; Gilg *et al.*, 2010; Jakubas *et al.*, 2011, 2012; Spencer *et al.*, 2014).

The summer position of the marginal ice zone around Svalbard has shifted in recent years from over the continental shelf, northward to the deep Arctic Ocean Basin (Hamilton *et al.*, 2015). This change has been associated with changes in the movement patterns and foraging behaviour of juvenile ringed seals, all of which indicate increased energetic costs for finding food in conditions with decreased sea ice (Hamilton *et al.*, 2015). The mechanism likely involves a decrease in habitat quality for ice-associated organisms such as the polar cod, which is a preferred prey species for ringed seals.

Sea ice is also used by seals and seabirds as a resting platform (Humphreys *et al.*, 2007) and is the major hunting habitat for polar bears (Amstrup, 2003). Polar bears are dependent on sea ice because their two most important prey species, ringed seals and bearded seals, live in association with ice and bears are only rarely

able to capture seals in open water (Stirling, 2011). Female bears are dependent on land-fast ice, in particular close to glacier fronts in Svalbard, in the early spring when they emerge from dens with young cubs. These are the prime ringed seal breeding habitats which provide the bears with predictable and abundant prey (i.e. ringed seal pups), allowing them to regain their condition after many months of fasting, while nursing their cubs in the den (Freitas *et al.*, 2012). Hunting on the sea ice in other seasons is of course also important; pregnant females that are unable to gain enough fat in the summer and fall to sustain the long winter denning period will not be able to rear cubs.

To date, the consequences of changes in sea ice on the foraging of Svalbard wildlife has only been quantified for the ringed seals (Hamilton *et al.*, 2015, 2016). However, considering the primary role of sea ice in the foraging of many other species, including the polar bear, the prediction that the ongoing decline in sea ice will negatively affect these species seems quite robust.

Climate change and interactions between the marine and terrestrial ecosystems

Terrestrial and marine ecosystems in the Arctic are tightly linked through both physical and biological processes. For example, sea ice losses contribute to near-surface warming over land across the Arctic (Screen *et al.*, 2012) and earlier annual sea ice melt and ice losses can influence seasonality in terrestrial ecosystems. Several studies have identified Arctic sea ice signals in the annual timing of vegetation emergence (i.e. timing and abundance of plant growth) in inland sites on Greenland (Bhatt *et al.*, 2010; Kerby & Post, 2013; Post *et al.*, 2013). Another example of the linkage between terrestrial and marine ecosystems is the transport of nutrients by marine birds from sea to land, which can increase primary and secondary production and species diversity markedly on a local basis (Ellis *et al.*, 2006; Stempniewicz *et al.*, 2006). Other links between the marine and terrestrial environments do exist, and some of them have changed in recent years in Svalbard as a response to climate warming (see below).

Changes in sea ice and predator–prey interactions

Changes in sea ice and especially land-fast sea ice affect some predator–prey interactions. For island-breeding sea ducks and geese, the time of break-up of the surrounding sea ice is an important factor determining the survival of eggs; Arctic fox predation is high when there is an ice bridge to land and almost non-existent if the island is surrounded by only water when egg-laying starts (Hanssen *et al.*, 2013). In western Svalbard,

reduced sea ice concentrations have been associated with higher numbers of breeding eiders (Hanssen *et al.*, 2013). However, reduced sea ice cover is also associated with a higher risk of nest depredation by polar bears for many ground-nesting bird species, such as the common eider, as has been observed in many Arctic areas (Smith *et al.*, 2010; Gaston & Elliott, 2013; Iverson *et al.*, 2014) including Svalbard (Prop *et al.*, 2015).

Changes in sea ice and predicted movements of terrestrial species

Sea ice allows dispersal (e.g. Svalbard reindeer, Hansen *et al.*, 2010) or broader access to feeding grounds for some terrestrial species. The Arctic fox uses both terrestrial and marine food webs, and this predator's movements can be affected markedly by changes in sea ice extent and dynamics. Decreases in sea ice extent and loss of sea ice habitat connectivity will likely impact the Arctic fox's foraging through the loss of ringed seal pups, polar bear carrion and reduced access to other marine foods (Fuglei & Ims, 2008; Ims *et al.*, 2013). Loss of sea ice connectivity between Arctic islands and continents will also likely cause isolation of the Arctic fox in Svalbard, with consequences for the genetic structure of this and other Arctic fox populations in the future (Carmichael *et al.*, 2007; Geffen *et al.*, 2007).

