North Atlantic Oscillation signatures in aquatic and terrestrial ecosystems—a meta-analysis

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Abstract

Climate variations over the Northern Hemisphere are to a substantial proportion associated with the North Atlantic Oscillation (NAO). Recently, many studies revealed the impacts of the NAO on the dynamics of organisms in different ecosystems but the results in the single studies were inconsistent. Here, we used meta-analysis techniques for a quantitative synthesis of results. We tested the influence of the NAO on the timing of life history events, on biomass of organisms, and on biomass of different trophic levels. We found a clear NAO signature in freshwater, marine, and terrestrial ecosystems. The response of life history events to the NAO was similar in all environments but less pronounced at higher latitudes. The magnitude of the biomass response was significantly related to the NAO, either positively in aquatic or negatively in terrestrial ecosystems. The response depended on longitude, the effect being less pronounced in Eastern Europe. The results stressed that a meta-analysis is a valuable tool in the field of climate-driven ecosystem responses and can identify more general ecological responses than single studies. We recommend the inclusion of nonsignificant results in order to archive an objective view of the strength of NAO and climate impacts in general.

Keywords: climate change, life history event, meta-analysis, NAO, trophic level

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Introduction

The last decade was the warmest in the Northern Hemisphere over the past thousand years and air temperature is predicted to increase even more in future, especially in winter (IPCC 2001). The central question arises as to how natural ecosystems respond to climate change and how they will change in future. Climate dynamics are complex and although global temperature has increased in the past century, large regional differences exist (Schlesninger & Ramankulty 1994). Temperature in Northern Europe has increased but at the same time decreased in Greenland and Northeastern America (Hurrell & Loon 1997). A substantial proportion of this variation in regional winter climate conditions in the Northern Hemisphere can be associated with variations in the atmospheric mass balance over the North Atlantic, which is known as the North Atlantic Oscillation (NAO) (Hurrell 1996). The NAO index is therefore considered to

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be a proxy for the climate variation over the North Atlantic, without characterizing a long-term climate-warming trend.

A positive winter NAO index implies a mild and rainy winter in Northern and Western Europe, while the opposite is the case in Eastern Canada.

Since the mid 90s, an expanded body of work has revealed distinct traceable effects of variation in the NAO on the dynamics of organisms in aquatic and terrestrial ecosystems. The most obvious and documented influence of the NAO on the organisms occurs through temperature (Ottersen *et al*. 2001). In European lakes, the timing for maximum biomass of phytoplankton and zooplankton in spring appeared earlier in mild winters during a positive NAO index (Weyhenmeyer *et al*. 1999; Gerten & Adrian 2000; Straile & Adrian 2000). In marine systems, the length of the growing season for phytoplankton (Reid *et al*. 1998), the zooplankton abundance (Fromentin & Planque 1996), and the growth rate of fish (Ottersen & Loeng 2000) were altered via temperature by the NAO. In terrestrial systems, the positive NAO caused an earlier breeding of amphibians and birds

(Forchhammer et al. 1998b), an earlier flowering of plants, and a higher biomass of ungulate calves (Post & Stenseth 1999). However, a separation from other winter variables like snow, ice cover or hydrodynamics in lakes and oceans is difficult as these factors are closely synchronized, and finding the forcing mechanism is often a difficult task (Ottersen et al. 2001). Therefore, the application of the NAO as an integrated climate parameter might be very advantageous in ecological studies.

Some inconsistencies were found between the different studies and organisms: On the species level it was documented that among plant and ungulate species the response was diverging (Post & Stenseth 1999). On the population level, Post et al. (1999b) found that the underlying mechanism of the NAO response might differ owing to the differences in regional responses to the NAO. However, the main focus in all NAO-ecology studies was on the timing of life history events, biomass, and the cascading effects.

Any impact of climate fluctuations and climate change will not be uniform across ecosystems and for different parts within ecosystems (Visser et al. 1998). A comparative ecosystem approach might provide new insights about general ecological phenomena, which has similarly been performed, e.g. in the field of acidification (Gunn et al. 1995; Wright & Schindler 1995).

