

REPORT

The Arctic Oscillation predicts effects of climate change in two trophic levels in a high-arctic ecosystem

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Abstract

During recent decades there has been a change in the circulation of atmospheric pressure throughout the Northern Hemisphere. These variations are expressed in the recently described Arctic Oscillation (AO), which has shown an upward trend (associated with winter warming in the eastern Arctic) during the last three decades. We analysed a 12-year time series on growth of *Cassiope tetragona* (Lapland Cassiope) and a 21-year time series on abundance of a Svalbard reindeer population. High values of the AO index were associated with reduced plant growth and reindeer population growth rate. The North Atlantic Oscillation index was not able to explain a significant proportion of the variance in either plant growth or reindeer population fluctuations. Thus, the AO index may be a better predictor for ecosystem effects of climate change in certain high-arctic areas compared to the NAO index.

Keywords

Arctic Oscillation, *Cassiope tetragona*, climate change, plant–herbivore interactions, Svalbard reindeer.

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INTRODUCTION

The climate on the earth is changing and the globe is currently warming (Overpeck *et al.* 1997; Mann *et al.* 1999). Accordingly, several studies have been able to relate many characteristics of individuals and populations to long-term changes in large-scale climatic phenomena like the North Atlantic Oscillation (NAO, Hurrell 1995) (e.g. Forchhammer *et al.* 1998a, b; Grenfell *et al.* 1998; Post & Stenseth 1999; Post *et al.* 2000; Sæther *et al.* 2000; Sillett *et al.* 2000). These biological responses are related to the fact that such large-scale climatic oscillations may explain a considerable proportion of annual variations in local temperature and precipitation patterns over large regions (Hurrell 1995).

Mean annual temperature has been shown to increase faster in large regions of the Arctic compared to the global average (Chapman & Walsh 1993). Global circulation models (GCM) suggest that future global warming will be most pronounced in Arctic regions (Maxwell 1997).

Accordingly, the index of the Arctic Oscillation (AO), a nearly axisymmetric spatial pattern of sea-level pressure (SLP) centred over the Arctic (Thompson & Wallace 1998, 2001), has shown an upward trend during the last three decades, and is closely related (Thompson & Wallace 1998; Shindell *et al.* 1999; Hartmann *et al.* 2000) to changes in mean annual temperature recorded at many locations in the Arctic (Overpeck *et al.* 1997). The AO index and the more familiar NAO index are the same physical entity and highly correlated (Thompson & Wallace 1998), but viewed as different paradigms (Wallace 2000; see Methods). The AO index explains more than half of the warming observed in the eastern Arctic, and less than half of the temperature trends over the western Arctic, where both warming (e.g. Alaska) and cooling (e.g. southern parts of Greenland) have been recorded (Rigor *et al.* 2000). Thus, Arctic regions may be suitable areas for studying ecosystem effects of regional climate changes. Nevertheless, few studies have linked ecological processes to

climate patterns in the Arctic, except for some important contributions on studying the effects of experimental warming on tundra ecosystems (e.g. Chapin *et al.* 1995; Arft *et al.* 1999).

In this paper we explore the contribution of regional climate variation (the AO index) on the observed variation in plant growth and the growth rate of a Svalbard reindeer population. We do this by using a 12-year time series on variation in growth characteristics of *Cassiope tetragona* (L) D. Don (Ericaceae) (Lapland Cassiope) and a 21-year time series of Svalbard reindeer (*Rangifer tarandus platyrhynchus*), respectively. We show that both plant growth and Svalbard reindeer population growth rate is negatively related to high AO index values, whereas no such relationship were found to the NAO index. We explain our findings by showing that the plant growth is directly affected through the AO index influence on local climate, and that the reindeer population growth rate decreases with a 1-year lag through a possible bottom-up trophic effect caused by reduced plant growth the previous year.

MATERIALS AND METHODS

Study area

The study area, Brøggerhalvøya, is located on the north-western coast of Svalbard (78°5'N, 11°5'E). Svalbard is located in one of the Arctic regions where the mean annual temperature has increased during the last decades (Hanssen-Bauer 2000). Brøggerhalvøya is a peninsula characterized (Aanes *et al.* 2000) by a mountainous area in the centre, surrounded by areas of lowland plain. The total area is approximately 221 km². The areas with vegetation coverage greater than 5% constitute 93.5 km² and areas with more than 50% coverage are *c.* 28 km². The Norwegian Meteorological Institute (DNMI) monitors local climate, with a meteorological station on Brøggerhalvøya at Ny-Ålesund.

