

## ORIGINAL ARTICLE

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## Long-term responses in arctic ungulate dynamics to changes in climatic and trophic processes

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**Abstract** Following predictions from climatic general circulation models, the effects of perturbations in global climate are expected to be most pronounced in the Northern Hemisphere. Elaborating on a recently developed plant–herbivore–climate model, we explore statistically how different winter climate regimes and density-dependent processes during the past century have affected population dynamics of two arctic ungulate species. Our analyses were performed on the dynamics of six muskox and six caribou populations. In muskoxen, variation in winter climate, mediated through the North Atlantic Oscillation (NAO), explained up to 24% of the variation in interannual abundance, whereas in caribou up to 16% was explained by the NAO. Muskoxen responded negatively following warm and snowy winters, whereas caribou responded negatively to dry winters. Direct and delayed density dependence was recorded in most populations and explained up to 32% and 90% of variations in abundance of muskoxen and caribou, respectively.

**Key words** Caribou · Density dependence · Muskox · North Atlantic Oscillation · Winter climate

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### Introduction

The forcing and feedback mechanisms of the arctic climate are considered to be a key element in the numerical modeling of global climate change (Manabe and Stouffer 1993). Recent studies on long-term atmosphere–ocean fluctuations strongly corroborate this link and emphasize the role of winter climate forcing by the North Atlantic Oscillation (NAO) (Dickson 1999). Hence, interactions between winter climate and ecosystem structure and functioning in the Arctic may provide us with important clues in understanding general ecological consequences following large-scale climatic changes, such as global warming (Oechel et al. 1997).

Experimentally altered abiotic conditions followed by monitoring of life histories have previously been applied on arctic plants and their community structure and function (Oechel et al. 1997), whereas such focused studies on arctic animals embracing intra- as well as intertrophic interactions are lacking. Ungulates have proven to respond, both phenotypically and in terms of population dynamics, to large-scale changes in winter climate (Forchhammer et al. 1998; Post et al. 1997, 1999; Post and Stenseth 1999). Of northern ungulates, the muskox (*Ovibos moschatus*) and the caribou (*Rangifer tarandus*) are the only species adapted to survive and reproduce in the Arctic. Both species occur naturally in Greenland, with muskox and caribou populations confined to Northeast and South/West Greenland, respectively (Vibe 1967; Ruby and Thing 1985; Forchhammer and Boertmann 1993). Overall, this spatial division of the geographic ranges of muskoxen and caribou populations, respectively, coincides with contrasting climate regimes, where Northeast Greenland is characterized by High-Arctic conditions and West Greenland being mostly Low- and Sub-Arctic. With respect to intertrophic interactions, muskoxen and caribou also display marked differences. First, muskoxen, but not caribou, have been exposed periodically to predators (Dawes et al. 1986) and, second, although muskoxen are generalist browsers, caribou feed selectively on high-quality forage (Ruby and Thing 1985;

Thing et al. 1987). Hence, from these trophic and climatic differences between the two species in Greenland, it is to be expected that their long-term population dynamics will display a dichotomy in response to interannual as well as decadal changes in large-scale climatic fluctuations. This study embarks on explaining, analytically, the long-term dynamics of muskox (1961–1989) and caribou (1908–1981) populations in Greenland. Elaborating on a plant–herbivore–climate model (Forchhammer et al. 1998), we focus, simultaneously, on the relative influences of changes in winter climate, mediated through the NAO, as well as intra- and intertrophic processes on the dynamics of muskox and caribou populations.

## Material and methods

### The species and the data

Muskox and caribou are indigenous ungulate species in Greenland. Both are sexually dimorphic, polygynous herbivores with mating seasons between August and October. With a gestation period of 7–8 months, the single calf is born in May–June (Muus et al. 1990). The average age of first reproduction of caribou and muskox females is in their second and third year, respectively (Ruby and Thing 1985; Olesen et al. 1994; Adams and Dale 1998).

The data on muskox abundance (individuals observed per square kilometer) in Northeast Greenland were compiled through the annual reconnaissance of the Danish military sledge patrol “Sirius.” In one population (Germania Land, GL), however, the Sirius data were too scarce to be used in autoregressive analyses. Instead, we used annual data collected through ground-truthing by the personnel at the weather station Danmarkshavn (Forchhammer and Boertmann 1993). The muskox data cover the dynamics of six populations from 1961 to 1989 (Fig. 1a).