In our study, we apply meta-analysis techniques to analyse the response of different organisms from aquatic and terrestrial habitats to the winter NAO. A meta-analysis permits the statistical synthesis of research results (Gurevitch et al. 1992)—in our study, the correlation coefficient—from a set of primary studies. The result is an aggregate test of numerous studies, which provides a more powerful test than the statistical test of individual studies (Osenberg et al. 1999). Meta-analysis generally offers a powerful set of tools for answering questions of great relevance in reviewing literature. It gives information on: (a) the overall magnitude of an effect, (b) whether that effect differs among contrasting categories of studies, and (c) how much variation are within and among categories (Gurevitch et al. 1992). Traditionally, reviews are often an attempt to place the results of studies into a general context, i.e. summarizing the literature verbally or by vote counting (see for example Gurevitch et al. 1992). The latter remain largely qualitative and subjective. In contrast, a meta-analysis is a quantitative synthesis, analysis, and summary of a collection of primary studies (Osenberg et al. 1999) and has been successfully implemented in ecological studies (Gurevitch et al. 1992; Brett & Goldman 1996; Downing et al. 1999; Gurevitch et al. 2000; Hillebrand et al. 2001). Meta-analysis allows first statistical testing of whether there is a general effect of NAO on biological parameters across studies. Secondly, it also enables us to analyse and compare the

effects for different response variables, ecosystems, groups of organisms, and trophic levels. We were able to use the same climate parameter (winter NAO) throughout. We applied for the first time a meta-analysis on the available literature to analyse the following objectives:

1. To quantitatively examine whether a positive NAO leads to an earlier life history event in different organisms in freshwater, marine, and terrestrial systems.
2. To estimate the effects of a warm winter (pos. NAO) on the biomass of different organisms in different systems.
3. To quantify the effects of the NAO on different trophic levels.

Methods

This analysis is based on published data which are obtained from the ASFA and BIOSIS database. To ensure unbiased comparison, we only included studies in which the winter (Dec.–Mar.) NAO Index (see Fig. 1) was applied to test for significant interactions. After this selection, 12 published papers were included in the database, which comprised 60 single analyses in total (see Table 1).

For each analysis, we used the correlation coefficient between the specific winter NAO and the target variable. As Osenberg et al. (1999) pointed out, the metric for the meta-analysis should be explicitly defined by the question and the ecological process of interest. In the NAO-ecology studies, the correlation analysis has remained the favoured method for the identification of NAO-ecology links (Ottersen et al. 2001). Moreover, the correlation coefficient is a suitable measure of effects because one variable—the NAO index—is the same in all correlations.
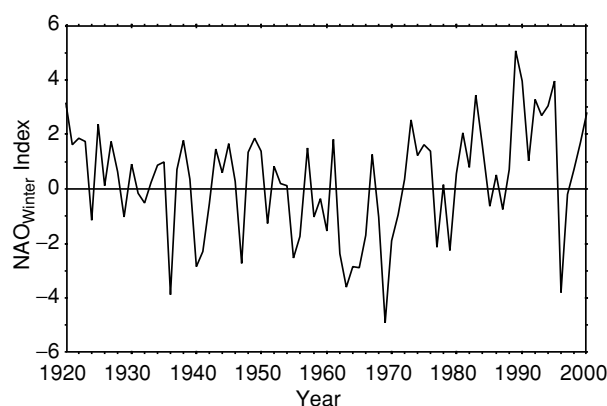
Fig. 1 The NAO winter index for the respective time period from the studies (1920–2000). The values in the graph differ slightly from those in Hurrell (1995) because the data were normalized relative to the 120-year period 1864–1983 (source:http://www.cgd.ucar.edu/~jhurrell/nao.html).