Svalbard reindeer data

In 1978 15 reindeer were transferred to Brøggerhalvøya from an area near Longyearbyen situated about 120 km south-east of the release point. Three individuals were lost during the first months, so 12 individuals (3 males and 9 females) represent the founding population. Personnel on snowmobiles have counted the number of Svalbard reindeer annually during April since the introduction. Favourable areas for reindeer on Brøggerhalvøya are open and individuals can be spotted from considerable distance. Additionally, rugged areas have been checked every April for presence of reindeer. Hence, we assume the yearly counts of reindeer in the area represent total counts, and

that the sample error is negligible. For further details, see Aanes *et al.* (2000).

During the winter of 1993/94 the reindeer population on Brøggerhalvøya crashed and the number of reindeer decreased from 360 individuals before calving in 1993 to 78 individuals before calving in 1994 (Aanes *et al.* 2000). The crash was related to extreme climatic events, possibly in combination with a high reindeer density in the area. The November month in 1993 was unusually warm and wet at Brøggerhalvøya, with a mean daily temperature of $-2.78 (\pm 1.24) ^\circ\text{C}$ and daily precipitation of $7.68 (\pm 1.79)$ mm. The November mean daily temperature and daily precipitation for the period 1978–97 was $-9.28 (\pm 0.25) ^\circ\text{C}$ and $1.23 (\pm 0.15)$ mm, respectively. The climatic conditions during November in 1993 with several periods with rain followed by temperatures below freezing-point resulted in terrestrial ice-crust formation throughout Brøggerhalvøya, and in some places the ice-layer was reported to be more than 10 cm thick (N.A. Øritsland own observations). In April 1994 the area was surveyed for reindeer, and a large number of carcasses was found on Brøggerhalvøya. Additionally, reindeer were found in previously unpopulated areas outside Brøggerhalvøya indicating that the crash was a combination of mortality from starvation and emigration.

Because of this extreme climatic event and response in the reindeer population, all analyses of reindeer population growth rate were performed with and without inclusion of the year 1993 (see Fig. 1a).

Plant data

Cassiope is a plant that grows with clear annual segments from an apical meristem. The individuals are long lived, and have been recorded up to 60 years old (Bliss *et al.* 1977). Senesced leaves are retained on the stem for up to 40 years (Callaghan *et al.* 1989), enabling this species to be used as a relatively long record of growth.

Previous studies indicate that *Cassiope tetragona* is an appropriate plant species to use for retrospective analyses similar to those used in dendrochronology (Callaghan *et al.* 1989; Johnstone & Henry 1997). *Cassiope tetragona* is not used as forage by reindeer (Callaghan *et al.* 1989). Nine individual shoots of *Cassiope tetragona* were sampled on Brøggerhalvøya during summer in 1999. All shoots collected had green tips and were air dried before being analysed. Using shoots from main stems, two alternate rows of leaves were carefully removed in strict sequence from the apex to the base of the shoot and the maximum length of each leaf was measured to 0.1 mm (Callaghan *et al.* 1989). The shortest leaf in a wave-like sequence of lengths was defined as the first leaf on a year segment (Callaghan *et al.* 1989; Havström *et al.* 1993). The number

