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Long-term monitoring at multiple trophic levels suggests heterogeneity in responses to climate change in the Canadian Arctic tundra

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Arctic wildlife is often presented as being highly at risk in the face of current climate warming. We use the long-term (up to 24 years) monitoring records available on Bylot Island in the Canadian Arctic to examine temporal trends in population attributes of several terrestrial vertebrates and in primary production. Despite a warming trend (e.g. cumulative annual thawing degree-days increased by 37% and snow-melt date advanced by 4–7 days over a 23-year period), we found little evidence for changes in the phenology, abundance or productivity of several vertebrate species (snow goose, foxes, lemmings, avian predators and one passerine). Only primary production showed a response to warming (annual above-ground biomass of wetland graminoids increased by 123% during this period). We nonetheless found evidence for potential mismatches between herbivores and their food plants in response to warming as snow geese adjusted their laying date by only 3.8 days on average for a change in snow-melt of 10 days, half of the corresponding adjustment shown by the timing of plant growth (7.1 days). We discuss several reasons (duration of time series, large annual variability, amplitude of observed climate change, nonlinear dynamic or constraints imposed by various rate of warming with latitude in migrants) to explain the lack of response by herbivores and predators to climate warming at our study site. We also show how length and intensity of monitoring could affect our ability to detect temporal trends and provide recommendations for future monitoring.

1. Introduction

The planet is currently warming and it is in the polar regions that this warming is proceeding at the fastest pace [1–3]. The effects of climate warming on the physical environment of the polar regions are well documented and include melting of icecaps and glaciers, deepening of the summer thawing of permafrost and decrease in snow and sea-ice cover [2,4–7]. Although some studies have documented similar impacts on Arctic biological systems [8–12], evidence remains limited and generally biased toward lower trophic levels (e.g. plants).

Arctic wildlife is often presented as being highly at risk in the face of current climate warming [1,13,14]. However, studies documenting clear, unequivocal impact of warming on Arctic wildlife are still scant, though exceptions exist (e.g. impact of receding sea ice on southern populations of polar bears, *Ursus maritimus* [15–17]). Several reasons may explain the paucity of evidence. First, the most studied taxa of tundra wildlife are endothermic animals, which are generally buffered from the direct impacts of temperature changes, unlike lower trophic levels (i.e. plants or detritivores). Second, animals show
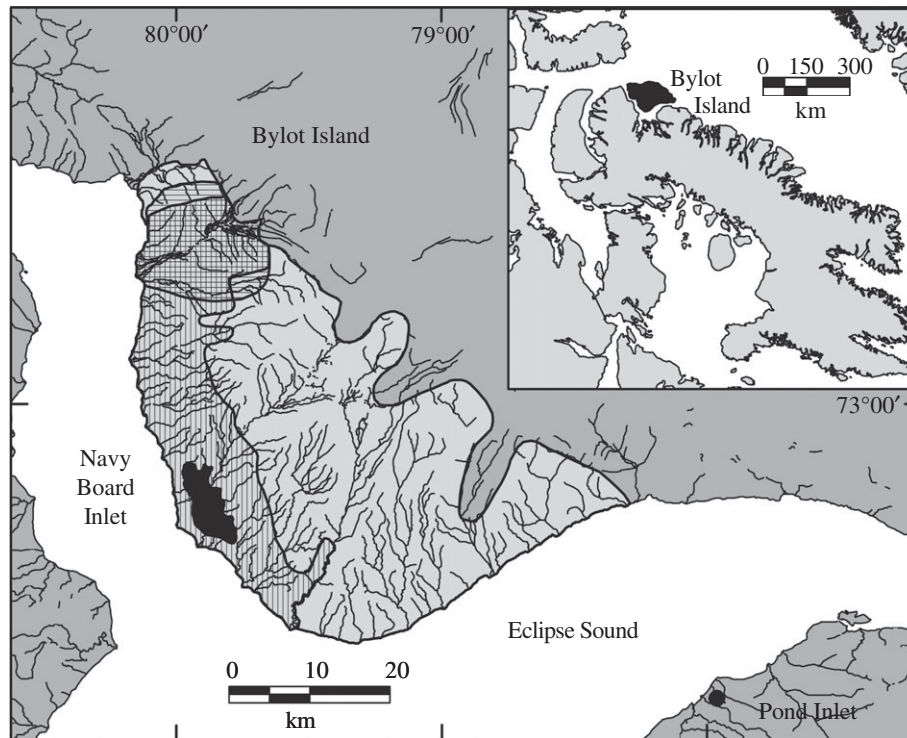
Figure 1. Localization of the study area. Light grey: South Plain of Bylot Island; horizontal hatch: Qarlikturvik Valley (main study area); vertical hatch: study area for foxes; black area: snow goose nesting colony.

phenotypic plasticity that allows them to cope with short-term environmental changes, though within some limits [18]. Third, the majority of breeding species are long-distance migrants that only come to the Arctic during the summer. For the rest of the year, they are exposed to different climatic regimes that may be changing at a different pace than in the Arctic [19,20]. Fourth, considering the large inter-annual variability in climate and the multiple drivers of animal populations besides climatic conditions [21–23], detecting temporal trends in animal populations (or their attributes, e.g. phenology) requires long-term datasets, which are rare in the Arctic [24].

We argue that a sound assessment of the impact of climate warming on Arctic wildlife requires three key elements. First, it must be based on long-term datasets. Second, it requires the intensive monitoring of several population attributes, in particular population size, demography and phenology. Third, it should involve multiple species and ideally key players at all levels of the food web (i.e. plants, herbivores and predators). The last point is important because, for endotherms inhabiting the tundra, it has been suggested that the most severe impact of climate warming may be indirect, through alterations in trophic interactions such as change in food availability, predation pressure, apparition of new competitors or mismatch between trophic levels [25–27]. Therefore, a food web approach is essential in order to fully understand the impact of climate warming on individual species [28].

Long-term monitoring of wildlife populations are especially scant in the vast Canadian Arctic but one site where such records are available is Bylot Island, Nunavut. This high Arctic site is located in the eastern Canadian Arctic Archipelago and several key components of the tundra food web have intensively been monitored during the past two decades [29–31]. Like many other Arctic sites, this region has experienced warming for the past 40 years [30]. We use the long-term records available at this site to first examine temporal trends in population attributes

(primarily phenology, abundance and productivity) of several herbivorous, insectivorous and carnivorous species of terrestrial birds and mammals, as well as in primary production. Second, we determine to what extent climatic conditions (primarily temperature and snow) can explain annual variation in these population attributes and, when detected, in temporal trends, and we discuss how this should impact these populations and ultimately the whole food web in the future. This also leads us to emphasize the difficulties associated with the detection of temporal trends or the attribution of annual variations and temporal trends to climatic variation. Third, considering the costs and efforts required to maintain long-term programmes in the Arctic, we also investigate how length and intensity of monitoring could affect our conclusions and we provide some recommendations for future monitoring programmes.

2. Material and methods

(a) Study site
Bylot Island is an 11 100 km^2 island located at the northern tip of Baffin Island, Nunavut, in the Canadian Arctic (figure 1). The island is dominated by mountains culminating at almost 2000 m and a large icecap except for the 1600 km^2 South Plain, which is bordered to the north by the mountains and to the south by the sea (Navy Board Inlet and Eclipse Sound). This portion of the island is characterized by flat lowlands and upland plateaus dissected by valleys, with elevation generally below 350 (m).a.s.l. It is covered by relatively lush tundra vegetation for the latitude due to the generally southern exposure and the relative protection offered by the mountains from the cold, northerly winds. Average annual temperature is −15°C [32]. The coldest month of the year is February and the warmest is July (average temperature during these two months is −34°C and +6°C, respectively). Snow typically covers the ground from late September to mid-June.

