Zooplankton and the North Atlantic Oscillation: a basin-scale analysis

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This study examines multiple, long-term zooplankton time series across the Atlantic region and its inland seas. Across a broad range of geographic regions and ecological environments, the impact of the North Atlantic Oscillation (NAO) on interannual changes in the zooplankton populations was evident. Across the mid-Atlantic, a correlation between the NAO and zooplankton abundance was present and remained positive from the northwestern Atlantic through the enclosed seas of the far eastern Atlantic. Following high NAO years, these regions experienced higher total zooplankton abundance or biomass. Following low NAO years, this trend was reversed. A time lag in the zooplankton response to the NAO was also evident, influenced more by the scale of the water basin than by latitudinal or longitudinal location. For some regions, the correlation between zooplankton and the NAO was higher when the NAO was substituted with its sub-components: the Azores High (AH) and the Icelandic Low (IL) atmospheric pressure systems. This suggests that decomposition of the NAO into its components might enhance the sensitivity of the analysis of biological time series with regard to climate change.

INTRODUCTION

The North Atlantic Oscillation (NAO) is the dominant mode of atmospheric fluctuation over eastern North America, the northern Atlantic Ocean and Western Europe. Recent explorations of the impact of the NAO on interannual sea-level patterns in the Mediterranean, deep-ocean convection and dust transport across the subtropical Atlantic reflect the scale of this event (Moulin *et al.*, 1997; Arpe *et al.*, 2000; Ribera *et al.*, 2000; Tsimplis and Baker, 2000). In high NAO years, enhanced wind stress generates intensive mixing in the upper water column, whereas low NAO years provide favorable conditions for earlier temperature stratification of the water column and onset of the spring phytoplankton bloom (Dickson *et al.*, 1988; Fromentin and Planque, 1996).

Among biological parameters measured in marine ecosystems, zooplankton biomass and abundance can be sampled using relatively simple equipment and techniques. As a result, multiple long-duration zooplankton sampling sites exist over a broad range of geographical regions. These zooplankton time series are a valuable tool in the analysis of climate change issues. Studies in the Gulf of Maine (Conversi *et al.*, 2001; Greene and Pershing, 2001; Piontkovski and Hameed, 2002) and in the northeastern Atlantic (Fromentin and Planque, 1996; Reid *et al.*, 1998) have evaluated correlations in the abundance response of copepods to the NAO. This article investigates these linkages over a broad range of regions, spanning different ecological situations as well as over a range of NAO influence.

METHODS

For this study, a longitudinal array was drawn from the western side of the Atlantic basin (exemplified by the

Gulf of Maine) to its eastern side (the North Sea), the enclosed seas of the Mediterranean basin and the Aral Sea (Fig. 1, horizontal arrow). The latitudinal array was assumed to stretch from the upper-Atlantic region through the subtropical to the tropical regions (Fig. 1, vertical arrow). Using zooplankton biomass and abundance data for regions along the arrays of influence, we examined the 'geographical threshold' of the NAO impact on zooplankton.

The NAO index was defined as the difference in normalized sea-level pressure (SLP) anomaly averaged over the December–March months, between the Azores region (Lisbon, Portugal) and Stykkisholmur, Iceland (Hurrell, 1995). The index values are high corresponding with years of anomalously high pressure over the Azores and anomalously low pressure over Iceland. An updated NAO index time series was taken from the Centers of Action-Northern Hemisphere website http://atmos.msrc.sunysb.edu/coa/data.shtml.

For the analysis of the longitudinal array, regularly sampled zooplankton data (time series) were used from the following regions.

The Atlantic Ocean 'western array region' was represented by 40 years of sampling (from 1961 to 2001) by the US National Marine Fisheries Service (NMFS) in the Gulf of Maine using a Continuous Plankton Recorder (CPR) with a mesh of 270 μm. NMFS-CPR measurements have been made with monthly frequencies on a series of transects across the Northeast US Shelf and the Northeast

Atlantic for over five decades (Jossi and Goulet, 1993; Warner and Hays, 1994).