The caribou population data analyzed in this study consist of yearly hunting records (total animals reported shot per hunter in every settlement) obtained by the local wildlife boards since 1900 and are available in several published game statistics (for details, see Meldgaard 1986). Previous studies (Cattadori et al. 1999; Forchhammer and Asferg 2000) have shown that hunting statistics, despite variations in hunting efficiency, provide a good proxy for actual abundance. The population data of caribou cover five populations in South and West Greenland over the period 1908–1981 and one from 1908–1957 (Fig. 1a).

Because of the multiplicative nature of population dynamics (Royama 1992) and to remedy heteroscedasticity, original abundances ( $N_t$ ) were  $\log_e$  transformed. This transformation allowed us to investigate the interactions between climate and ungulate abundance on a log-linear scale (for details, see Forchhammer et al. 1998).

### The NAO and local winter weather in Greenland

The NAO is, in terms of its impact on regional and global climatic regimes, similar to its Pacific counterpart, the El

Niño Southern Oscillation (Hurrell and van Loon 1997). Specifically, the NAO quantifies the meridional oscillation in atmospheric mass over the North Atlantic with action centers over Iceland and the Azores and acts as a pressure corridor affecting the speed and direction of westerly surface winds across the Atlantic Ocean from North America to northern Europe (van Loon and Rogers 1978; Hurrell and van Loon 1997). Although operating throughout the year, the NAO is most pronounced during winter (Hurrell 1995). This NAO winter index is defined as the annual winter (December through March) deviance from the average difference in sea level pressure measured at Lisbon (Portugal) and Stykkisholmur (Iceland).

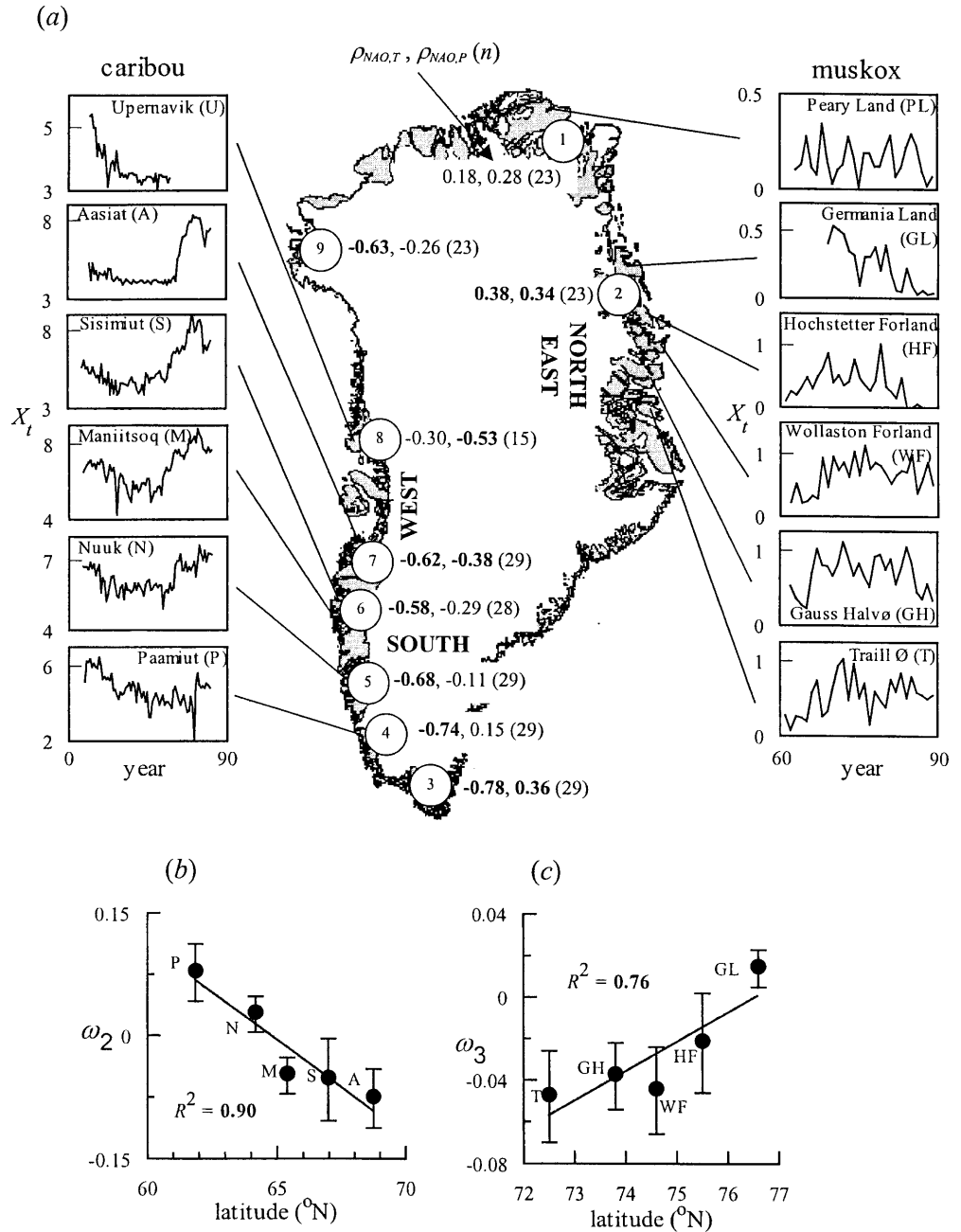
Through its association with changes in westerlies across the Atlantic, the NAO induces regional variations in winter temperature and precipitation on both sides of the North Atlantic. When the atmospheric mass balance is centered over the Azores (high positive NAO index), the cross-Atlantic westerlies increase in strength and northern Europe experiences increasingly warmer and wetter winters whereas eastern North America experiences cold and dry winters. In contrast, a weakening of the high pressure over the Azores (low negative NAO index), winters in northern Europe become cold and dry, whereas winters in eastern North America are warm and wet (Hurrell and van Loon 1997). We used the NAO index available at the National Center for Atmospheric Research (<http://www.cgd.ucar.edu/~jhurrell/nao.html>).