We can recognize three main plant communities on Bylot Island, which are largely determined by soil moisture and elevation. Wetlands occur in low-lying areas such as along streams and shallow ponds and, most commonly, in low-centre tundra polygons created by the growth of ice wedges in the permafrost. These sites are typically moss-covered fens dominated by grasses and sedges such as *Dupontia fisheri*, *Carex aquatilis* and *Eriophorum scheuchzeri*. Mesic tundra covers most of the landscape on plateaus and gentle slopes and frequently forms hummocks. The most common plants of the mesic tundra are prostrate shrubs (*Salix arctica*, *Vaccinium uliginosum*) and forbs (e.g. *Cassiope tetragona*, *Luzula* spp.) along with some grasses (*Arctagrostis latifolia*, *Poa arctica*) and mosses. Finally, exposed areas with dry, gravel soil such as ridges or high-elevation sites have a very sparse vegetative cover consisting of only a few plant species such as *Dryas integrifolia* or *Saxifraga oppositifolia* [33,34].

The main herbivore at the study site during the summer is the colonial-nesting greater snow goose (*Anser caerulescens atlanticus*). During nesting, geese are restricted to a small area but during brood-rearing families disperse throughout the South Plain of the island [35]. Two species of small mammals are present, the brown (*Lemmus trimucronatus*) and collared (*Dicrostonyx groenlandicus*) lemmings. The former species has regular, high-amplitude cycles of abundance with a 3–4-year periodicity whereas the collared has weak, low-amplitude cycles [36]. Other herbivores such as the rock ptarmigan (*Lagopus mutus*) and Arctic hare (*Lepus arcticus*) are also present but in low numbers. Large mammalian herbivores such as muskox (*Ovibos moschatus*) or caribou (*Rangifer tarandus*) are absent. Insectivorous migratory birds are abundant and include a few passerines (mostly Lapland longspur, *Calcarius lapponicus*) and several species of shorebirds (primarily *Calidris* spp. and *Pluvialis* spp. [30]). The mammalian predator guild is dominated by two species that are year-round residents, the Arctic fox (*Vulpes lagopus*) and the stoat (*Mustela erminea*). Red foxes (*Vulves vulpes*) have been present in low numbers in the region since the 1950s [37]. Numerous avian predators are present during the summer, especially the snowy owl (*Bubo scandiacus*), rough-legged hawk (*Buteo lagopus*), long-tailed jaeger (*Stercorarius longicaudus*), parasitic jaeger (*S. parasiticus*) and glaucous gull (*Larus hyperboreus*), though the abundance of the first three species can vary considerably with the phases of lemming cycle [38].

Our activities are conducted primarily at two sites on the island, the large Qarlikturvik Valley (approx. 100 km^2; 73° 08′ N; 80° 00′ W), and a secondary site 30 km to the south (approx. 30 km^2; 72° 53′ N, 79° 55′ W) in the centre of the large greater snow goose nesting colony (figure 1). However, some of the monitoring activities (e.g. for foxes and for some avian predators) encompass a 60-km long coastal area (approx. 520 km^2) including these two sites.

(b) Field methods

We have maintained since 1994 a fully automated weather station operating year-round in the Qarlikturvik Valley (located at 20 (m).a.s.l.). The station recorded on an hourly basis air temperature and humidity (at 2 m), soil temperature (10 cm deep), wind speed and direction (at 3 m), snow depth and solar radiation [39]. Snow-melt was monitored from 1 June until snow disappearance by visually estimating snow cover in the Qarlikturvik Valley from a vantage point at 2-day intervals. We also retrieved weather data from the Environment Canada weather station located at the Pond Inlet airport on Baffin Island (72°41′ N, 77°59′ W; 80 km southeast from the Qarlikturvik Valley weather station). Weather data from our automated station and Pond Inlet over the period 1995–2004 were highly correlated and thus could be used to extend the time series of climatic data from our station (once properly adjusted, following the approach of Dickey *et al.* [40]). We also retrieved monthly values of the North Atlantic Oscillation

(http://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/norm.nao.monthly.b5001.current.ascii.table) to look at temporal trends for the months of interest (May to September).

We have monitored the annual plant production and goose grazing impact in wetlands of the Qarlikturvik Valley since 1990. Each year, 12 new exclosures (1 × 1 m) made of chicken wire and spread over approximately 1 km^2 area were installed in late June to prevent goose grazing. At the end of the plant growing season (i.e. mid-August), we sampled the vegetation by removing a 20 × 20 cm piece of turf inside and outside of each exclosure. Live above-ground plant biomass was cut, sorted out, dried and weighed. Live above-ground biomass inside exclosures in mid-August is a good measure of annual production of graminoids, which account for more than 90 per cent of the vascular plant biomass in wetlands [41]. Goose grazing impact was assessed by the difference in biomass inside and outside exclosures [42]. In some years, graminoids (*E. scheuchzeri* and *D. fisheri*) were also sampled inside exclosures at 10- to 14-day intervals and dried samples were analysed for nitrogen concentration to determine seasonal variations in plant nutritive quality (see [43] for details).

An annual index of lemming abundance in the Qarlikturvik Valley has been obtained in mid-July using snap-traps (greater than or equal to 1000 trap-nights each year) since 1993. Since 2004, monthly density of brown and collared lemmings has been estimated via capture–mark–recapture methods using live-trapping data from two 11-ha grids in the same area. Each grid had 144 traps laid out every 30 m in a 12 × 12 Cartesian plan (see [36,44] for details). Using the relationship between annual lemming density estimated from live recapture (N) in July and the abundance index (I) derived from snap-trapping over the period 2004–2011 ($\log(N) = 1.33 \log(I) + 0.55$; $r^2 = 0.82$), we obtained a time series of annual lemming density from 1993 to 2012 [31].

We have monitored annually the reproductive activity of a large number of birds. The longest time series available are for the snow goose (since 1989), snowy owl (since 1993), Lapland longspur (since 1995) and the long-tailed jaeger (since 2004). Nests of these species were found during systematic searches of the study area, except for longspurs for which nests were found opportunistically. Because geese nest colonially, nest density in this case refers to the central portion of the colony that was monitored annually. Nests were revisited periodically to determine their content (clutch size), phenology (laying date) and success (number of young hatched or fledged). For snow geese, arrival date in early June was also monitored by counting birds on the first snow-free areas at 2-day intervals (see [29,45] for methods). These data provide information on annual abundance, phenology and reproductive success of these species.

We monitored fox dens opportunistically from 1993 to 2002 and systematically throughout the study area since 2003 [46]. Known dens were checked for breeding activity of Arctic and red foxes every year in summer [47]. Since 2003, adult and juvenile Arctic foxes were captured, marked with ear tags and sampled (blood and hairs) in summer for analysis of carbon and nitrogen isotopic ratios [48].