Snow conditions on land and effects on reproduction of marine birds

Breeding of species such as common eiders and little auks are affected by late snow melt. Moe *et al.* (2009) found that for little auks breeding on the west coast of Spitsbergen, the timing of egg laying was determined by temperature and snow melt in the colony. The common eider in Kongsfjorden initiates breeding earlier in years with early sea ice and snow cover retreat (Hanssen *et al.*, 2013). More generally, the predicted earlier snow melt and shorter snow cover duration in the Arctic (Liston & Hiemstra, 2011), which is supported by local meteorological observations in Svalbard (Fig. 3), is likely to have positive effects on ground-nesting species by allowing an earlier onset of reproduction. Another possible consequence of earlier snow melt is access to new breeding grounds at the limits of the species' range (Jensen *et al.*, 2008), with a displacement of the population towards undisturbed habitats in more northerly areas.

Importance of glacier fronts

Recent studies in several Arctic regions, including Svalbard, stress the importance of tidewater glaciers as key

foraging areas for various predators such as seabirds, seals and Arctic whales (Arimitsu *et al.*, 2012; Lydersen *et al.*, 2014; Hamilton *et al.*, 2016). Glacier fronts also represent important hunting areas for Arctic foxes in the spring (Lydersen *et al.*, 2014). Additionally, glacier pieces drifting at the surface near glacier fronts are used as resting platforms for many seabirds and seals (Lydersen *et al.*, 2014); the latter's use of this habitat means that it is also important hunting habitat for polar bears throughout the spring, summer and fall. It has been suggested that glacier melting and the increase in glacier discharge may counterbalance, at least over the short term, the negative consequences of sea ice loss by increasing coastal productivity. Indeed, little auks in Franz Josef Land recently switched from foraging at the sea ice edge to feeding close to glacier fronts, while maintaining the same chick growth rate (Gremillet *et al.*, 2015). However, the current mass balance for most of Svalbard's glaciers is negative, and the rate of ice loss has accelerated in the recent decades (Kohler *et al.*, 2007). Continued warming is expected to reduce the number of tidewater glaciers and also the overall length of calving fronts around the Svalbard Archipelago (Lydersen *et al.*, 2014). Thus, these important foraging hotspots for Svalbard's marine mammals and seabirds will gradually become fewer and will likely eventually disappear.

Diseases and parasitism

Rising temperatures can favour the emergence of new diseases or parasites (Epstein, 2001; Harvell *et al.*, 2002), and also exacerbate the impacts of contaminants (e.g. Kallenborn *et al.*, 2012), with potentially important consequences on wildlife population dynamics. This is likely to be exaggerated in the Arctic where changes in host–parasite relationships have already been linked to temperature shifts (Kutz *et al.*, 2005). In Svalbard, several studies have emphasized direct or indirect effects of climate warming on parasitism and disease risk. For example, the prevalence of ticks *Ixodes uriae* on the Brünnich's guillemot is strongly linked to the average winter temperature (Descamps, 2013) and an increase of 1 °C in the average winter temperature was associated with a 5% increase in the number of birds infected by these ectoparasites. Another example is the increase in toxoplasmosis in the Svalbard Arctic fox population, which is thought to be related to increasing goose populations breeding in Svalbard (Prestrud *et al.*, 2007). Similarly, toxoplasmosis prevalence in polar bears, ringed seals and likely also bearded seals has increased in recent decades (Jensen *et al.*, 2010). Oocysts may have increased survival when brought north with ocean currents from areas off coastal Norway, due to

warmer sea water (Jensen *et al.*, 2010). Even if the changes documented so far have no detrimental effect on the host population trends, an increase in parasite load or prevalence clearly represents an additional stressor on populations already challenged by other physical and biotic changes in their environment(s).

Perspectives

Model projections indicate that we are just beginning to experience dramatic increases in temperature in the Arctic (Intergovernmental Panel on Climate Change, 2014). The combination of extreme values occurring with higher frequencies both in summer and winter seasons suggests that Svalbard will experience 'new climate' regimes if current trends continue (Ims *et al.*, 2014). Projections for year 2100 suggest an annual temperature increase of +2–8 °C (Førland *et al.*, 2012) and mid-winter temperatures close to 0 °C (Hansen *et al.*, 2014), with the southern vegetation growth seasons expected to move >20 latitudinal degrees north (Xu *et al.*, 2013). This means an expected bioclimate for Svalbard similar to the present one found in Denmark. Implications of such changes are difficult to comprehend, and consequences for Arctic ecosystems are hard to predict, although they are expected to be profound.