Table 1 References used for the meta-analysis, including information about time period of the study, habitat, latitude, longitude, trophic group, species group, the inclusion of the extreme negative NAO year 1996 and if the biomass was log transformed. Variables in the trophic group were abbreviated as follows: ph = physical, p = plant, h = herbivore, pr = predator, o = other (birds and amphibians), Variables in the species group were abbreviated as follows: wt = water temperature, ice = ice cover of lakes, snow = snow cover, phy = phytoplankton, zoo = zooplankton, p = plant, un = ungulate, am = amphibian, bi = bird, pr = predator

Reference	Time period	Habitat	Latitude	Longitude	Trophic group	Species group	Extreme year	Log-transformed
Weyhenmeyer et al. (1999)	1954–1998 (no constant)	lake	59.4	18.2	ph, p	ice, phy	yes	no
Gerten & Adrian (2000)	1979–1998	lake	52.4	13.6	ph, p, h	wt, phy, zoo	yes	partly
George (2000)	1956–1968	lake	54.3	− 2.9	ph, h	wt, zoo	no	no
Straile (2000)	1979–1994	lake	47.6	9.4	ph, p, h	wt, phy, zoo	no	yes
Belgrano et al. (1999)	1985–1996	marine	58	11	ph, p	wt, phy	yes	no
Irigoien et al. (2000)	1993–1999	marine	50.2	− 4.2	p	phy	yes	yes
Post & Stenseth (1998)	1957–1985	terrestrial	46	9.5	ph	snow	no	
Post & Stenseth (1999)	1928–1977 (plants)	terrestrial	61.8	8.3	p, h	p, un	no	no
Post et al. (1999b)	1964–1993	terrestrial	61.8	8.3	h	un	no	yes
Post et al. (1999c)	1958–1997	terrestrial	46	9.5	p, h, pr	p, un, pr	yes	partly
Loison et al. (1999)	1977–1997	terrestrial	63.5	9.5	ph, h	snow, un	yes	partly
Forchhammer et al. (1998a)	1925–1995	terrestrial	50.2	− 4.2	o	am, bi	no	
Przybylo et al. (2000)	1980–1995	terrestrial	57.2	18.3	o	bi	no	no

The specific winter NAO Index originated from the same year or from previous years, depending on when the authors found the highest response to the ecological variable. All correlation coefficients (r) were Z-transformed (r_z) to establish the effect size:

$$r_z = \frac{1}{2} \ln \left[\frac{1 + r}{1 - r} \right]$$

r_z is a common effect size of meta-analyses and allows the performance of a weighted analysis, where the effect size is weighted (w_i) for the ith study by the inverse of its sampling variance.

The sampling variance (v_z) of r_z was calculated from the number of observations (n):

$$v_z = \frac{1}{n - 3}$$

First of all, we calculated the overall effect (overall effect size, E^{++}) of the NAO on (a) the timing of the life history event and (b) the biomass of the organisms. Secondly, we tested if the magnitude of the NAO effects on (a) and (b) differed for groups, particular characteristics (group effect size, E^+) which we believed might affect the outcome of the relationship between the NAO and the target variable in the individual study. Seven characteristics were chosen to test if the magnitude of the NAO impact varies between ecosystems ('habitat'), location of the study site ('latitude' and 'longitude'), on a trophic level

('trophic group'), and on different species levels ('species level'). Furthermore, the inclusion of the extreme negative NAO year (1996) in the time period of the primary study ('extreme year') could influence the result, as extremes tend to influence the correlation. Additionally, we tested whether a log transformation of an organism biomass in the primary studies affects the relationship between the NAO and the target organism biomass ('log transformed'). The primary studies were not clustered with respect to geographical position (longitude and latitude) and thus possible impacts on effect sizes were not owing to a single cluster of analyses from one site.

The 95% confidence intervals (CI) and the E^{++} were calculated for all phenological events and biomass data as outlined by (Rosenberg et al. 2000).

$$E^{++} = \frac{\sum_{i=1}^{n} w_i * E_i}{\sum_{i=1}^{n} w_i}$$

E_i is the calculated effect size of the individual ith study.

The variance of E^{++} is a function of the individual weight:

$$S_{E^{++}}^2 = \frac{1}{\sum_{i=1}^{n} w_i}$$

Using $s^2_{E^{++}}$, the CI around E^{++} is:

$$CI = E^{++} \pm t_{\alpha/2[n-1]} * S_{E^{++}}$$

where t is the two-tailed critical value found from Student's t-distribution at the critical level α.

An effect is significant if the CI does not overlap 0 (Gurevitch *et al.* 2000). In general, a positive effect size means also a positive impact of the NAO on the particular variable. For example, a positive effect size of all life history events means that the timing of all varied life history events is later during a positive NAO year.