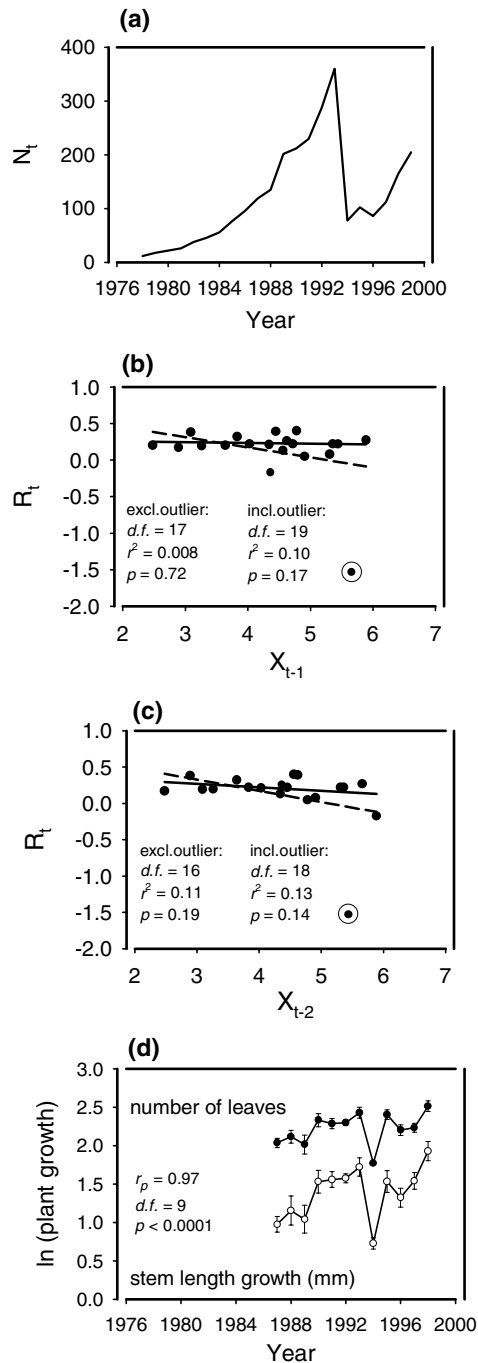


Figure 1 Dynamics of the two trophic levels on Svalbard, Norway. (a) The population development of Svalbard reindeer on Brøggerhalvøya during the period 1978–99. (b–c) The regression of population growth rate (R_t) against the lagged logged abundances in $t - 1$ and $t - 2$, respectively (encircled point refers to the outlier value in R_t). (d) Annual variation in the mean number of leaves (± 1 SE) and stem length growth (mm) (± 1 SE) of *Cassiope tetragona*.

of leaves and stem length (mm) for each segment were recorded for each year (Fig. 1d).

We obtained data on eight individuals for 1987–89, nine individuals for 1990–97, and eight individuals for 1998. We used natural-logarithm-transformed values of mean number of leaves and stem length growth (mm) to remedy heteroscedasticity. There was a close correlation between annual variation in number of leaves and stem length growth in *Cassiope tetragona* ($r = 0.97$, $d.f. = 12$, $P < 0.0001$).

The Arctic Oscillation

The AO is a natural climate cycle in the Northern Hemisphere (Thompson & Wallace 1998, 2001; Shindell *et al.* 1999, 2001; Hartmann *et al.* 2000). The more familiar North Atlantic Oscillation (NAO Hurrell 1995) may be viewed as the signature of the AO in the Atlantic sector (Overland & Adams 2001). The NAO index is measured as the mean deviation from the average SLP between Iceland and the Azores from December through March. In contrast, the AO index reflects the mean deviation from the average SLP measured throughout the Northern Hemisphere at longitudes poleward of 20°N (see Wallace (2000) for a detailed discussion about the relationship between AO and NAO indexes). Similarly to the NAO index, the AO index is primarily evaluated and modelled during winter months (Shindell *et al.* 1999; Hartmann *et al.* 2000), and the indexes are highly correlated (Thompson & Wallace 1998). Nevertheless, although the AO is commonly viewed as a winter phenomenon, recent atmospheric pressure reductions have been observed during summer months also, partly reflecting the same nature as the AO winter index (Serreze *et al.* 1997, 2000) but with less vigorous variation. This may indicate that the AO index during the warm season may be important when evaluating climate change in seasons other

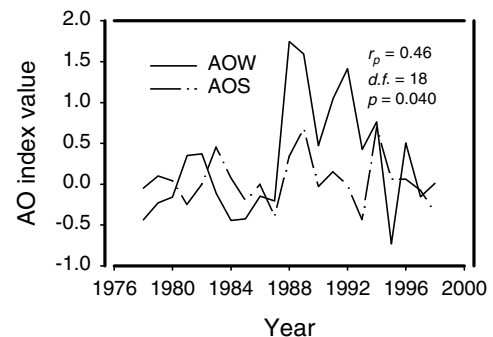


Figure 2 The variation in the Arctic Oscillation (AO) during the study period 1978–98. AOW refers to the months November through April (winter index), whereas AOS refers to the months June through September (i.e. summer index reflecting the plant growth season).

than winter. We used the AO index (source: <http://tao.atmos.washington.edu/data/ao/>) based on the NCEP/NCAR Reanalysis Project (see: <http://wesley.wvb.noaa.gov/reanalysis.html>).