Based on 15–29 years of local weather data from nine weather stations, we established the association between the NAO and local winter temperature and precipitation in Greenland (Fig. 1a). In years with high NAO values, Northeast Greenland (stations 1, 2) has relatively warm winters with more than average snow, whereas winters in South and Southwest Greenland (stations 3, 4) are colder but still more snowy than average. In contrast, West Greenland (stations 5–9) experiences unusually cold and dry winters during high NAO years (Fig. 1a). These winter conditions reverse during years with low NAO indices.

### Statistical analyses

In a recent plant–herbivore–climate model predicting the relative effects of density and climate on herbivore population dynamics, only a direct effect of climate on herbivore overwinter mortality was considered (Forchhammer et al. 1998). However, winter climate conditions have been shown to exert lagged and, probably, cumulative effects on ungulate abundances (Mech et al. 1987; Post and Stenseth 1998). This lagged influence can result from trophic interactions (Post and Stenseth 1999) as well as changes in life history traits, such as fecundity (Albon et al. 1987; Loison and Langvatn 1998) and early growth (Albon and Clutton-Brock 1988; Post et al. 1997, 1999). Hence, taking into account that lagged effects of climate on population growth may, as a result of different life histories, vary between species, we can, under  $\log_e$ -linear approximation, write a

**Fig. 1.** **a** Temporal dynamics of  $\log_e$ -transformed abundances ( $X_t$ ) of caribou (*left*) and muskoxen (*right*) in Greenland. *Inserted circles with numbers* are locations of the weather stations providing data (Statistics Greenland 1967–1996) used in the analyses. With each station are associated three numbers: least square correlation coefficients between the NAO index and average winter (December–March) temperature ( $\rho_{NAO,T}$ ), and between the NAO index and average winter precipitation ( $\rho_{NAO,P}$ ); sample sizes ( $n = \text{years}$ ) are given in *parentheses*. Northeastern, southern, and western regions of Greenland are indicated on the map. **b** Latitudinal variations in the 2-year lagged influence of the NAO ( $\omega_2$ ; see Table 1) across caribou populations. **c** Latitudinal variations in the 3-year delayed influence of the NAO ( $\omega_3$ ; see Table 1) across muskox populations. In **b** and **c**, the *solid line* indicates the linear regression line and error bars  $\pm$ SEM. *Capital letters* refer to those in Table 1 and Fig. 1a



more general version of the previous population model by Forchhammer et al. (1998):