Then, the E^+ and the CI were calculated for the seven characteristics (j):

$$E_j^+ = \frac{\sum_{i=1}^{kj} wi_j * E_{ij}}{\sum_{i=1}^{kj} w_{ij}}$$

where kj is the number of studies in the characteristic group j and w_{ij} and E_{ij} are the weight and effect size for the ith study in the jth group. For each E^+, the 95% CIs were calculated with bootstrapping 9999 randomizations. This distribution-free method creates a distribution of effect sizes based on the actual data set without assuming underlying distributions.

Non-overlapping CIs indicate a significantly different group effect size. Differences of effect sizes between the characteristic groups were tested with an analysis of heterogeneity (Q) within groups (Q_{wj}) and between groups (Q_M), which is analogous to an analysis of variance.

The heterogeneity within the jth group is:

$$Q_{wj} = \sum_{i=1}^{kj} w_{ij}(E_{ij} - E^+)^2$$

The heterogeneity between groups is calculated as:

$$Q_M = \sum_{j=1}^{m} \sum_{i=1}^{kj} w_{ij}(E^+ - E^{++})^2$$

where m is the number of groups.

All calculations were done with MetaWin 2.0 (Rosenberg *et al.* 2000).

Results

NAO effects on life history events

We found seven published papers, with 29 single studies on phenology. These life history events ranged from timing of the phytoplankton spring bloom (Weyhenmeyer *et al.* 1999; Gerten & Adrian 2000; Irigoien *et al.* 2000), timing of
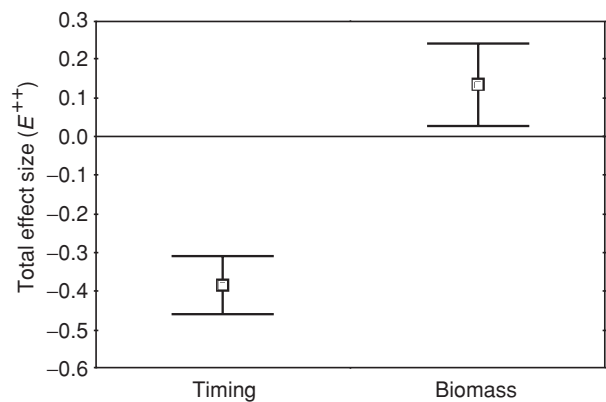

Fig. 2 The E^{++} and the CIs (95%) of all primary studies on timing of life history events and biomass of the organisms.

maximum zooplankton biomass (Gerten & Adrian 2000; Straile 2000) and first flowering date of plants (Post & Stenseth 1999) to first spawning date of amphibians (Forchhammer *et al.* 1998a), first egg-laying date of birds (Forchhammer *et al.* 1998a; Przybylo *et al.* 2000) and timing of first reproduction by different ungulates (Post & Stenseth 1999). All these life history events were significantly negatively influenced by the winter NAO (Fig. 2), implying an earlier onset of the target process after warm winters (pos. NAO). The E^{++} was significantly >0, indicating a general impact of the NAO across ecosystems. The analysis of heterogeneity revealed a significant decrease of the effect with latitude (Table 2). This indicates that the effect of the NAO on timing in general was stronger in the South of Germany than in Northern Scandinavia. No differences between effects were found between aquatic and terrestrial systems (Table 2, Fig. 3). Also, the inclusion of the extreme negative NAO year 1996 (lowest value ever measured) did not affect the result. Additionally, the type of organism on study was of less importance, even though the ungulates varied largely between negative and positive responses to the NAO (Table 2, Fig. 4).

NAO effects on biomass

Ten publications containing 24 relationships between biomass and NAO could be obtained. The primary studies covered phytoplankton (Belgrano *et al.* 1999; Weyhenmeyer *et al.* 1999; Gerten & Adrian 2000; Irigoien *et al.* 2000; Straile 2000), zooplankton (George 2000; Straile 2000) plants (Post & Stenseth 1999), ungulates (Loison *et al.* 1999; Post & Stenseth 1999; Post *et al.* 1999b; Post *et al.* 1999c) and predators like wolf (Post *et al.* 1999c). In contrast to the timing, the overall effect here showed a significantly positive response, indicating that a higher NAO value was associated with a higher

biomass of the specific organism (Fig. 2). The general effect was significantly >0 (see also Fig. 3). However, a significant difference between the effects in aquatic and terrestrial habitats was found (Table 2). In aquatic systems, the biomass responded positively to a high NAO, whereas in terrestrial environments it decreased after warm winters (Fig. 3). In addition, the longitude seems to be important for the response of biomass to the NAO, indicating a stronger impact of the NAO in the West than in the East of Europe (Table 2). The effect strength was not significantly affected by latitude, species group, trophic group, extreme year, or log transformation.