(c) Data analysis

The following variables were extracted from the field data. Cumulative thawing degree-days (TDD) was defined as the sum of the daily mean temperature above 0°C up to a given date. Daily snow depth values from the first snowfall until snow-melt were averaged to obtain mean winter snow depth (see [49] for details). Laying date was defined as the day that the first egg of a nest was laid and clutch size as the maximum number of eggs recorded in a nest after the start of incubation. Hatching success was the

probability that at least one egg would hatch in a clutch and nesting success was the probability that at least one young would successfully leave the nest.

Doiron *et al.* [43] showed that date of 50 per cent maximum normalized difference vegetation index (NDVI) was a very good predictor of date of peak nitrogen concentration in graminoids at our study site. Because the former variable was measured during only 10 years, we extended the time series by retrieving annual NDVI values from our study site and applying the equation of Doiron *et al.* [43] to predict date of peak nitrogen concentration in graminoid plants from the date of 50 per cent maximum NDVI. However, NDVI was not a good predictor of the actual peak nitrogen concentration and thus we could not extend the time series for the latter variable.

For birds, abundance estimates are based on nest density and thus incorporate only the breeding segment of the population. In some species, annual variation in reproductive effort can be large and may depend on abiotic (e.g. temperature in spring for geese [40]) or biotic factors (e.g. lemming abundance for predators [29]). Therefore, variation in breeding density may not always be indicative of genuine change in population size. In the case of the snowy owl, as breeding occurs only when lemming abundance is high and non-breeding adults are rarely seen [29], we excluded years without nesting owls from the analysis.

Arctic fox productivity is defined as the proportion of monitored dens where an Arctic fox litter emerged (natal dens). The nitrogen isotopic ratio in fox blood is used here as a trophic index, assuming that higher $\delta^{15}N$ generally indicates foraging at higher trophic levels [50]. On Bylot Island, a higher $\delta^{15}N$ also reflects stronger reliance of foxes on marine food [48].

We used linear regression to examine temporal trends in the data. However, temporal series are often subject to autocorrelation problems, which could bias the parameter estimates of the regression [51]. To test for that, we computed the Durbin–Watson statistic and we adjusted first- and second-order autoregressive models (procedure autoreg in SAS, [52]). We used the AICc to determine whether a model with autoregressive terms fitted our data better than a simple regression model. We present parameter values of the best fitting model (i.e. either with or without the autoregressive terms). When needed, data were log-transformed (or arcsine-transformed for proportion) to respect normality and homogeneity of variance.

Data used in this paper have been deposited in the Polar Data Catalogue (http://www.polardata.ca).

3. Results

(a) Climate

Average monthly temperature over the past 24 years showed a strong warming trend in both spring and summer on Bylot Island (see the electronic supplementary material, figure S1). The increasing trends ranged from 0.3°C per decade in June to 1.1°C per decade in May and August. The average number of frost-free days also increased from 97 in 1989 to 106 in 2011 (see the electronic supplementary material, figure S2) and the average annual cumulative number of TDD by 37 per cent (from 381 to 521 TDD; figure 2). Cumulative TDD to 15 August, when we sampled plants, showed the same trend. Temperature at nearby Pond Inlet revealed similar warming trends over the same period with generally steeper slopes (see the electronic supplementary material, table S1). However, annual mean ground temperature at 10 cm did not show any trend on Bylot Island ($\beta = 0.002$°C per year; overall mean, -10.9°C).
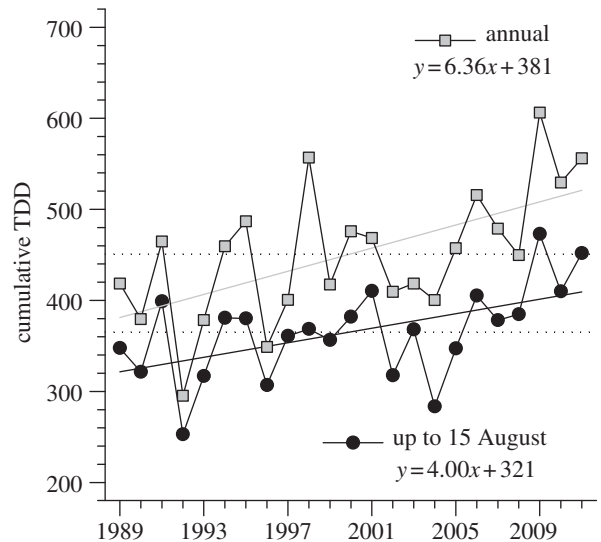

Figure 2. Cumulative thawing degree-days (TDD = degree-days above 0°C) in the Qarlikturvik Valley of Bylot Island from 1989 to 2011. The dotted lines show the mean for the whole period. The regression lines show the temporal trends (1989 = year 0 in the regression equations).

The North Atlantic Oscillation (NAO), a large-scale climatic index that has previously been shown to affect wildlife populations on Bylot Island [40,53], has changed during the spring and summer over the same time period. Average monthly NAO from May to September showed a strong decreasing trend over the past 24 years (see the electronic supplementary material, table S1). On average, it decreased from 0.36 in 1989 to −0.77 in 2012. Negative NAO values are associated with warm temperature on Bylot Island [53], which fits well with the observed warming trend.

Mean winter snow depth increased by 48 per cent from 1994 to 2010 (figure 3*a*). Despite this deeper snow cover, there was a trend for an advance in snow-melt; average date at which the ground was 50 per cent snow-free advanced by 4.1 days from 1989 to 2012 (figure 3*b*). However, one point (i.e. the very early snow-melt in 1993) is highly influential in this relationship; excluding this point, the advance in snow-melt date was 6.6 days.

(b) Phenology

Date of peak nitrogen concentration of graminoid plants showed large inter-annual variability but no clear temporal trend (table 1 and figure 4*a*). Despite the trend for warmer spring and earlier snow-melt in recent years, we found little evidence for changes in the phenology of nesting birds. Laying date of snow geese, the species for which we had the longest record (24 consecutive years), did not show any temporal trend (figure 5*a*). We found similar results for snowy owl and Lapland longspur laying dates (table 1). Peak arrival date of snow geese in spring showed a weak trend to occur later over the past 17 years (2.0 days per decade) but the relationship was not statistically significant (table 1).

Considering the lack of temporal trends in our phenological data, we examined how inter-annual variability in the timing of snow-melt affected phenology, focusing on the datasets for which we had the longest record, snow geese and their graminoid food plants. There was a positive relationship between the date of 50 per cent snow cover in spring and annual median
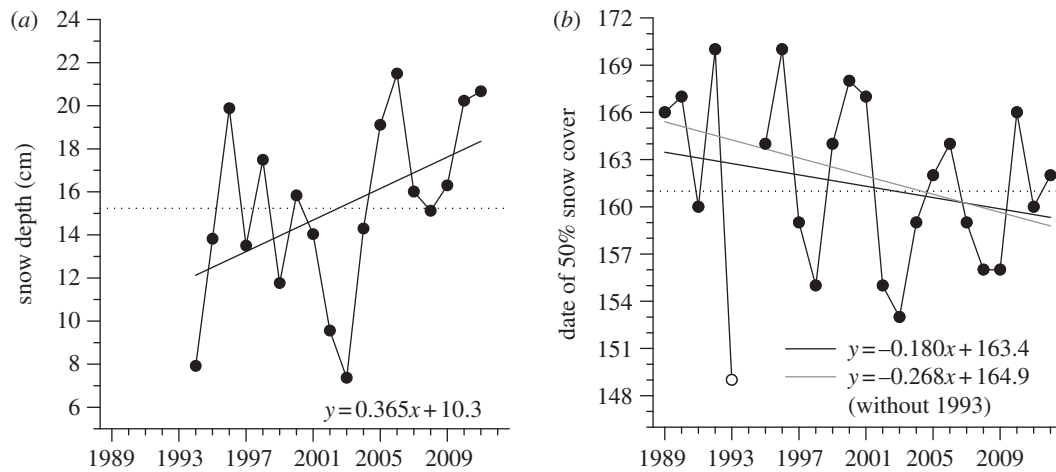
Figure 3. (a) Mean annual winter snow depth (cm) and (b) date of 50% snow cover (day of the year) in the Qarlikturvik Valley of Bylot Island from 1989 to 2012. The dotted lines show the mean for the whole period. The regression lines show the temporal trends (1989 = year 0 in the regression equations).