The Atlantic Ocean 'eastern array region' was represented by two sampling programs. First was 30 years of sampling (from 1974 to 2004) at Helgoland Roads (54°11′18″N 7°54′E), in which copepod abundance was sampled with a HYDROBIOS 0.17-m diameter net fitted with a 150 μm mesh (Greve et al., 2004). Second was 14 years of sampling (from 1988 to 2002) at the Plymouth L4 station (04°13′W, 50°15′N). Copepod abundance was vertically sampled from 50 m to the surface using a 200-μm WP2 net. These data were downloaded from the Plymouth L4 website at http://www.pml.ac.uk/L4.

The Adriatic Sea was represented by 29 years of sampling (from 1970 to 1999) in the Gulf of Trieste, northern Adriatic Sea (Cataletto et al., 1995; Fonda-Umani et al., 1996). Mesozooplankton were vertically sampled from the bottom (∼21 m) to the surface using a 200-μm WP2 net.

The Black Sea was represented by 29 years of sampling (from 1959 to 1988) in the offshore deep regions of the sea (Mashtakova, 1985; Kovalev et al., 1998) excluding its northwestern part. Samples were vertically sampled, from 100 m to the surface, using Juday nets with a mouth diameter 0.8 m and fitted with a 168-μm mesh. The time series was constructed from the biomass (mg m^{-3}, wet weight).

The Caspian Sea was represented by 41 years of sampling (from 1939 to 1980) in the northeastern part. Data sampled in the summer (June) of each year were retrieved from the archives of the Zoology Institute (Azerbaijan), as well as published articles (e.g. Kasymov and Rogers, 1996; Voropayev, 1997). Zooplankton samples were collected by Juday nets with a mouth diameter of 0.8 m and fitted with 168-μm mesh.

The Aral Sea was represented by 35 years of sampling (from 1969 to 2004) in the minor part of the Aral Sea ('Small Sea'). Data were vertically sampled from the bottom (∼18 m) to the surface using Juday nets fitted with 133-μm mesh. This time series was construction from archived materials and databases from the Institute of Zoology (Russia), Institute for Fishery and the Institute of Zoology (Kazakhstan).

For the analysis of the latitudinal array, zooplankton data nearest to the mid-Atlantic region and extending outward were used. These included the NMFS-CPR data (above) and the following additional data.

The Atlantic Ocean 'subtropical region' was represented by 5 years of sampling (from 1994 to 1998) at the Bermuda Atlantic Time-series Study site (BATS; 31°50′N, 64°10′W). Zooplankton biomass (wet mass) was vertically sampled from ∼200 m to the surface using a 1-m² rectangular net fitted with 202-μm mesh. For this study, we
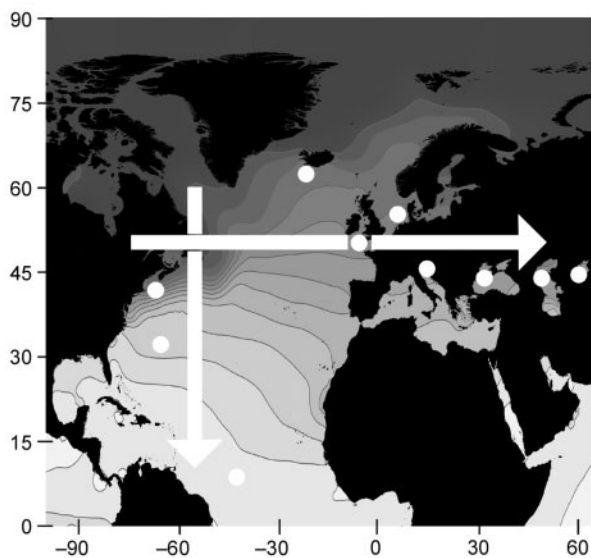

Fig. 1. Annual mean sea surface temperature (modified from Stephens et al., 2002). White arrows illustrate the latitudinal and longitudinal arrays analyzed in this article.

used the mean, daylight-sampled, zooplankton biomass values from Madin *et al.* (Madin *et al.*, 2001).

The Atlantic Ocean 'tropical and subtropical regions' were represented by data from the Pelagic Ecosystems of the Tropical Atlantic Ocean (PETAO) database (Greze, 1984; Piontkovski and Williams, 1995; Finenko *et al.*, 2003), which is comprised of the expeditions conducted by the former Soviet Union from 1950 to 1989. In this database, we restricted ourselves to samples collected in the tropical zone (from 23°N to 23°S) using Bogorov-Rass nets and the oceanic model of the Juday net (0.8 m mouth diameter) with mesh sizes from 112 to 200 μm. All tows were taken in a vertical or in an oblique manner in the upper 100 m.