NAO effects on trophic levels

We tested if the response of the relationships of physical parameters (see Table 1) as well as biomass of different trophic levels to the NAO declines from physical to herbivore level. Six published papers (Belgrano *et al.* 1999; Weyhenmeyer *et al.* 1999; George 2000; Gerten & Adrian 2000; Irigoien *et al.* 2000; Straile 2000) with a total 21 single variables were used in the test. No significant effect was found owing to the overlapping of the CI (Fig. 5). However, a tendency of a decline in the response to the NAO from physical to phytoplankton and finally zooplankton became evident (Fig. 5). Still, the number of published studies were too limited to draw general conclusions from this test.

Discussion

Our results clearly demonstrated that a positive NAO value (warm winter) induced earlier timing of life history events for a variety of organisms and across ecosystems in Europe. The magnitude of biomass was also significantly related to the NAO, either positively in aquatic or negatively in terrestrial ecosystems. The effect of the NAO impact was clearly related to the geographical position of the study site. Additionally, the response of different trophic levels to the NAO was not significant, whereas a tendency towards a decline in the response can be seen.

Timing effects

The timing of life history events was strongly altered by the NAO signal because phenology in general is strongly influenced by temperature and precipitation (Hughes 2000) and, additionally, climatic constraints on life-history events have implications for the fitness of organisms in variable environments (Post *et al.* 2001a). The meta-analysis revealed a similar magnitude of response in aquatic and terrestrial systems as well as organism

Table 2 Tests of heterogeneity (Q) for the timing of life history events (timing) and biomass relationships between (Q_M) and within (Q_{wi}) the different (a-f) characteristic groups. Significance levels were obtained from randomizations (Rosenberg *et al.* 2000)

(a) Habitat (aquatic and terrestrial)

	Timing			Biomass		
	d.f.	Q	p	d.f.	Q	p
Between	1	1.04	0.347	1	8.5	0.014
Within	29	29.5		24	33.0	

(b) Trophic group (physical, plant, herbivore, amphibians and birds)

	Timing			Biomass		
	d.f.	Q	p	d.f.	Q	p
Between	3	4.3	0.241	1	3.07	0.123
Within	27	27.7		23	29.84	

(c) Species group (phytoplankton, zooplankton, amphibians, birds, plants, ungulates and predators)

	Timing			Biomass		
	d.f.	Q	p	d.f.	Q	p
Between	6	10.5	0.144	4	12.4	0.053
Within	24	24.5		26	34.8	

(d) Extreme year (the year 1996 included: yes or no)

	Timing			Biomass		
	d.f.	Q	p	d.f.	Q	p
Between	1	0.69	0.444	1	1.55	0.271
Within	29	29.53		24	31.0	

(e) Latitude (46–65°N)

	Timing			Biomass		
	d.f.	Q	p	d.f.	Q	p
Between	1	8.25	0.004	1	0.22	0.642
Within	29	29.17		24	34.82	

(f) Longitude (9.5–25.8°W)

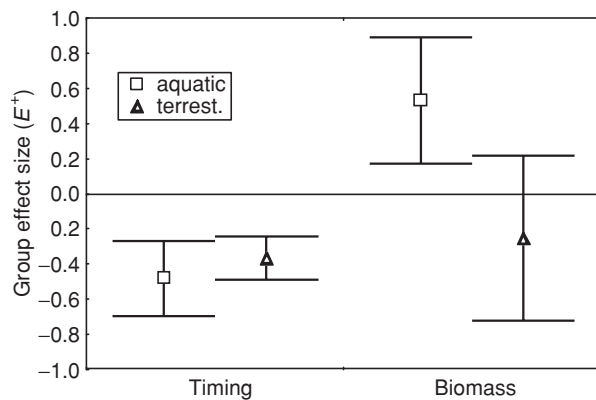|	Timing			Biomass		
	d.f.	Q	p	d.f.	Q	p
Between	1	0.25	0.616	1	4.86	0.027
Within	29	29.44		24	30.45	

Fig. 3 The E^+ and the CIs (95%) of the aquatic and terrestrial environment on the timing of life history events and biomass of the organisms.