$$N_t = N_{t-1} \exp\left(\beta_0 + \sum_1^{i=d} \beta_i X_{t-i} + \sum_1^{j=k} \omega_j U_{t-j}\right) \quad (1)$$

where  $N_t$  is herbivore abundance at time  $t$ ,  $X_t = \log_e(N_t)$ ,  $U_{t-j}$  is the abiotic (i.e., climatic component), and  $\beta_0$  represents the intrinsic growth rate of the herbivore population without intrinsic and extrinsic influence (Forchhammer and Asferg 2000). Following Forchhammer et al. (1998), taking the natural logarithm on both sides of Eq. 1 we obtain a  $d$ -dimensional, univariate autoregressive (AR( $d$ )) model with the summed climatic effects ( $U_{t-j}$ ) as covariate:

$$X_t = \beta_0 + (1 + \beta_1)X_{t-1} + \beta_2 X_{t-2} + \beta_3 X_{t-3} + \dots + \beta_d X_{t-d} + \sum_1^{j=k} \omega_j U_{t-j} + \varepsilon_t \quad (2)$$

The coefficients  $(1 + \beta_1)$  and  $\beta_i$  (for  $i > 1$ ) are the AR coefficients,  $\omega_j$  are the covariate regression coefficients, and  $\varepsilon_t$  is the remaining variance not specified by the specified model parameters of Eq. 2. Generally, an AR(1) population model suggests that direct density dependence is the most important determining temporal dynamics (Stenseth et al. 1998b; Forchhammer and Asferg 2000). On the other hand, AR(2) population dynamics suggest that direct interactions with another trophic level also are influential, whereas AR(3) population dynamics indicate that the dynamics are

influenced by two additional levels (Stenseth 1995; Stenseth et al. 1998b; Forchhammer and Asferg 2000; Post and Forchhammer 2001).

To simultaneously estimate the relative effects of winter climate and density dependence on muskox and caribou dynamics, we applied the analysis of AR with the NAO as a covariate. To cover the reproductive phenology of both muskoxen and caribou (see above) in our analyses, we considered the alternatives of lagged covariates (i.e.,  $U_{t-j}$ ) up to  $j = 3$  years combined with dimensions  $d$  equaling 0–3 in the AR( $d$ ). When, in our process of comparing the fit of different models, the data are first used to estimate model parameters and, then, to calculate goodness-of-fit, a more complicated model will always give a better fit than a simpler model because of the larger number of parameters (Hjort 1994). In contrast, theoretical information criteria are better measures of the appropriateness of various models. Several alternative criteria exist (Priestley 1981). Here we follow the procedures of previous studies involving analyses of linear and nonlinear structural population dynamics (Bjørnstad et al. 1995; Forchhammer et al. 1998; Stenseth et al. 1996, 1999; Post and Stenseth 1999; Aanes et al. 2002) and use the Akaike information criterion,  $AIC = -2LL + 2p$ , where  $LL$  is the maximized log likelihood of the fitted model and  $p$  is the number of parameters in the model (Sakamoto et al. 1986). The most parsimonious model from all combinations of  $k$  and  $d$  was then found by choosing the model with lowest AIC, where a difference in AIC between models lesser than 1 is considered insignificant (Sakamoto et al. 1986).

AR and covariate coefficients were estimated using the PROC AUTOREG with maximum-likelihood estimation in SAS 6.12 for Windows (SAS Institute 1996). Stationarity of time series is required for AR procedures (Priestley 1981). Hence, time (i.e., year) was added as a covariate in the AR procedures (for details, see SAS Institute 1990) to remedy nonstationarity and spurious interactions caused by trends in the data. Similarly, the influence of trends in the NAO was tested by comparing AR results using nondetrended and detrended (cubic spline smoothed,  $df = 5$ ; see MathSoft Inc. 1997) NAO time series, respectively.

Although previous theoretical work has focused on the power of tests detecting density dependence (i.e., avoiding type II error: rejection of density dependence when present in dynamics), only recently the effect of type I errors (i.e., detection of density dependence in density-independent population processes) in population studies has come into focus (Shenk et al. 1998). Type I errors may be a potential problem in many population studies because census error may generate spurious density dependence and most studies do not involve either exact error-free counts or multiple census. Indeed, type I error may be a problem in this study because, as in many previous long-term studies (Elton 1924; Keith 1963; Stenseth et al. 1998a), the population dynamics of caribou and muskoxen in Greenland are based on consecutive single annual estimates of abundance. Therefore, because AR analyses of density dependence in the time series may result in type I errors (Shenk et al. 1998), we addressed this potential problem in two ways.