To further supplement the geographic extent of both arrays, we added a sub-polar Atlantic data series off Iceland to the analysis. This region was represented by 41 years of sampling (from 1961 to 2002). Zooplankton biomass was sampled vertically from the bottom (∼50 m) to surface using a Hensen Net (1961–91) or WP-2 Net (1992–2002) fitted with 202-μm mesh. Annual mean dry weight values were used, as published in the Icelandic Marine Research Institute's Annual Status Report on Environmental conditions in Icelandic Waters (Anonymous, 2004).

For all of the regions above, the zooplankton time series were de-trended and used in a regression and cross-correlation (time lag) analyses. The trends were subtracted as follows: $x_2 = x_1 - (a + b * t)$, with coefficients a and b estimated from the data using the least squares method. The iterative regression (Piontkovski and Hameed, 2002) was used to fill in the missing values in the interannual time series for the Gulf of Maine. Our analysis was tailored to look for statistically significant linkages between NAO and zooplankton rather than the optimization of the regression curves fitting the correlation found. Zooplankton and NAO index data were annually averaged and used for the time series analysis. Before averaging, zooplankton time series were logarithmically transformed. The cross-correlation functions have been applied to estimate linkages between the plankton and NAO.

RESULTS

A summary of the parameters of each time series and correlation with the NAO index is provided in Table I. All correlations and slopes were significant at the 95% confidence level.

The longitudinal array

In the Gulf of Maine, western array region, three species of copepod—*Pseudocalanus sp.*, *Centropages typicus* and *Calanus finmarchicus*—contribute ∼75% of the total abundance in the Gulf of Maine (Sherman *et al.*, 1988). In this region, we found that total copepod abundance, lagged by 3 years, was positively correlated with the NAO index (Fig. 2). This supports previous NAO–zooplankton correlations found in this region (Conversi *et al.*, 2001; Piontkovski and Hameed, 2002).

In the eastern array region, the Plymouth L4 and Helgoland Roads time series each had a positive correlation between total copepod abundance and the NAO, with a 3-year to 4-year time lag.

In the Adriatic Sea, a few dominant species such as *Acartia clausi*, *Temora* and *Oithona* genera contribute most of the total copepod abundance. In this region, we found the same (positive) correlation between copepod abundance and the NAO, with a 0-year to 1-year time lag (Fig. 3).

In the Black Sea offshore regions, the most abundant taxa are copepod species (*Pseudocalanus elongatus*, *Paracalanus parvus*, *A. clausi* and *Calanus euxinus*), *Noctiluca scintillans* and some *Chaetognatha* species. The correlation between mesozooplankton biomass and the NAO was positive, with a time lag of 3 years.

In the eastern Caspian Sea, total copepod biomass was composed of four most abundant species: *Calanipeda aquae dulcis*, *Limnocalanus grimaldii*, *Eurytemora grimme* and *Halicyclops sarsi*. Here, total biomass was also positively correlated with the NAO, with a time lag of 3 years.

In the Aral Sea, the taxonomic composition of mesozooplankton was characterized by a few species, among which *C. aquae dulcis*, *Arctodiaptomus salinus*, *Mesocyclops leuckarti*, *Thermocyclops crassus*, *Halicyclops rotundipes aralensis*, *Ceriodaphnia reticulata*, *Moina mongolica*, *Podonevadne camptonyx*, *Evadne anonyx* and *Cercopagis pengoi* were the most abundant. Mesozooplankton biomass was positively correlated with the NAO, with a time lag of 2 years (Fig. 4).

The latitudinal array

As discussed above, the Gulf of Maine zooplankton were positively correlated with the NAO, with a time lag of 3 years. From the northern latitudes southward, to the subtropical zone, we analyzed the BATS zooplankton biomass data. Copepods contribute ∼70% of the total mesozooplankton abundance and ∼48% of mean displacement volume of samples. In these samples, the calanoid copepod genera (*Clausocalanus*, *Ctenocalanus*, *Paracalanus* and *Pleuromamma*) were among the most abundant (Deevey, 1971). We found the interannual variation of zooplankton daily mean biomass to be negatively correlated with the NAO index (Table I), with a time lag of 1 year. It should be noted, however, that the BATS zooplankton time series is still too short for the