AO index for two different parts of the year (Fig. 2): (1) the winter AO index (AOW) refers to the commonly used index (Shindell *et al.* 1999; Hartmann *et al.* 2000) based on the months November through April; (2) the summer AO index (AOS) reflects the plant growth season. The AOS was obtained by using monthly values to calculate mean annual index for the months June through September, which are the snow-free months on Svalbard and hence the growing season for plants. There was a positive correlation between the current AOS and following AOW during the study period ($r_p = 0.46$, d.f. = 18, $P = 0.040$).

Data analyses

We used linear regressions to explore the relationships between biological parameters (dependent variables) and climate factors (predictor variables), and between reindeer population growth rate (dependent) and plant growth (predictor). Autoregressive (AR) models (Royama 1992) were used to evaluate the combined influence of regional climate changes and delayed effects of density on reindeer population growth rate using current and previous year population growth rates. The measure on reindeer population growth rate, R_t , equals the first difference of the abundance series, i.e. $R_t = X_{t+1} - X_t$ (Diggle 1990; Royama 1992), where $X_t = \log_e N_t$ and N_t is the population size at time t . This means that the R_t series mirrors the detrended version of the abundance series. The second-order alternative of the AR model is

$$R_t = \beta_0 + \beta_1 R_{t-1} + \beta_2 R_{t-2} + \alpha_1 AO_{t-k} + \varepsilon_t \quad (1)$$

where β_i and α_1 are the auto-regressive coefficients (Box & Jenkins 1970), and AO_{t-k} is the regional climate (i.e. the AO index). The term $t - k$ denotes the year AO was found to influence R_t in the bivariate analyses, and k may be 0, 1 or 2. The term ε_t represents the noise parameter, assumed to have zero mean and a constant variance (see Royama 1992; Stenseth *et al.* 1996). The first-order model is obtained by removing the term $\beta_2 R_{t-2}$. We used SPSS Trends ARIMA using maximum likelihood estimation (SPSS 1994) in the AR modelling. SPSS uses Kalman Filtering (see Brockwell & Davis 1996, chapter 8.6) to estimate dummies for missing values, as in those cases when the year 1993 was excluded from the analyses. The most parsimonious model was selected by the corrected Akaike information criterion, AIC_c (Hurvich & Tsai 1989); the model with the lowest AIC_c being considered the most parsimonious. Owing to few degrees of freedom we did not perform AR analyses including plant growth.

RESULTS

The influence of climate on plant growth

Plant growth on Svalbard (as estimated from the performance of *Cassiope tetragona*) was strongly related to summer climate. Both number of leaves and stem length growth were positively related to the mean temperature during the snow-free season (i.e. June through September) at Svalbard (number of leaves: $\beta = 0.218$, $r^2 = 0.51$, d.f. = 11, $P = 0.009$, stem length: $\beta = 0.364$, $r^2 = 0.49$, d.f. = 11, $P = 0.011$). The mean temperature during the two warmest months (July and August) explained most of the annual variation in stem length growth and number of leaves (Fig. 3a). Similarly, we found a strong direct relationship between plant growth and the AO summer index (AOS), with high values of the AOS associated with decreased plant growth (Fig. 3b). The latter may be explained by the influence of regional climate on local climate as the mean temperature during July and August was negatively related to the AOS for the whole study period 1978–98 ($r_p = -0.45$, d.f. = 18, $P = 0.046$). Average temperatures in July and August were negatively related to amount of

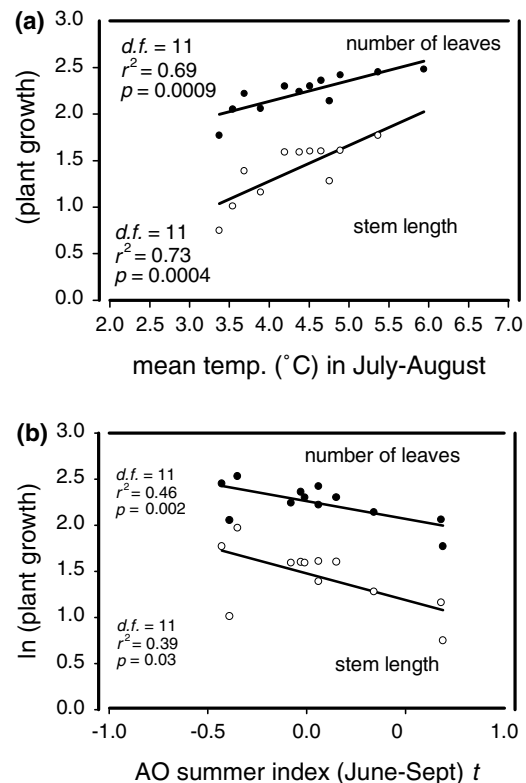


Figure 3 (a) The relationship between mean temperature during July – August and plant growth in *Cassiope tetragona*. (b) Decline in plant growth associated with increase in the AO summer index values.