Changes in Svalbard's physical environment are already impacting wildlife within the archipelago, directly and indirectly. Even though a few species may be considered 'climate warming winners' (e.g. pink-footed geese and harbour seals), most of the Arctic endemic species in Svalbard are suffering negative consequences from a warming environment (Table 1). The changes in the physical environment are occurring so rapidly (and unidirectionally) that species can only adapt or respond via (micro) evolution or phenotypic plasticity, or dispersal to more suitable habitats (Parmesan, 2006; Gilg *et al.*, 2012; Carlson *et al.*, 2014). If they are not able to respond in these ways, local extinction is expected. For long-lived species, adaptation through evolution (i.e. evolutionary rescues, Carlson *et al.*, 2014) is very unlikely, considering the speed of the current environmental change (Berteaux *et al.*, 2004). Potential for dispersal is also limited, especially for terrestrial species considering Svalbard's remote, isolated location and declining sea ice situation; sea ice has in the past acted as a transport corridor between land masses in some years. In theory at least, some species may show short-distance movements, moving to East Svalbard, for example, which is colder (Svendsen *et al.*, 2002), or shifting altitudinal distribution to remain in cold environments, but such shifts are unlikely to represent long-term solutions for most species; East Svalbard is

only a temporary refuge as it too is warming. Phenotypic plasticity might allow some marine species to switch their diets towards new prey types (e.g. switch from polar cod to capelin in Brünnich's guillemot in Canada, Gaston *et al.*, 2012; increased use of seabird eggs and chicks by polar bear in Hudson Bay, Iverson *et al.*, 2014; and in Svalbard, Prop *et al.*, 2015), or perhaps to change their foraging habitats to maintain their current diets into the future.

Understanding and predicting the population- and ecosystem-level impacts of climate warming on wildlife is an extremely challenging task. Our review indicates that most measured or predicted effects of a warming climate are, or will be, detrimental to Arctic wildlife. However, some of these effects remain speculative or are based on short-term measurements (Table 1), leaving many of these findings in the realm of solid predictions rather than confirmed outcomes. Moreover, there might also be some environmental changes that will affect wildlife in unexpected ways. Climate warming is associated with changes in many biotic (e.g. predator–prey relations) and abiotic environmental parameters and interactions simultaneously (e.g. timing of ice break-up, warming of the sea, increased frequency of ROS events) at various periods of the year. Populations of birds and mammals are driven by changes in survival and reproduction, and in some cases, also by emigration/immigration processes. Each of the demographic parameters might respond differently, and not necessarily linearly, to changes in the environment. Some species or parameters might be affected most by changes in summer conditions while others might be most affected by changes in winter conditions, for example, and the directions of the effects are not necessarily the same. In this context, it is important to consider the potential positive effects of environmental changes on a short-time scale. In particular, climate warming increases glacier discharge which may partly counterbalance the negative consequences of sea ice loss over the short term by increasing coastal water productivity (Gremillet *et al.*, 2015). However, continued warming will reduce the number of glacier fronts that make contact with the sea, which are important foraging hotspots, notably for Svalbard's marine mammals and seabirds (Lydersen *et al.*, 2014). Similarly, contracting sea ice will have detrimental consequences for sea ice-associated marine mammals, including the ringed seal and polar bear. However, over the short term, reduced sea ice extent may have positive consequences on polar bears, through higher seal densities (that gathered within smaller ice-covered areas) and thus temporarily better foraging conditions in the spring. This remains speculative, but emphasizes the need to incorporate

potential positive short-term effects associated with climate warming into our predictive models.

Finally, past histories of exploitation and relative carrying capacities also need to be taken into account for some species (Laidre *et al.*, 2015). Some long-lived, top trophic animals in Svalbard such as walrus have been increasing despite environmental change that is likely lowering the carrying capacity markedly for the species, because their numbers were artificially low due to past overexploitation (Kovacs *et al.*, 2014). This population level vs. carrying capacity issue might also be a factor in how little Svalbard's polar bears have been affected thus far. The polar bear population was protected in 1973 after more than 100 years of intensive hunting that had markedly depleted this population.

To understand the impact of climate warming on population growth rates, it is essential to understand the main trophic interactions between the different components of the food webs, including the interactions between marine and terrestrial ecosystems (Post *et al.*, 2009). This task is challenging and requires long-term monitoring of demography and population sizes combined with tracking and diet studies to identify key habitats, foraging areas and prey (and thus trophic relationships). Such studies should take advantage of, and expand upon, the development of new technologies and analytical tools which enable year-round studies including the nonbreeding season (Marra *et al.*, 2015). Long-term (i.e. multidecadal) adaptive ecosystem-based monitoring (Lindenmayer & Likens, 2009) would facilitate understanding the mechanisms involved in negative impacts, increase our predictive power and allow appropriate management actions to be undertaken to conserve Arctic flora and fauna. An adaptive monitoring scheme would facilitate tracking early signs of unexpected effects of climate warming on wildlife, which are likely to be numerous. There are few sites in the Arctic where such ecosystem monitoring is conducted (see fig. 2a in Legagneux *et al.*, 2014). The research effort to evaluate the impact of climate warming in the Arctic is thus rather limited (see Wassmann *et al.*, 2011 for a similar view). Maintaining ongoing ecosystem monitoring programmes into the future should be viewed as a priority. These programmes, many of which focus mainly on the terrestrial (tundra) environment, should be expanded to take into account trophic interactions between marine and terrestrial ecosystems.

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