Table I: Time lags and regression estimates for each zooplankton time series at $P_{0.05}$

Region and time series	'Plankton-NAO' time lag in years	r	Slope	Intercept	Years of sampling	Sampled parameter
North Atlantic (Iceland)	3–4	0.5	0.18	−0.20	1961–2002	Zooplankton Biomass
Western Atlantic (Gulf of Maine)	3	0.6	0.13	−0.02	1961–1991	Copepod Abundance
Eastern Atlantic (Helgoland Roads)	3–4	0.6	0.17	−0.13	1975–2003	Copepod Abundance
Eastern Atlantic (UK-L4)	3	0.4	0.05	−0.07	1988–2002	Copepod Abundance
Adriatic Sea	0–1	0.5	0.13	−0.10	1970–1999	Copepod Abundance
Black Sea (open regions)	3	0.5	0.12	0.05	1959–1988	Zooplankton Biomass
Caspian Sea	3	0.4	0.13	0.06	1939–1980	Copepod Biomass
Aral Sea	2	0.6	0.17	−0.06	1969–2004	Zooplankton Biomass
Subtropical Atlantic (BATS)	1 (lack of data)	−0.7	−0.06	0.03	1994–1998	Zooplankton Biomass
Tropical Atlantic (PETAO)	3	−0.4	−0.12	−0.04	1950–1989	Zooplankton Biomass

BATS, Bermuda Atlantic Time-series Study; PETAO, Pelagic Ecosystems of the Tropical Atlantic Ocean.
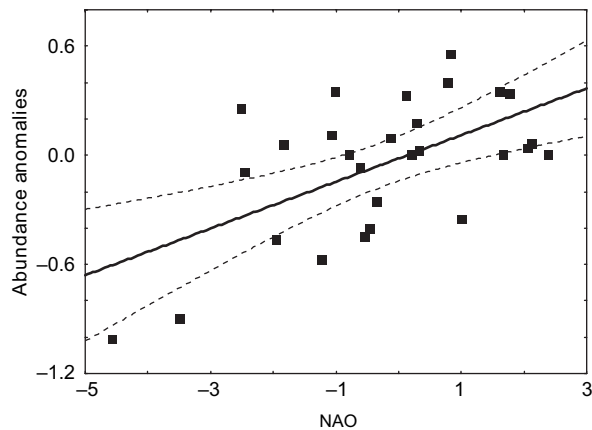

Fig. 2. Gulf of Maine, continuous plankton recorder data: the relationship between total copepod abundance (3 years lagged) and North Atlantic Oscillation index. Dashed lines indicate 95% confidence interval.
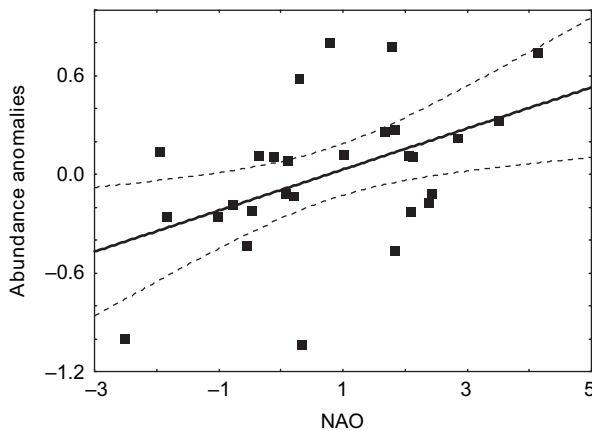

Fig. 4. Aral Sea: the relationship between the total zooplankton biomass (2 years lagged) and North Atlantic Oscillation index. Dashed lines indicate 95% confidence interval.

Fig. 3. Adriatic Sea: the relationship between total copepod abundance (1 year lagged) and North Atlantic Oscillation index. Dashed lines indicate 95% confidence interval.
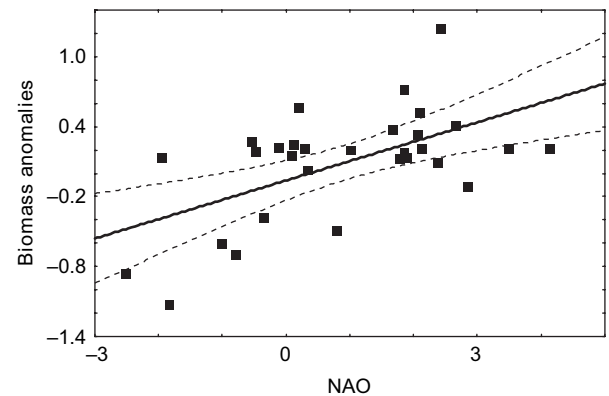
sustainable statistical estimates of interannual changes. So we consider the above results as preliminary, complementing the other time series and regions involved.