precipitation in the same months ($r_p = -0.66$, d.f. = 9, $P = 0.026$). Thus, high AOS values were associated with colder, cloudier and wetter weather conditions reducing plant growth in the study area.

Plant growth was not correlated with the NAO index, testing for direct (t) and delayed ($t - 1$) effects (number of leaves: NAO_t , $r_p = 0.12$, d.f. = 9, $P = 0.72$, NAO_{t-1} , $r_p = 0.18$, d.f. = 9, $P = 0.59$, stem length: NAO_t , $r_p = 0.13$, d.f. = 9, $P = 0.70$, NAO_{t-1} , $r_p = 0.10$, d.f. = 9, $P = 0.81$).

The influence of plant growth and climate on reindeer dynamics

A positive relationship was found between the reindeer population growth rate and variation in the growth of individuals of *Cassiope tetragona* the preceding year (Fig. 4). Although *Cassiope tetragona* is not eaten by reindeer this may suggest a bottom-up effect in the ecosystem through a decrease in the available plant biomass associated with high values of the AOS (Fig. 3b) reducing the growth rate of the reindeer population. Accordingly, annual variation in the population growth of reindeer was negatively related to both the AOW and AOS with a delay of 1 year (Fig. 5a,b). The strongest relationship was found with the AOS the previous year. Similarly to plant growth, reindeer population growth rate was not correlated with the NAO index (Aanes *et al.* 2000).

Earlier we have shown that annual variation in growth of the reindeer population is closely related to winter climate conditions through a direct negative relationship to the amount of precipitation (Aanes *et al.* 2000). In the present study we found that precipitation during winter was positively related to the AO index the previous year

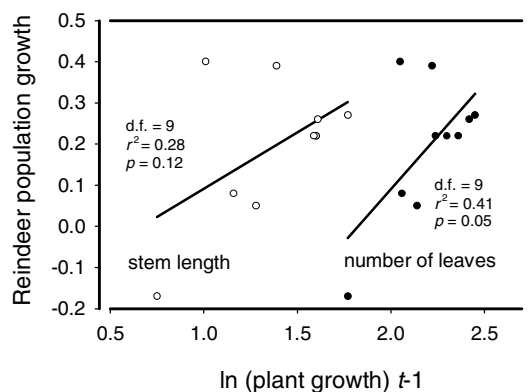


Figure 4 The 1-year delayed negative relationship between plant growth and reindeer population growth (R_t) excluding 1993. Including the extreme value of R_t in 1993 (see Methods) in the analysis gave a nonsignificant relationship between reindeer population growth and plant growth ($\beta = 0.107$, $r^2 = 0.001$, d.f. = 10, $P = 0.91$ and, $\beta = -0.080$, $r^2 = 0.002$, d.f. = 10, $P = 0.89$, for number of leaves and stem length growth, respectively).