First, because short-term population censuses, additional and independent of those used in this study (see above), were available for caribou population P (Meldgaard 1986) and muskox population GL (M.C. Forchhammer, unpublished data), we can in these populations assess variation to in census error in relation to the variation of the population time series used in this study. Therefore, we compared in the two mentioned populations the coefficient of variation ( $CV = \sigma/\mu$ ) (Zar 1984) of census errors (i.e., difference between the two population censuses) and the CV of the population census data used in our autocovariate analyses (see above). If the latter exceeds the former, then variance in census error is minor compared to real variation in population abundances, whereas if there is no difference in the CV, variations in actual population size and census errors are difficult to disentangle (Freckleton et al., in manuscript). Differences in CV's were evaluated using Fisher's variance ratio test (Zar 1984).

Second, having only a point estimate, that is, one population estimate in each of the 12 muskox and caribou time series, we evaluated the robustness of the estimated best-fit AR models, using the bootstrap technique of resampling (Efron and Tibshirani 1993). Bootstrapping was performed in S-PLUS 4 for Windows using the BOOTSTRAP function with 1000 replications (MathSoft 1997).

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## Results

### Effects of the NAO and density dependence

In both muskoxen and caribou, the most parsimonious autoregressive model found in five of six populations was of the order  $d \leq 2$  (Table 1). No remaining pattern was found in the residuals for any of the populations, except the Gauss Halvø muskox population (Table 1).

For caribou, high NAO winters, which were associated with cold and snowy winters in South Greenland and cold and dry in West Greenland (Fig. 1a), had a 2-year delayed positive effect on southern populations but a 2-year delayed negative effect on western populations (Table 1; Fig. 1b).

For muskoxen, warm snowy winters (high NAO index; Fig. 1a) had, overall, a 3-year delayed negative effect on muskox abundances (Table 1). Spatially, this effect decreased toward the north (Fig. 1c; Table 1). A direct negative effect of high NAO winters was only found in the Germania Land population (Table 1).

Overall, the state of the NAO had its largest impact on southern arctic ungulate populations, accounting for up to 24% and 16% of the temporal variance in muskox and caribou dynamics, respectively (see Table 1).

Significant direct, negative density dependence ( $(1 + \beta_1) < 1$ ) was recorded in four muskox and all caribou populations, whereas significant delayed density dependence ( $\beta_2$ ) was documented in three muskox and one caribou populations (Table 1). A 3-year delayed density-dependent component entered the most parsimonious model in one muskox and one caribou population (see Table 1).

**Table 1.** Summary of the autoregressive analyses of the six muskox (1961–1989) and six reindeer (1908–1981) populations in Greenland

Population ( <i>n</i> )	AIC	<i>d</i>	Most parsimonious model, $\phi\{\cdot\}$	AR coefficients			NAO coefficients			DW <sup>d</sup>	$R^2_{TOT}$	$R^2_{NAO}$
				$(1 + \beta_1)^a$	$\beta_2^b$	$\beta_3^b$	$\omega_1^c$	$\omega_2^c$	$\omega_3^c$			
Muskox												
T (29)	-0.8	0	$\phi\{NAO_{t-3}\}$	-	-	-	-	-	-0.048*	1.9	0.23	0.23
GH (29)	-8.2	2	$\phi\{X_{t-1}, X_{t-2}, NAO_{t-3}\}$	0.695	-0.401*	-	-	-	-0.038*	1.6*	0.49	0.24
WF (29)	-1.5	2	$\phi\{X_{t-1}, X_{t-2}, NAO_{t-3}\}$	-0.008*	0.537*	-	-	-	-0.045*	2.0	0.49	0.24
HF (29)	1.3	1	$\phi\{X_{t-1}, NAO_{t-3}\}$	0.341*	-	-	-	-	-0.022	1.9	0.30	0.12
GL (23)	-41.5	3	$\phi\{X_{t-1}, X_{t-2}, X_{t-3},$ $NAO_{t-1}, NAO_{t-3}\}$	-0.486*	-0.414	-0.464	-0.022*	-	0.014	2.0	0.35	0.12
PL (29)	-58.2	2	$\phi\{X_{t-1}, X_{t-2}\}$	0.053*	-0.567*	-	-	-	-	2.0	0.32	0.00
Caribou												
P (74)	118.1	1	$\phi\{X_{t-1}, NAO_{t-2}\}$	0.593*	-	-	-	0.077*	-	2.0	0.58	0.16
N (74)	65.5	3	$\phi\{X_{t-1}, X_{t-2}, X_{t-3},$ $NAO_{t-2}\}$	0.538*	0.041	0.294*	-	0.027	-	1.9	0.67	0.03
M (74)	99.0	1	$\phi\{X_{t-1}, NAO_{t-2}\}$	0.840*	-	-	-	-0.049*	-	2.1	0.81	0.14
S (74)	181.5	2	$\phi\{X_{t-1}, X_{t-2}, NAO_{t-2}\}$	0.522*	0.256	-	-	-0.054	-	2.0	0.75	0.11
A (74)	159.1	2	$\phi\{X_{t-1}, X_{t-2}, NAO_{t-2}\}$	0.477*	0.392*	-	-	-0.077*	-	2.0	0.81	0.11
U (50)	93.1	1	$\phi\{X_{t-1}\}$	0.827*	-	-	-	-	-	2.1	0.91	0.00