laying date of geese ($F_{1,21} = 15.1$, $p < 0.001$, figure 5b) but the slope was only 0.38 (95% CI = 0.18–0.58), significantly less than unity. Geese undercompensated since, for a change in snow-melt of 10 days, they adjusted their laying date by only 3.8 days. Date of peak nitrogen concentration in plants was also related to date of 50 per cent snow cover ($F_{1,16} = 11.5$, $p = 0.004$) but this time the slope did not differ significantly from unity ($\beta = 0.71$, 95% CI = 0.27–1.15; when excluding 1993, an outlier, $\beta = 0.91$, 95% CI = 0.46–1.36; figure 4b). Thus, contrary to geese, the timing of plant growth appears to track rather well the timing of snow-melt in spring.

(c) Abundance

Primary production in wetlands showed a strong and unequivocal increasing trend over time. Average above-ground graminoid biomass increased by 123 per cent over 23 years (table 1 and figure 6a). Annual variation in plant biomass was associated with summer climatic conditions. Indeed, graminoid biomass was positively related to cumulative TDD until 15 August ($r^2 = 0.285$, $F_{1,19} = 7.95$, $p = 0.011$, $y = 0.149x - 7.15$) and negatively to the July–August NAO ($r^2 = 0.409$, $F_{1,19} = 14.6$, $p = 0.001$, $y = -13.3x + 46.1$).

There was little evidence of a temporal trend in lemming density (table 1) but the large inter-annual variability in density due to cyclic population fluctuations makes the detection of such a trend difficult (figure 7). To smooth out those variations, we looked at the 3-year running mean of density. This analysis suggested a possible decreasing trend in summer lemming density (table 1). Lemming populations were especially low during the period 2002–2009 but we note that the most recent peak (2011) was relatively high (figure 7). Characteristic of the snow cover can account for some of the annual variations in lemming density at our study site [49].

Annual nesting density of snow geese and long-tailed jaegers showed no temporal change (table 1). Although not statistically significant, nesting snowy owl abundance tended to decrease over time, which is consistent with the apparent decreasing trend in lemming density (table 1).

(d) Productivity

In snow geese, the clutch size, nesting success and ratio of young to adults near fledging did not show any temporal trend (table 1). Similarly, no temporal trend in the clutch size or nesting and hatching success of Lapland longspurs was detected. There was evidence for a decreasing trend in snowy owl clutch size (a reduction of 0.7 egg per decade or 10% over 18 years) though this was based on only 7 years of data (table 1). However, snowy owl clutch size was not related to lemming density ($F_{1,5} = 0.85$, $p = 0.400$).

The productivity of Arctic foxes did not show any significant temporal trend (table 1 and figure 8). Productivity was strongly linked to annual lemming abundance ($r^2 = 0.619$, $F_{1,16} = 26.3$, $p < 0.001$, $y = 0.080 \log(x) + 0.11$) and thus showed large fluctuations according to the phase of the lemming cycle. Annual fox productivity was not related to climatic variables such as the timing of snow-melt and the number of TDD. We also tested for a temporal trend while accounting for the effect of lemming abundance on fox productivity, but there was still little evidence of change over time despite a slight positive trend ($r^2 = 0.113$, $F_{1,16} = 2.03$, $p = 0.17$, $y = 0.0046x - 0.066$).

(e) Other attributes

The nitrogen concentration of graminoid plants at its peak did not show any temporal trend for the 10 years of data available spanning a 20-year period (table 1). Goose grazing impact lessened over time as the average percentage of wetland graminoids consumed by snow geese decreased from 47 per cent in 1990 to 15 per cent in 2012 (table 1, figure 6b), although the absolute amount of biomass grazed did not change over time ($r^2 = 0.003$, $F_{1,20} = 0.07$, $p = 0.79$).

The annual Arctic fox trophic level, as indexed by its ^{15}N isotopic signature, was highly variable among years and did not show any temporal trend over a 9-year period (table 1). This large annual variability was due to lemming cycles as lemming abundance was strongly linked to this index ($r^2 = 0.818$, $F_{1,7} = 31.4$, $p < 0.001$, $y = -1.65 \log(x) + 8.31$).

At the community level, the number of red fox natal dens did not change through time, since we never detected more than one pair of red fox breeding in the study area and their presence (in 1996, 1998–2001, 2004, 2008 and 2011–2012) was relatively stable.

Table 1. Temporal trends in biological parameters monitored on Bylot Island. The t-statistic is for the slope parameter of interest. Autoregressive terms (ARs) were retained in the model when significant. The r^2 is only for the regression parameter of interest and excludes the autoregressive component when significant (1989 = year 0 in the regression equations). n.s., non-significant ($p > 0.05$).

variable	period	n	mean	CV	r^2	intercept	slope	s.e.	t	p	AR
phenology											
graminoids—date[a] of peak nitrogen concentration	1991–2010	18	181	3.60	0.006	182	−0.089	0.290	0.31	0.764	n.s.
snow geese—peak arrival date[a]	1996–2012	17	161	3.27	0.037	163	−0.201	0.264	0.76	0.458	n.s.
snow geese—median laying date[a]	1989–2012	24	164	2.07	0.009	163	0.046	0.100	0.46	0.651	n.s.
Lapland longspur—median laying date[a]	2000–2012	13	169	2.28	0.004	168	0.066	0.298	0.22	0.829	n.s.
snowy owl—median laying date[a]	1993–2010	7	141	3.34	0.004	142	−0.045	0.328	0.14	0.896	n.s.
abundance											
graminoids—primary production (g m⁻²)	1990–2012	22	49.5	31.2	0.343	29.0	1.731	0.558	3.10	0.006	AR1[e]
brown lemming—summer density (nb ha⁻¹)[b]	1993–2012	20	4.74	147	0.075	1.84	−0.051	0.042	1.21	0.243	n.s.
brown lemming—summer density (3-year running mean, nb ha⁻¹)[b]	1993–2012	18	4.24	73.4	0.147	2.13	−0.050	0.030	1.66	0.116	n.s.
snow geese—nest density (nb ha⁻¹)	1993–2012	19	4.17	58.0	0.099	2.20	0.132	0.097	1.37	0.190	n.s.
long-tailed jaeger—nest density (nb ha⁻¹)	2004–2012	8	0.61	54.5	0.083	0.42	0.007	0.011	0.67	0.530	AR1,2[f]
snowy owl—nest density (nb km⁻²)[c]	1993–2010	7	0.11	84.3	0.362	0.23	−0.009	0.005	1.69	0.153	n.s.
productivity											
snow geese—clutch size	1989–2012	24	3.7	8.54	<0.001	3.7	0.0003	0.009	0.03	0.978	n.s.
snow geese—nesting success[d]	1989–2012	24	0.66	32.1	0.015	0.91	0.004	0.007	0.58	0.568	n.s.
snow geese—young-adult ratio near fledging	1990–2012	23	1.04	22.5	0.009	1.08	−0.003	0.007	0.43	0.673	n.s.
Lapland longspur—clutch size	1995–2012	18	5.4	5.17	0.009	5.5	−0.005	0.013	0.38	0.708	n.s.
Lapland longspur—nesting success	1995–2012	18	0.48	49.0	0.049	0.61	−0.010	0.010	0.91	0.375	n.s.
Lapland longspur—hatching success	1995–2012	18	0.64	31.7	0.010	0.58	0.004	0.009	0.40	0.696	n.s.
snowy owl—clutch size	1993–2010	7	7.0	8.79	0.523	7.9	−0.069	0.030	2.34	0.064	n.s.
Arctic fox—proportion of natal dens	1995–2012	18	0.12	0.73	0.048	0.07	0.003	0.004	0.82	0.380	n.s.
other attributes											
Graminoids—peak nitrogen concentration (%)	1991–2010	10	3.12	10.5	0.027	3.21	−0.007	0.016	0.47	0.653	n.s.
goose—grazing impact (% biomass removed)	1990–2012	22	30.4	54.0	0.339	48.3	−1.438	0.449	3.20	0.005	n.s.
Arctic fox—isotopic signature (δ¹⁵N, ‰)	2003–2011	9	8.42	18.4	0.062	11.0	−0.141	0.207	0.682	0.517	n.s.