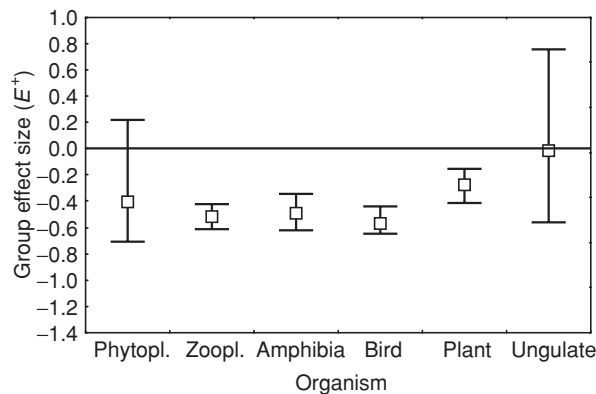**Fig. 5** The E^+ and the CIs (95%) for the effect on the trophic level of the aquatic environment including the physical (ice cover, water temperature), phytoplankton, and zooplankton level.

Fig. 4 The E^+ and the CIs (95%) on the timing of the life history events of all organisms under study, i.e. Phytoplankton (phytopl), Zooplankton (zoopl), amphibia, bird, plant, and ungulate.

groups, which is interesting with respect to the different environmental adaptations and the different body sizes of the organisms included.

Also, the proximate causes of timing differ among the organisms: Phytoplankton spring blooms are strongly dependent on solar radiation (Irigoien *et al*. 2000), which in Northern Europe is strongly mediated by the cover of ice (Weyhenmeyer *et al*. 1999; Gerten & Adrian 2000), while the timing of maximum zooplankton biomass is related to water temperature (George 2000; Straile & Adrian 2000; Straile 2000). Breeding phenology of birds and amphibians responded to growing season length as well as increased food availability (Forchhammer *et al*. 1998a). Flowering of plants was mainly dependent on the timing of snow melt (Post & Stenseth 1999 and literature therein). The timing of fecundity depends on two factors—directly on winter conditions and indirectly on plant phenology (Post & Stenseth 1999). The sum of this
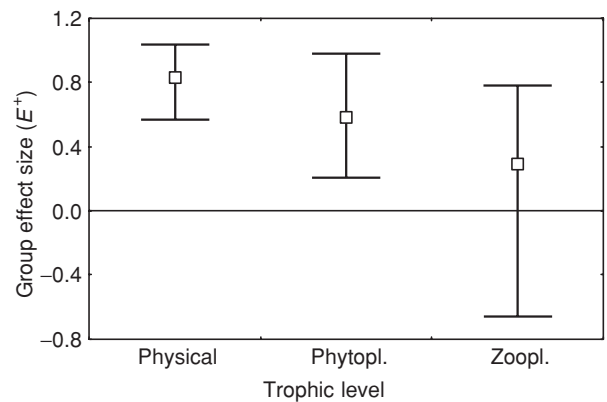
wide variation of proximate causes for the timing of life history events seems to be substantially influenced by the NAO. Our findings reinforce the assumption made by Iwasa & Levin (1995) that an evolutionary stable strategy in many species might be to reproduce as early as possible when environmental conditions are favourable. These environmental conditions concerned are all influenced by the NAO. However, detailed mechanisms are still unclear and need further investigations. Studying the effects of birds, it is documented that only for some species the increasing spring temperature results in an earlier egg laying, whereas some species did not show any response (Visser *et al*. 1998).