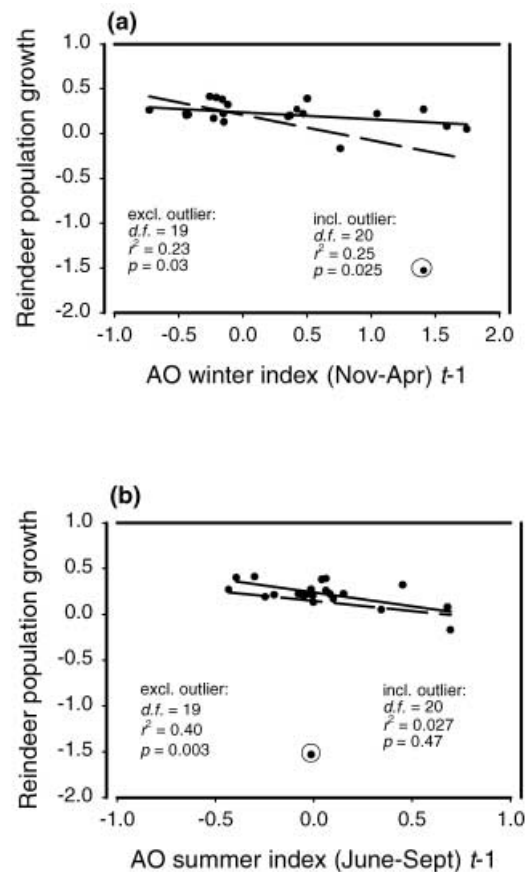


Figure 5 The fluctuations in the reindeer population growth in relation to (a) AOW_{t-1} , and (b) AOS_{t-1} . Full regression lines represent regressions where the outlier for R_t (encircled point in figures) is excluded (see Methods), and dashed lines represent all data.

(AOS ; $r_p = 0.56$, d.f. = 18, $P = 0.010$, AOW ; $r_p = 0.38$, d.f. = 18, $P = 0.095$).

The autoregressive models for the complete time series (i.e. including year 1993) showed that the AOW significantly influenced reindeer population growth rate (Table 1a). No significant density-dependent effects were found in these models (Table 1a). When 1993 was excluded (Table 1b) both the AOS and the AOW were found to explain a significant proportion of the variance in R_t . The AIC_c showed that a second-order density-dependent process, including the AOW, was the most parsimonious model in explaining the dynamical pattern of the population (Table 1b). The delayed density-dependence patterns were strengthened by the linear regression of population growth rate against the 1- and 2-year lagged log-abundances, respectively (Fig. 1b,c). This suggests that delayed density dependence and regional climate variation in combination contribute to fluctuations in Svalbard reindeer density.

Table 1 Estimated autoregressive coefficients from eqn 1 shown for both 1- and 2-order models, explaining the variation in population growth rate (R_t) as influenced by regional climate (i.e. AO). Bold AR coefficients are statistically significant ($P < 0.05$), and bold AIC_c denote the most parsimonious models if significant AR coefficients are present. AR models including the year 1993 are given in (a), and models excluding 1993 are given in (b). In the second column AOS refers to the AO summer index, whereas AOW refers to the AO winter index (see Methods).

Dependent variable	Climate variable	N	AR(1)-coeff.	Clim.-coeff.	AIC_c	AR(2)-coeff.	Clim.-coeff.	AIC_c	
			β_1^\dagger	α_1^\S		β_1^\dagger	β_2^\ddagger		α_1^\S
(a) Including 1993									
R_t	AOS	20	-0.170	-0.139	28.73	-0.067	0.078	-0.084	34.22
R_t	AOW	20	0.137	-0.248	22.98	0.219	0.044	-0.246	28.50
(b) Excluding 1993									
R_t	AOS	19	-0.234	-0.296	-23.45	-0.225	-0.339	-0.146	-22.26
R_t	AOW	19	-0.119	-0.083	-17.78	-0.049	-0.412	-0.082	-31.04

† Two-tailed t -test, $H_0: \beta_1 = 0$.

‡ Two-tailed t -test, $H_0: \beta_2 = 0$.

§ Two-tailed t -test, $H_0: \alpha_1 = 0$.

DISCUSSION

We have shown that a high (positive) polarity of the AO index decreased plant growth (Fig. 3b) and reindeer population growth rate (Fig. 5, Table 1), and hence is likely to affect trophic interactions, in a high Arctic ecosystem on Svalbard. These relationships appear because of a relationship between regional and local climate (Hurrell 1995). When the AO index is in the high and positive phase the atmospheric pressure over the Arctic is lower than average. This is associated with an increase in winter temperature and amount of precipitation (Thompson *et al.* 2000). In contrast, low atmospheric pressure during summer result in cloudier and wetter conditions, and thus decreased temperatures. Accordingly, local climate on Brøggerhalvøya was related to variation in the AO index, with high index values associated with colder and wetter summer climate (in t) and increased winter precipitation (in $t + 1$) (see Results). Whether the latter finding is the result of spurious correlations or can be explained by a distinct geophysical mechanism is still unclear. However, it deserves attention as it has been shown elsewhere that oceans may have long-term memory of climatic events, like a high NAO polarity (Dickson *et al.* 1999) or a strong El Niño/Southern Oscillation event (Melsom *et al.* 1999), lasting over many years and long distances.