[a]Date expressed in day of the year (1 January = 1).
[b]Data were transformed ($\ln(y)$) for regression analysis.
[c]Exclude years where snowy owls did not nest due to low lemming abundance.
[d]Data were arcsine-transformed for regression analysis.
[e]First-order autoregressive coefficient significant (AR1 = −0.55, $p = 0.011$).
[f]First- and second-order autoregressive coefficients significant (AR1 = 1.09, $p = 0.006$; AR2 = 0.91, $p = 0.003$).
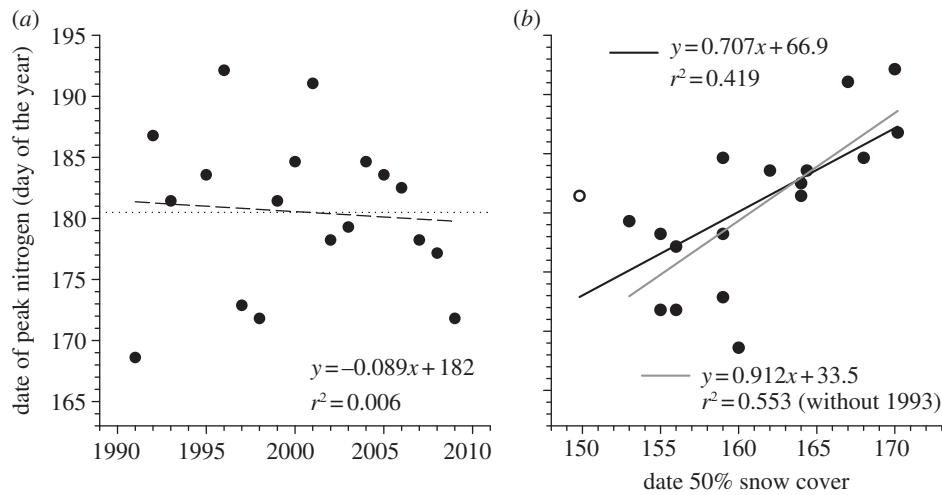
Figure 4. (a) Annual date of peak nitrogen concentration (day of the year) in wetland gramioids and (b) relationship between date of peak nitrogen concentration and date of 50%snow cover (day of the year) in the Qarlikturvik Valley of Bylot Island from 1990 to 2010. The dotted line shows the mean for the whole period. The regression lines show the temporal trends (1989 = year 0 in the regression equations). The white dot in (b) is year 1993.
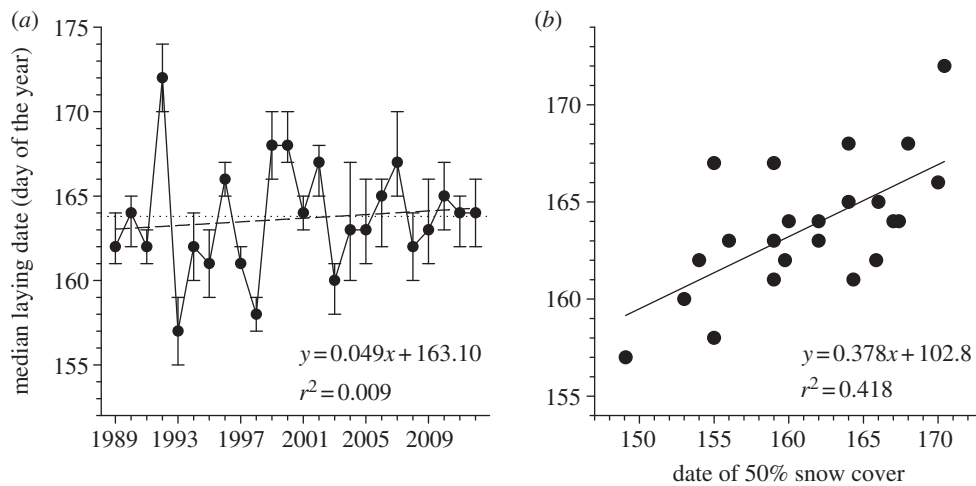

Figure 5. (a) Annual median goose laying date (day of the year) with 25% and 75% percentiles and (b) relationship between median goose laying date and date of 50% snow cover (day of the year) in the Qarlikturvik Valley of Bylot Island from 1989 to 2012. The dotted line shows the mean for the whole period. The regression lines show the temporal trends (1989 = year 0 in the regression equation with year).
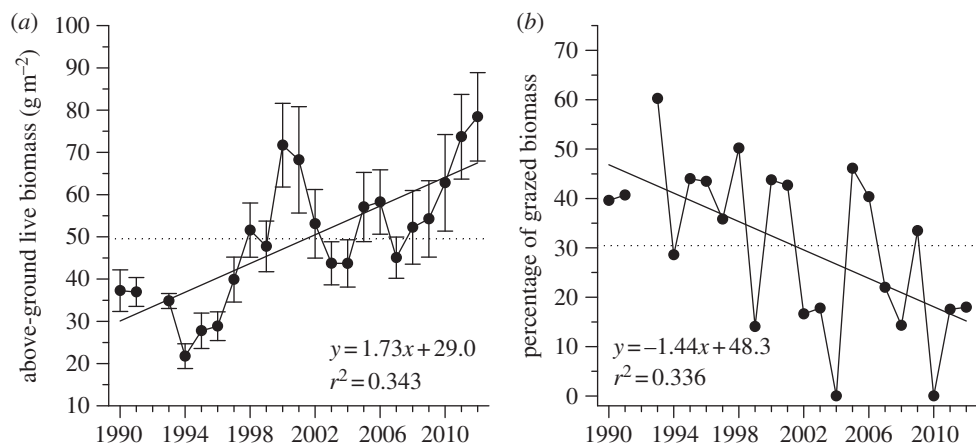