Population codes refer to those given in Fig. 1. The Akaike Information Criterion (AIC) and the order (*d*) are given for the most parsimonious model. The AR and covariate coefficients refer to those specified in Eq. 1. DW is the Durbin–Watson statistic (Durbin and Watson 1971) for the model residuals.  $R^2_{TOT}$  is the total explained variance and  $R^2_{NAO}$  is the amount by which  $R^2_{TOT}$  increased by including NAO as a covariate in the AR model. Use of “-” indicates that the variable did not enter the most parsimonious model

\*  $P < 0.05$

Two-tailed *t* test,  $H_0$ : <sup>a</sup> $(1 + \beta_1) = 1$ , <sup>b</sup> $\beta_2 = 0$ , <sup>c</sup> $\omega_i = 0$ , <sup>d</sup>DW = 2

## Evaluation of the population data

For the caribou population P, the coefficient of variation (CV) of log-transformed hunting indices (1.98) did not differ from the CV of log-transformed fur-trading indices (1.78) ( $F_{35,34} = 1.34$ ,  $P > 0.20$ ). However, the CV of the annual census errors (0.71) was significantly less than the CV of population estimates used in the AR analyses (i.e., hunting indices) ( $F_{35,34} = 2.80$ ,  $P < 0.005$ ). In the muskox population GL, no significant difference was found between the CV of log-transformed ground-truthing indices (1.00) and the CV of the comparative log-transformed Sirius indices (0.63) ( $F_{14,6} = 2.79$ ,  $P > 0.10$ ); the CV of census errors (0.35) was, however, significantly less than the CV of population estimate used in our AR analyses (i.e., ground-truthing) ( $F_{14,6} = 6.43$ ,  $P < 0.05$ ).

Bootstrap resampling of the muskox and caribou time series showed that AR and covariate coefficients estimated through AR modeling (Table 1) were robust: 1000 bootstrap samples obtained by randomly sampling from the original time series produced virtually no bias in relation to the original estimates (Fig. 2a,b).

## Discussion

Our statistical analyses document that variation in large-scale winter climate, mediated by the North Atlantic Oscillation (NAO), and density dependence are important components of the developmental processes of muskox and caribou dynamics in Greenland. Also, between as well as within the two species, the analyses revealed significant spa-