The overall pattern in aquatic systems derived from our meta-analysis (Fig. 3) showed a distinct negative relationship (negative effect size) to the NAO, i.e. a positive NAO year leads to an earlier timing of the response variables. However, the large CIs of phytoplankton and ungulates (Fig. 4) indicated that the effects of timing differ between studies. Irigoien *et al*. (2000) found no direct relationship for the timing of the maximum biomass of all phytoplankton species, but only with the maximum biomass of diatoms. With regard to ungulates, contrasting influences of the NAO were found. A primary study on the island Rum, Scotland, indicated that a positive NAO value was associated with typically mild and snow-free winters, and increased body mass of red deer, while the winter conditions in West-central Norway were snowy, associated with lower body mass of red deer (Post & Stenseth 1999). Given two opposing local weather situations, depending on the study area, either positive or negative responses of the fecundity of ungulates were documented.

The response of timing to NAO was in general dependent on latitude, i.e. a less pronounced response to the NAO at higher latitudes. Post & Stenseth (1999) found

no relationship to latitude, but they did distinguish a difference in the response of timing to the NAO for some plant species with a stronger correlation in Southern than in Northern Norway. Our study included different timing events on a broader geographical scale and revealed a significant impact of latitude on the timing response to the NAO. However, no effect of longitude was found. Furthermore, the fact whether the extreme negative NAO year 1996 was included or not, did not affect the magnitude of response. Therefore, the result of the analysis of long-term data generally was not influenced by the extreme year, whereas short-time series might be affected (Irigoien *et al*. 2000).

Biomass

Generally, biomass responded positively to the NAO, but significant differences appeared between the aquatic and terrestrial environment. In aquatic systems, the biomass of all organisms under study increased after warm winters. Straile (2000) and George (2000) established a strong dependence of the NAO via water temperature on the growth of zooplankton. In general, direct temperature effects on zooplankton have been found (Vijverberg 1980; Lampert & Muck 1985). Fromentin & Planque (1996) found contrasting responses of two zooplankton species to water temperature and NAO, indicating the complex interactions of physical factors with biological and physiological processes.

As discussed for timing, the results of the terrestrial studies were biased owing to different weather responses to the NAO of Scotland and Scandinavia, which also lead to different biomass responses. Additionally, the responses of the populations of ungulates and their calf masses differed extremely in the literature (Post *et al*. 1999b; Aanes *et al*. 2000; Ottersen *et al*. 2001) owing to linkage between the NAO and precipitation. For example, a positive correlation with snow and NAO was found above 400 m (Post *et al*. 1999a), whereas the same correlation was negative below 400 m (Mysterud *et al*. 2000) where the red deer stay over winter (Ottersen *et al*. 2001). This shows the complex responses of different variables as indicated by the large CI in our study.

We found a strong impact of longitude in the way that the magnitude of biomass response was less pronounced in Eastern Europe. A similar effect was discovered for lynx populations in Canada, where the response of the data-series along an east-west gradient to the NAO ranged from negative to positive and finally to a nondetectable effect owing to persistence of the atmospheric circulation over the North Atlantic (Stenseth *et al*. 1999). Overall, the biomass of organisms is affected by the NAO, but the direction and the magnitude of the response differs with habitat and longitude.

Trophic levels

The timing and biomass generally responded strongly to the NAO. However, some organisms showed contrasting results, implying the problem of analysing species responses to climate in an isolated context. Generally, organisms are affected by other trophic levels, which are also partly influenced by climate. As there are a limited number of studies considering the NAO influence on different trophic levels, we only tested the response from physical processes to two trophic levels in aquatic systems. The effect of the NAO response on the different levels was not significantly different. However, we found a tendency towards a decline in the response from physical to herbivore level (Fig. 5). The spring is mainly controlled by the physical processes in the aquatic system (Weyhenmeyer *et al*. 1999), indicated by the fact that the physical factors showed the highest magnitude of response. It is well documented that temperature can directly affect zooplankton growth (Vijverberg 1980; Lampert & Muck 1985). However, the declining tendency was very much influenced by the negative biomass response of the zooplankton in Lake Constance in July, which was a result of an earlier growth in spring and a suppression in summer (Straile 2000). This explains the lower magnitude of response of zooplankton than phytoplankton and demonstrates the difficulty when analysing climate effects on organisms, which follow natural successional changes. A contrasting response was shown in a study where the size of wolf packs depends on snow cover (and NAO), influencing the vulnerability of moose to predation and browsing on balsam fir (Post *et al*. 1999c). In this study, a climate signal was apparent on all trophic levels, but the effect altered at different trophic levels. Therefore, species interactions and density dependence (Post *et al*. 2001a,b) play major roles in determining the magnitude of climate-driven responses (Ives 1995), indicating that climate can affect the ecosystem function. Additionally, there might also be synergistic effects, where not only the meteorological parameters influence the organism but also other climate-affected variables, for example salinity or oceanic hydrodynamics (Kröncke *et al*. 1998).