Figure 6. (a) Annual above-ground production of wetland graminoid plants (mean ± s.e.) and (b) percentage of above-ground biomass of wetland graminoid plants removed by geese in the Qarlikturvik Valley of Bylot Island from 1990 to 2012. The dotted lines show the mean for the whole period. The regression lines show the temporal trends (1989 = year 0 in the regression equations).
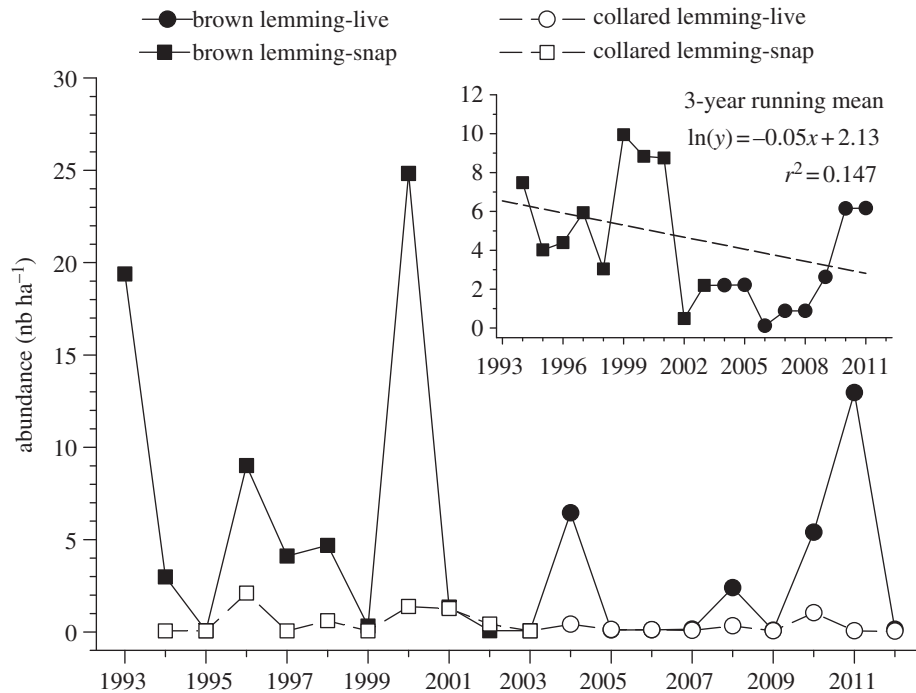
Figure 7. Annual abundance of two lemming species estimated by snap-trapping (up to 2003) and live-trapping (after 2003) in the Qarlikturvik Valley of Bylot Island from 1993 to 2012. The inset shows the 3-year running mean abundance for brown lemmings over the same period. The regression line shows the temporal trend (1989 = year 0 in the regression equations).
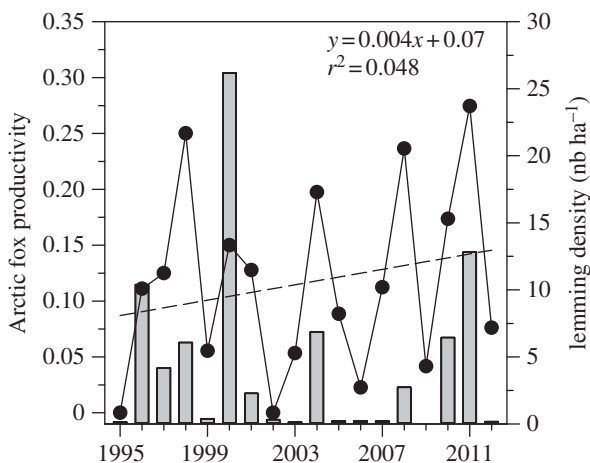

Figure 8. Annual productivity of Arctic foxes (proportion of monitored dens with fox litter) on Bylot Island from 1995 to 2012. The regression line shows the temporal trend in productivity (1989 = year 0 in the regression equations). Grey bars show annual lemming density.

(f) Length and intensity of monitoring

To explore how length or intensity of monitoring could have affected our ability to detect significant biological trends, we re-analysed subsets of the most significant temporal trend that we detected, namely the increase in graminoid biomass in wetlands (figure 6a). Significant positive trends were still detected when the length of monitoring was reduced by half (11 years), though slopes were inflated (see the electronic supplementary material, table S2). However, when monitoring was reduced to 7 or 8 years, a significant positive trend was detected only in the most recent period whereas the middle period showed an almost significant negative trend. Sampling only every other year would have yielded similar results to those obtained with annual monitoring.

4. Discussion

The most surprising outcome of our analyses has been that, generally, we found little evidence for changes in the phenology, abundance or productivity of several species of vertebrates on Bylot Island despite the warming trend that has affected this area over the past three decades. The only clear change that we detected in the food web over the past 20 years has been with primary production, which more than doubled in wetland vascular plants. Similar increases in plant production have recently been reported elsewhere in the Canadian Arctic [8–10]. These increases are probably linked to improved growth conditions brought by climate warming as we found a strong association between annual climatic conditions (both at local and regional scales) and plant biomass on Bylot Island.

Why, then, are we not detecting temporal changes in population attributes of higher trophic levels (i.e. herbivores and predators) at our study site, especially considering the relatively large spatial scale of our monitoring? Phenology, for instance, has been shown to respond rapidly to climate warming in many areas [54–56] even sometimes at the genetic level [57]. We offer several explanations to this apparent paradox.

First, our time series are perhaps too short to detect trends. For plants, which are likely to be quite responsive to environmental conditions, we showed that 11 years of monitoring would have been sufficient to detect the increasing trend in biomass found with the full time series, but generally not with shorter time series. The majority of our datasets (16 out of 22) met this criterion, with some series spanning two decades or more (e.g. geese, lemmings). For cyclic populations such as small rodents and the predators that depend upon them, a higher number of years may be needed to detect trends, given the large inter-annual variability in population densities. However, extreme changes such as a

total collapse of cycles [58] are probably easier to detect from relatively short time series and we clearly did not observe such changes.

Second, inter-annual variation may be especially large in the Arctic. For instance, annual reproductive success in geese can vary enormously, with alternating 'boom' and 'bust' years [53], and this may contribute to masking long-term changes in the data. This also raises the issue of the statistical significance of a trend. In presence of high annual variability, it will be difficult to demonstrate the statistical significance of weak or even moderate trends (in terms of slope parameter value) unless sample size is large (e.g. more than 40 years). In such situations, we would argue that discussing a trend based solely on the magnitude of its slope parameter, even if the confidence interval overlaps zero, may be justified, though within some limits. Indeed, this should apply to situations where the measurement error of the variable of interest is small relative to the mean observed change and to time series that are reasonably long (e.g. more than 10 years; see above). A related issue is the relative importance of making type I versus type II errors when it comes to detecting effects of climate change. If important conservation issues are at stake, then type II error is as damageable as type I error [59], and it may be wise to raise the threshold of statistical significance from 0.05 to 0.10 or 0.20 in those cases.