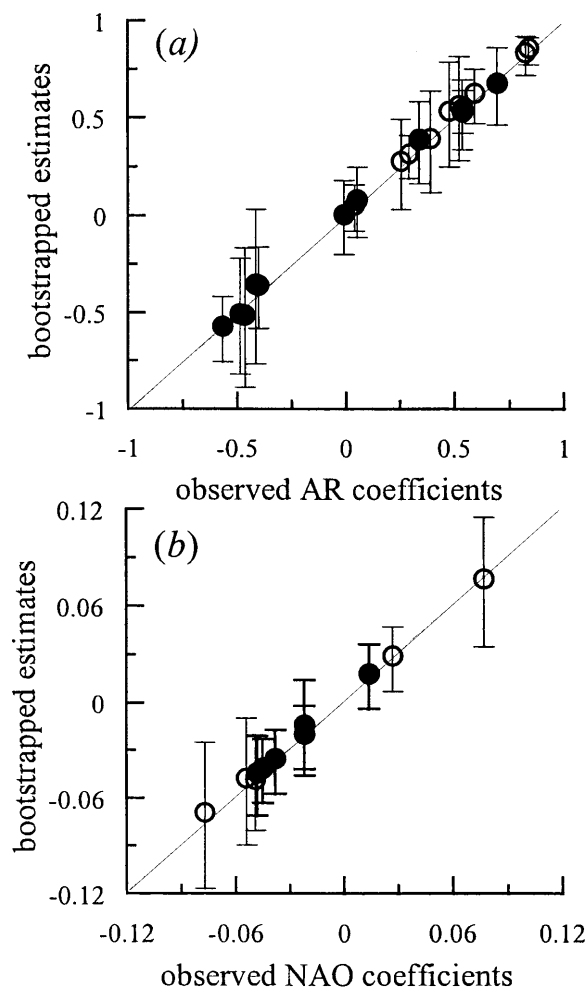
tiotemporal variations in the structural components of their population dynamics.

The analyses of coefficient of variation demonstrating the importance of population variance (and not census error) in two populations and the robustness of the estimated AR models (Fig. 2a,b) in all populations clearly indicate that our results reflect population processes and not spurious dynamics arising from census errors. Furthermore, additional independent, mostly scattered and short-term data on muskox abundances in Greenland compiled by various expeditions (Boertmann and Forchhammer 1992) corroborate the dynamics demonstrated in this article. Similarly, in caribou, additional independent data (Vibe 1967; Meldgaard 1986) support the presented hunting-based dynamics in Fig. 1a.

One could argue that being based on hunting statistics, the presented caribou population dynamics could reflect temporal changes in hunting behavior. However, if such an intertrophic interaction was important, AR analyses would show strong negative delayed density dependence (Stenseth et al. 1998b), which they did not (Table 1). Based on this and previous results (Cattadori et al. 1999; Forchhammer and Asferg 2000), we believe that the population indices used here parallel changes in population sizes.

## Responses to variations in the NAO

The observed consistency by which the 3-year and 2-year delayed effects of the NAO entered the most parsimonious models for muskoxen and caribou dynamics, respectively, combined with the reported age at maturity in the two species (see above), suggest that variations in the NAO



**Fig. 2.** Relationships between bootstrapped estimates and observed **a** AR ( $1 + \beta_1, \beta_2$ ) and **b** NAO ( $\omega_2, \omega_3$ ) coefficients. The symbols ● and ○ refer to muskox and caribou populations, respectively; horizontal bars,  $\pm$  bootstrapped SEM; diagonal lines,  $y = x$

primarily influence fecundity and survival/recruitment of offspring of arctic ungulates in Greenland. This hypothesis is corroborated by empirical studies on several northern ungulates documenting a profound influence of abiotic conditions on early development of individuals in utero as well as during postnatal development (Albon et al. 1987; Albon and Clutton-Brock 1988; Post et al. 1999; Forchhammer et al. 2001). For example, in red deer (*Cervus elaphus*), individuals born following warm, snowy winters showed significant delays in their early development of body weight, eventually postponing time of first reproduction (Langvatn et al. 1996; Loison and Langvatn 1998). Also, in moose (*Alces alces*) and Soay sheep (*Ovis aries*), effects on early development imposed by the state of the NAO persist into adulthood, creating cohort differences in survival as well as reproductive output (Post and Stenseth 1999; Forchhammer et al. 2001).

Although probably affecting temporal patterns of fecundity and recruitment in both muskoxen and caribou, the effect of NAO was clearly different in the two species (Table 1). Our results suggest that muskoxen are influenced

by both precipitation and temperature during winter. First, muskoxen foraging in deep snow increase energy expenditure at the expense of overwinter body condition (Adamczewski et al. 1995). Second, warmer than average winters may accentuate negative effects of snow depth by increasing the probability of ice crust formation (Forchhammer and Boertmann 1993). Deterioration of body condition following such high NAO winter conditions may in particular affect pregnant females (Adamczewski et al. 1995) and consequently their fetuses, as reported for red deer and Soay sheep (Post et al. 1999; Forchhammer et al. 2001). Indeed, the progressive latitudinal decreasing effect of the NAO across muskox populations (Fig. 1c) coincides with a south–north gradient, where muskox dynamics were, because of the sheltering effects of the extensive sea ice, decreasingly influenced by the warmer and more variable maritime North Atlantic environment (Forchhammer and Boertmann 1993).