Therefore, studies of climate effects on a single species or even trophic group might be compensated by other trophic levels, which might result in a minor climate effect on the ecosystem. The compensation of responses to environmental change has been documented for acidification of aquatic ecosystems (Frost *et al*. 1995). Species composition may change but not necessarily ecosystem processes such as production. Alternatively, there are time-lag responses of different organisms and ecosystems to the atmospheric forcing (Reid *et al*. 1998), which has been shown by Post & Stenseth (1998), and Post *et al*. (1999b).

Furthermore, biological responses in general might be nonlinear (May 1986), as recently shown for the response of wild and domestic herbivores to the NAO (Mysterud *et al.* 2001). Therefore, long-term studies on an ecosystem level, including physical, chemical variables as well as different trophic levels, might provide a more holistic view on climate-driven responses in ecosystems.

Publication bias and recommendations

The validity of meta-analysis results can be reduced by publication bias (Gurevitch & Hedges 1999). Especially for correlation studies, there might be an unproportional publication of significant correlations, whereas nonsignificant results are not published. From the 60 single studies in our database, 50 (83%) reported a significant relationship, which indicates a need for unbiased and careful examination of long-term data sets including the publication of nonsignificant results. However, we attempted to reduce this bias by (i) selecting studies by clear criteria, (ii) including nonsignificant results from the primary studies, when available, and (iii) testing our hypotheses based on a statistical, quantitative meta-analysis, which increases the objectivity of a review.

A combination of small-scale and large-scale studies will improve the statistical power to detect climate signature in ecology (Root & Schneider 1995). Large explanatory analyses always reveal many statistically significant relationships and it is therefore likely that a prominent fraction of suspicious ones will be detected (Ottersen *et al*. 2001). In our meta-analysis, the arguments are matched because the primary studies altogether are transformed into a large-scale study (the meta-analysis output) and therefore the result is more than the sum of the individual studies.

All in all, synthesizing many primary studies in a meta-analysis can lead to more overarching conclusions than individual studies do, in terms of spatial differences and the delay of the effect of the NAO. Therefore, we recommend an increase in the application of meta-analyses in the climate–ecology topic. Only by including nonsignificant results also can we enhance our understanding of climate-driven responses of ecosystems. With the NAO being a proxy for interannual climate variability, the response of climate impacts on ecosystems on annual or decadal variation can be analysed. The high sensitivity of the ecosystem processes to climate fluctuations contributes to our understanding of the impact of long-term warming trends on organisms and ecosystem function. This will allow us to provide decision-makers with an improved basis for discussions about implications of nature in a changing climate.

Conclusion

The meta-analysis of the relationships between different target variables and the NAO clearly demonstrated a NAO signature in freshwater, marine, and terrestrial ecosystems. The timing of life-history events was strongly and similarly influenced by the NAO in all environments, indicating an earlier timing owing to high NAO values (warm winters). Additionally, the response of the timing was less pronounced at higher latitudes. The biomass of organisms was also significantly related to the NAO, but the response differed in aquatic and terrestrial environments. Furthermore, the magnitude of biomass response to the NAO was more pronounced in Western than Eastern Europe. The trophic levels did not significantly differ in the response to the NAO, but a tendency towards a decline in the response from physical processes to the herbivore level was shown. This study clearly illustrates that aquatic and terrestrial ecosystems responded very sensitively to year-to-year climate variations. From these, we might improve our understanding of complex processes and interactions which are forced by a long-term climate trend and which might alter the ecosystem function persistently.

Finally, a meta-analysis appears to be a very suitable and objective tool to review climate-driven responses in ecosystems.

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