Third, the amplitude of the observed climate change may not be large enough yet to elicit a response. In arthropods, species at higher latitudes have broader thermal tolerance than those at lower latitudes and they are living in climates that are currently cooler than their physiological optima [60]. A similar phenomenon may occur in some of the vertebrates we are monitoring in the high Arctic as the climate changes may have not yet exceeded their phenotypic plasticity and thus their capacity to cope with these changes [18]. It is also possible that the benefits associated with a response to some environmental changes, for instance, in terms of advancement in phenology, may not yet outweigh the potential costs, and thus the lack of response could be beneficial under certain circumstances [61].

Fourth, the tundra food web may be slower to respond to changes than other biomes. This could be especially true in the high Arctic where the inertia could be greater than in the low Arctic, for instance, owing to the greater stability of some physical components of the environment such as the permafrost or snow cover. Responses to environmental changes in many Arctic species may not be linear but could occur rather suddenly when some thresholds are exceeded [56,62,63]. For instance, abrupt changes could occur when the annual ground temperature increases above $0°C$, resulting in disappearance of the permafrost, or when the ecosystem switches from a herbaceous to an erect shrub-dominated vegetation [64]. At our site, permafrost has rather been stable so far as ground temperature showed little temporal trend, probably because winter temperature has not warmed up over the past 40 years [30].

Fifth, constraints can prevent short-term adjustments in some species. In migratory birds, population attributes can be strongly affected by environmental factors encountered away from the Arctic breeding grounds [53,65,66]. Spring migration phenology, and hence timing of breeding, may be constrained by the timing of life-cycle phases preceding migration, by different climatic variations in the wintering areas and along the migratory route, or by depleted genetic variance in migration traits [67]. For instance, delays in snow goose spring migration resulting in lagged arrival on the breeding grounds with respect to snow-melt may be partly driven by different rates of advancement of spring between the Arctic and temperate terrestrial biomes.

Despite the relative stability of the Bylot Island vertebrate food web over the past two decades, our analyses still provide some insights into which components are most likely to be affected by future climate warming and how. By relating reproduction phenology with environmental conditions using a common metric (i.e. date), we showed that snow geese undercompensated in response to change in the timing of snow-melt as they laid after the 50 per cent snow-melt date in early years but before it in late years. This probably illustrates two different constraints faced by geese at each end: in early years, they do not arrive early enough to take advantage of the good conditions and in late years, they have to start laying even if conditions are not quite right owing to the shortness of the summer (if they delay more, they may run out of time at the end to complete their breeding cycle, [45]). In contrast, the timing of growth of their graminoid food plants (in terms of peak nitrogen concentration) seems to adjust rather well to annual change in snow-melt date (i.e. slope close to unity). In years of very early snow-melt, there is evidence that this leads to a reduction in growth of goslings, probably due to a mismatch between the timing of gosling hatch and the timing of peak plant nutritive quality [40]. Thus, as climate continues to warm, we should expect a greater mismatch between geese and their food plants, with negative consequences for the population. Increased mismatch between the timing of breeding of insectivorous shorebirds and the timing of emergence of their insect prey in years with early springs, which led to reduced chick growth, has also been reported at our site [68].

In the case of predators such as the Arctic fox, future change in their population may be more related to changes in the absolute abundance of their prey rather than on the seasonal timing of their availability. We found that both their diet and annual productivity were strongly affected by cyclic fluctuations in lemming abundance, as found elsewhere [69–71]. Even though lemming peaks may have been less pronounced during the 2000s than in the previous decade on Bylot Island, this had no long-term effect on fox productivity. This may not be surprising considering that the effect of lemming abundance on fox productivity was nonlinear as it was only at the lowest lemming density that it declined abruptly (see also [29]). In some regions of the Arctic, lemming cycles have recently collapsed [58] and change in the duration and quality of the snow cover has been invoked to explain this [72,73]. Although snow depth and density can affect the amplitude of lemming oscillations at our study site, the usually dry snow pack of the Canadian high Arctic has probably been less affected so far by climate warming than in regions exposed to the warm water of the northeast Atlantic Ocean [49]. Nonetheless, any serious disruption of lemming cycles due to future climate warming could have devastating effects for Arctic foxes, as observed in Fennoscandia [74].

Invasion by new competitors such as the red fox is another threat faced by tundra species. The red fox breeds on Bylot Island where it competes with Arctic foxes, but its abundance has not increased over the past two decades.

A similar stability was also observed in the western Canadian Arctic (Yukon) despite recent warming [75].

5. Conclusion

We suggest that the most serious impacts of climate warming on Arctic vertebrate species will probably be indirect, due to disruption of trophic interactions caused by mismatches, decline in prey abundance and appearance of new competitors or predators [28]. Recent findings provide evidence that migratory birds are becoming ecologically mismatched in temperate regions and that failure to respond to climate change can have severe negative impacts on their populations [76]. Increasing trophic mismatch between migrating herbivores or insectivores and their food resources may thus be a widespread threat to Arctic food webs. It will be important to track migratory species during their entire annual cycle to identify potential constraints preventing adjustment to rapid changes happening on their Arctic-nesting grounds.

Because of their simplicity, Arctic food webs may especially be prone to exhibit nonlinear dynamics in response to climate warming and to show abrupt changes owing to threshold effects and feedback processes [56,62,63]. Therefore, great care is needed when trying to extrapolate future ecological responses (or lack of them) observed at the early stage of warming, especially considering that upcoming warming should greatly exceed what has been observed so far [1]. In order to better understand the complex mechanisms and processes behind the responses of individual species to climate change, increased efforts should be devoted to understanding the interactions and strengths of linkages among species.

There is currently an international effort underway to implement a coordinated, circumpolar programme to monitor future changes in Arctic ecosystems [77]. Our results can provide some guidance on how such programmes should be implemented. For instance, our analysis suggests that length of monitoring is critical and that conclusions based on short time series should be viewed with caution. Monitoring spanning a decade appears to be a minimum before drawing some conclusions, and probably more for cyclic species and predators that depend upon them. For some components of the environment showing moderate year-to-year variability such as primary production, we showed that less intensive monitoring (e.g. every other year rather than annual) could be sufficient to detect long-term trends, which could reduce costs. However, this recommendation would not apply to cyclic species, which require annual monitoring because cycles typically show irregularities in periodicity.

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Long-term monitoring at multiple trophic levels suggests heterogeneity in responses to climate change in the Canadian Arctic tundra

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Table S1. Temporal trends in summer climate in Pond Inlet, Nunavut, Canada (TDD = thawing degree-days, i.e. degree-days > 0°C) and in the North-Atlantic Oscillation (NAO).

Variable	Period	*n*	Mean	Equation
Mean temperature in May (°C)	1989-2012	19	-8.6	$y = 0.174x - 10.8$
Mean temperature in June (°C)	1989-2012	19	2.8	$y = 0.080x + 1.8$
Mean temperature in July (°C)	1989-2012	19	7.3	$y = 0.070x + 6.5$
Mean temperature in August (°C)	1989-2012	19	5.5	$y = 0.133x + 3.8$
Mean temperature in September (°C)	1989-2012	19	-0.6	$y = 0.054x - 1.2$
Cumulative TDD until 15 August (°C)	1989-2012	19	425	$y = 5.86x + 350$
Cumulative TDD for the whole year (°C)	1989-2011	18	517	$y = 9.23x + 405$
Number of frost-free days (d)	1989-2011	18	101	$y = 0.541x + 94$
NAO (May to September)	1989-2012	24	-0.198	$y = -0.060x + 0.598$

Table S2. Temporal trend in total graminoid biomass (g m^{-2}) monitored at peak growth in mid-August on Bylot Island using various monitoring schemes. The temporal trend detected using the full dataset (full study) is compared to shorter monitoring obtained by splitting the dataset in two (first and second halves of the study) or three (first, second and last third), or with a less intensive monitoring (every other year, using even or off years). Autoregressive terms (AR) were retained in the model when significant. The r^2 is only for the regression parameter of interest and excludes the autoregressive terms when significant (1989 = year 0 in the regression equations). NS = non-significant (P > 0.05).