Variation in plant growth characteristics of *Cassiope tetragona* was closely related to changes in the AOS, with high index values associated with reduced plant growth (Fig. 3b). One explanation for this relationship is that a high AOS may be associated with unfavourable growth conditions (e.g. cold and wet weather) during the growing season. The demonstrated links between growth of *Cassiope tetragona*

and summer climate (Callaghan *et al.* 1989; Havström *et al.* 1993; Molau 1997) may represent a direct coupling between high-Arctic inter-annual climate variations and plant growth for a broad range of plant species and growth forms. Independent support for this hypothesis is provided by carbon balances in comparable ecosystems further south (*c.* 60 km from our study site) on the west coast at Eidembukta (Wütrich *et al.* 1999). These observations indicate that cold and cloudy summer conditions resulted in suboptimal plant growth and net ecosystem carbon losses (caused by an excess of respiration over photosynthesis) at several high arctic community types, including those dominated by foliose lichens. Nevertheless, the present study suffers from a short time series on plant growth, and more important, lack of quantitative data on the correlations in plant growth between *Cassiope tetragona* and representative food plants for Svalbard reindeer.

In a recent paper (Aanes *et al.* 2000) we reported that the local amount of winter precipitation on Brøggerhalvøya was the main factor influencing the fluctuations in growth rate of this Svalbard reindeer population. Here we have shown that large-scale climate variability (i.e. the AO) as well as climate-modulated plant growth may contribute to the observed population growth rate fluctuations. Thus, the population dynamics of Svalbard reindeer are likely to be influenced by a climate-mediated trophic bottom-up effect. These results complement several studies that have demonstrated effects of plants on ungulates in northern ecosystems through correlations between summer weather and weight gain and (or) reproduction in ungulates (e.g. Sæther 1985; Langvatn *et al.* 1996; Solberg *et al.* 1999), in addition to direct effects of food supply on reindeer body

condition and calf survival (White *et al.* 1981; Eloranta & Nieminen 1986). This bottom-up effect may however, be density dependent. At higher reindeer densities top-down trophic interaction may become more important, with grazing having profound effects on forage species and plant communities (e.g. Leader-Williams *et al.* 1981, 1987; Helle & Aspi 1983; McInnes *et al.* 1992; Danell *et al.* 1994).

If an increase in the mean and the variance of temperature and precipitation is likely in a future Arctic climatic scenario this will probably have large consequences for Svalbard reindeer population dynamics. The Intergovernmental Panel on Climate Change (IPCC 1996) has suggested that a more pronounced warming, as well as a tendency towards more extreme climatic events, will be likely in the future Arctic. Our analyses do in fact show that the year 1993 strongly influenced the dynamics of the reindeer population (Fig. 5a,b and Table 1) because of extreme weather conditions during the winter. So far, ecologists have been mostly concerned with predicting the consequences of a change in mean climate (e.g. Sæther *et al.* 2000). Our results suggest that increasing attention should also be paid to changes in the temporal variance of key climate variables. An increased frequency of the climate conditions (i.e. environmental shocks) of the kind experienced during 1993 will have a strong impact on the dynamics of the reindeer population. Accordingly, the outcome of reintroductions of animals may be strongly dependent on the unpredictable climate. The reintroduction of reindeer to Brøggerhalvøya in 1978 must be considered successful. If the reintroduction had been done in 1993 the probability of success would most likely have been much lower. Therefore, several successive reintroductions may be necessary to obtain a viable population in areas with highly variable climate.

This study has demonstrated that plant growth characteristics as well as reindeer population growth rate were negatively related to the AO indexes. Thus, if the positive trend (Shindell *et al.* 1999) in the AO index continues it is likely that the population dynamics of the high arctic reindeer, proposed as an indicator species for environmental health status in the Arctic (CAFF/AMAP Anonymous 2000), will be strongly affected. Climate models applied to the AO (Shindell *et al.* 1999) show that it is likely that the observed warming in the Northern Hemisphere is anthropogenic (through greenhouse gases), and that we can expect a further increase in average temperature in the near future. Our data have suggested, through a negative impact of a positive AO polarity on both reindeer and plants, that this may affect trophic interactions in arctic ecosystems. We found no relationship between the NAO index and plant growth (this study) or reindeer population growth rate (Aanes *et al.*

2000), suggesting that in some areas the AO index may be a better predictor of ecological consequences resulting from climate change than the NAO index, possibly because the NAO may have a more spatially limited effect on key climate variables than the AO, with the latter capturing more (or other areas) of the Arctic.

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