Caribou dynamics, on the other hand, seem to be primarily influenced by winter precipitation. As shown by the latitudinal gradient of the influence of the NAO (Fig. 1b), all caribou populations were, during high NAO winters, exposed to colder than usual winter conditions (Fig. 1a). But, although the southern regions of Greenland also experienced more snow, the western regions experienced dry winters during high NAO conditions (Fig. 1a). Following high NAO winters, southern populations increased but western populations decreased (see Table 1). Hence, our analyses suggest that increased amounts of snow during winter positively affect caribou abundance with a 2-year lag. This finding seems to contradict earlier findings describing direct (nonlagged) and negative effects of increased snow depths (Skogland 1989; Adams and Dale 1998). However, empirical evidence strongly suggests that two conditions, combined or separately, may have caused the observed delayed positive response seen in Greenland. First, caribou favour sites with persistent snow over snowfree sites for calving (Eastland et al. 1989). Second, following snowy winters caribou arriving on their summer grounds experience improved forage conditions (Walsh et al. 1996) and prolonged availability of newly emergent plants (Post and Stenseth 1999). Although deep snow leads to a shorter plant growth season and lower plant biomass ( $\text{g/m}^2$ ) production (Post and Klein 1999), calving caribou select foraging areas with high biomass concentration ( $\text{g/m}^3$ ), which increases with delayed snow melt and abbreviation of the plant growing season (Post and Klein 1996). In corroboration, recent analyses suggest that increased (high NAO) winter severity has a direct negative effect on juvenile survival but a delayed positive effect on adult survival and fecundity of Soay sheep cohorts, the latter probably being mediated through improved spring forage conditions following high NAO winters (Forchhammer et al. 2001).

#### Responses to variations in density

Our results also documented that temporal forcing of direct and delayed density dependence are major population processes of muskoxen and caribou, respectively (see Table 1).

Statistical direct density dependence ( $1 + \beta_1$ ) has been shown to represent ecological density dependence, that is, intrinsic interactions, whereas statistical delayed density dependence ( $\beta_2$ ) also includes extrinsic intertrophic interactions (Stenseth et al. 1998b; Forchhammer and Asferg 2000). Hence, our statistical results suggest that intrinsic competitive processes are important for both muskoxen and caribou, throughout their ranges (Table 1).

The positive intertrophic interaction between caribou and their forage inferred by the positive  $\beta_2$  coefficients (Table 1) has been previously suggested for caribou in Alaska. Experimentally induced grazing over a range of caribou feeding habitats induced a strong positive growth response in forage characteristics, such as biomass density, shoot density, and concentrations of nutrients and minerals (Post and Klein 1996). Because caribou grazing is sensitive to local variations in forage quality and quantity (Post and Klein 1996), a positive feedback loop may explain the observed positive delayed density dependence (see Table 1).

The same mechanism may be responsible for the positive delayed density dependence seen in muskox population WF. However, the negative delayed density dependence reported in muskox populations GH, GL, and PL probably reflects an increased impact of polar wolves (*Canis lupus arctos*), which, after 70 years of absence, recolonized Northeast Greenland in the early 1970s (Dawes et al. 1986) and now are breeding in central eastern Greenland (Gauss Halvø, GH) (Marquard-Petersen 1998). Indeed, the remaining pattern found in the model residuals of population GH (Table 1) suggests that muskoxen here may recently have become significantly squeezed from above; that is, a three-trophic-level model integrating the effects of wolves may be more appropriate here.

Our results demonstrate a complexity with respect to how, specifically, large-scale climatic perturbations, such as global warming, influence population dynamics of long-lived organisms in a relatively simple ecosystem, such as the Arctic. As shown through the dichotomous effect of changes in the NAO in Greenland, spatial variability of climatic changes is important. Indeed, it has recently been documented that it is the variability rather than the trend of change of extreme events that probably affects environmental conditions (Hasselmann 1999). Evidently, integration of atmospheric circulation modes, like the NAO, may be of major importance in understanding impacts of large-scale climatic change on ecosystem structure and functioning in the Northern Hemisphere.

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