Monitoring scheme	Period	n	Mean	CV	r^2	Intercept	Slope	SE	t	p	AR
Full study	1990-2012	22	49.5	31.2	0.343	29.0	1.73	0.55	3.10	0.006	AR1[1]
First half of study	1990-2001	11	42.4	37.9	0.515	20.6	3.20	1.04	3.09	0.013	NS
Second half of study	2002-2012	11	56.6	20.2	0.592	8.8	2.65	0.74	3.61	0.006	NS
First third of study	1990-1997	7	32.5	20.0	0.061	35.4	-0.62	1.10	0.57	0.595	NS
Second third of study	1998-2005	8	54.6	19.3	0.573	84.7	-2.28	1.00	2.28	0.085	AR2[2]
Last third of study	2006-2012	7	60.7	19.6	0.691	-30.9	4.58	1.37	3.34	0.021	NS
Even years only	1990-2012	11	50.9	33.8	0.537	27.6	1.81	0.56	3.23	0.010	NS
Odd years only	1990-2012	11	28.1	29.3	0.540	29.4	1.56	0.48	3.25	0.010	NS

[1] First-order autoregressive coefficient significant (AR1 = -0.55, P = 0.011)

[2] Second-order autoregressive coefficient significant (AR2 = 0.88, P = 0.008)
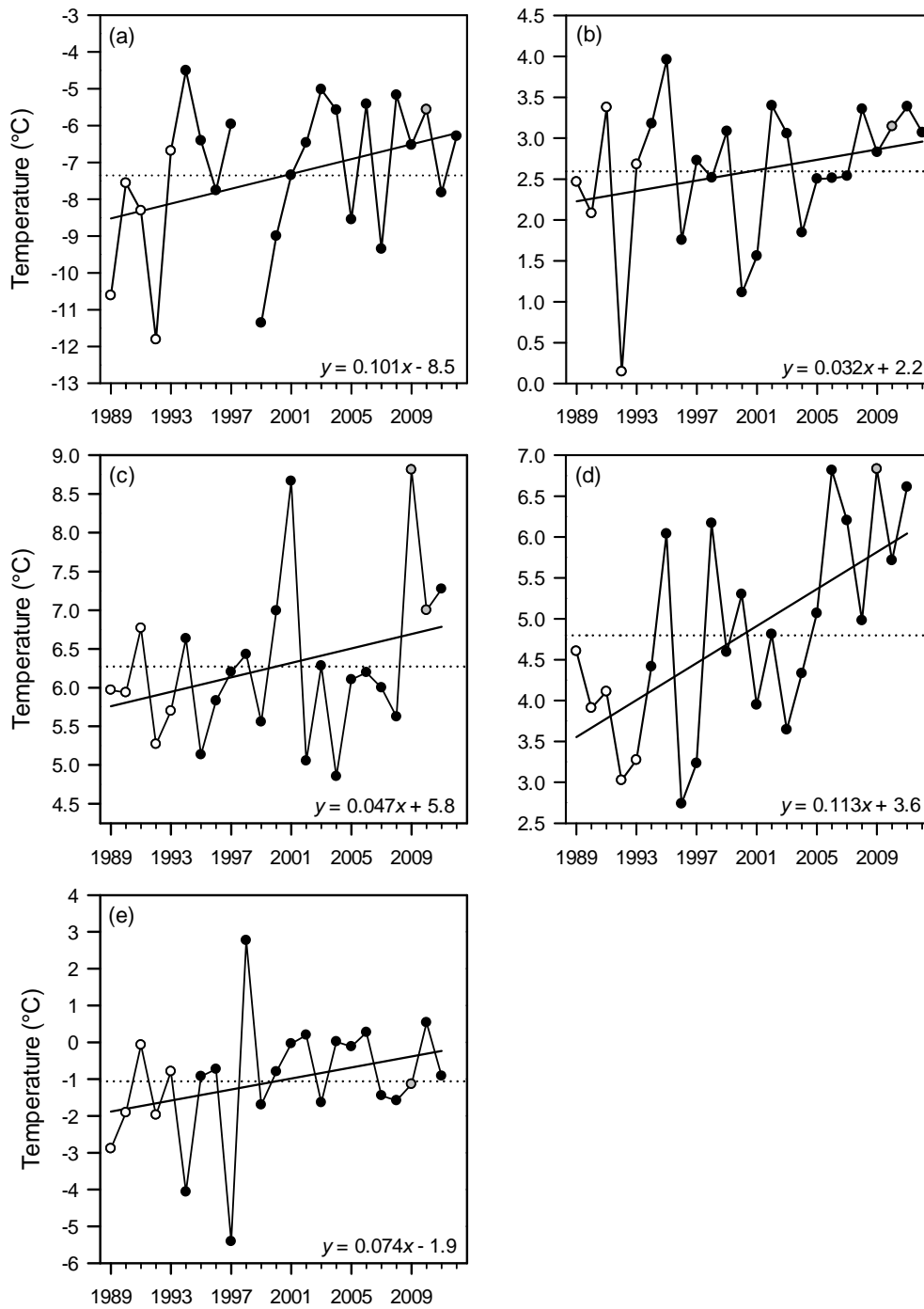
Figure S1. Average monthly temperature in the Qarlikturvik Valley of Bylot Island from 1989 to 2011 for (a) May, (b) June, (c) July, (d) August and (e) September. The dotted line shows the mean for the whole period. Data represented by white and gray circles were extrapolated from temperature data collected in Pond Inlet and another, nearby station on Bylot Island, respectively. The regression lines show the temporal trends (1989 = year 0 in the regression equation with year).
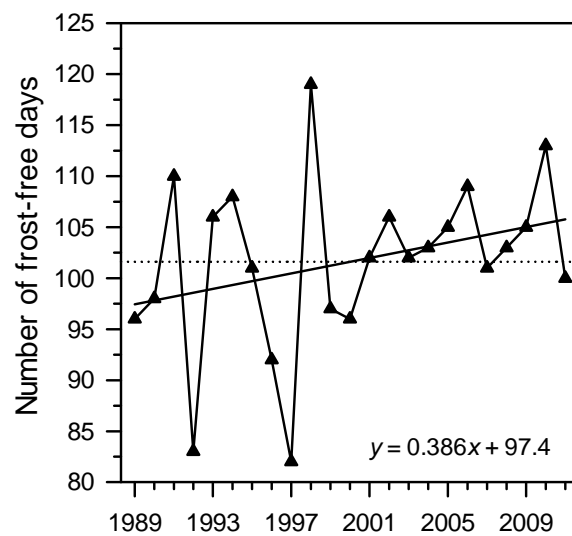
Figure S2. Annual number of frost-free days in the Qarlikturvik Valley of Bylot Island from 1989 to 2011. The dotted line shows the mean for the whole period. The regression lines show the temporal trends (1989 = year 0 in the regression equations).