In the offshore waters of the tropical zone, copepod species comprised 70–90% of mesozooplankton abundance. In the eastern tropical part, for instance, copepods were the dominant mesozooplankton group accounting for 197 species, of which 23 species contributed to 75% of mesozooplankton abundance (Zuyev *et al.*, 1990). The list of abundant species included *Calanus minor, Undinula vulgaris, Rhincalanus nasutus, Calocalanus pavo, Calocalanus pavoninus, Delius nudus, Clausocalanus furcatus, A. clausi, Scolecithrix brady, Scolecithrix dana, Pleuromamma abdominalis, Pleuromamma gracilis, Lucicutia flavicornis, Heterorhabdus papilliger, Euchaeta marina, Oithona plumifera, Oncaea venusta, Oncaea mediterranea, Oncaea conifera, Oncaea media, Corycaeus speciosus, Microsetella rosea* and *Macrosetella gracilis*. These species were noted through all the eastern part in which copepods contributed ~53%

of the total mesozooplankton biomass versus ∼66% reported for the western tropical Atlantic (Greze, 1984). A negative correlation between zooplankton biomass and the NAO index with a lag of 3 years was calculated. Minimum values of the biomass were observed in the high NAO years.

In the opposite direction, far north of the array, the Icelandic time series was used to investigate interannual variation along the most northern extent of the NAO influence. In this region, zooplankton biomass and primary production are strongly influenced, often doubling, by the periodic inflow of warm Atlantic water (Astthorsson and Gislason, 1998; Astthorsson and Vilhjalmsson, 2002). We found a positive correlation between the NAO and zooplankton biomass, with a response time lag ranging from 3 to 4 years.

DISCUSSION

We analyzed zooplankton data over a broad range of geographical regions and ecological situations, from waters with oceanic salinity to the brackish waters of the biggest lakes represented by the Caspian and the Aral Seas. The impact of the NAO on interannual changes of zooplankton abundance or biomass was pronounced through all the studied regions, from the Gulf of Maine to the Aral Sea (along the longitudinal array) and from the northern-most to tropical latitudes in the Atlantic Ocean (along the latitudinal array). In all regions of the Atlantic Ocean basin and its enclosed seas which have been considered, zooplankton interannual changes were related to the impact of the NAO, regardless of distinct differences in taxonomic composition over regions.

Along the latitudinal array (north to south), the correlation between NAO and the total zooplankton changes its sign from positive [in the upper- and mid latitudes (Iceland, Gulf of Maine)] to negative (in the subtropical and tropical regions (BATS, PETAO). Following high NAO years, upper array regions will experience high zooplankton abundance or biomass, whereas lower array regions experience low zooplankton abundance or biomass. Following low NAO years, this trend would be reversed in all regions.

Along the longitudinal array (west to east), the correlation between NAO and total zooplankton remains positive from the northwestern Atlantic (Gulf of Maine) through the enclosed seas of the Atlantic Ocean (Adriatic, Black, Caspian and Aral Seas). Following high NAO years, all regions along the longitudinal array will experience higher total zooplankton abundance or biomass. Following low NAO years, this trend

would reverse consistently across the array. This consistent correlation is not seen at the individual species level. Conversi *et al.* (Conversi *et al.*, 2001) found a positive correlation between the NAO and *C. finmarchicus* in the Gulf of Maine, whereas Fromentin and Planque (Fromentin and Planque, 1996) found a negative correlation between *C. finmarchicus* and the NAO in the northeastern Atlantic.

The NAO has different effects on the two sides of the ocean basin: positive anomalies in the pressure difference between Iceland and Azores (high NAO index) are associated with warmer than normal winters in Western Europe and colder than normal temperature in eastern Canada (and vice versa when the NAO index is low). The NAO also affects the circulation of the western (Taylor and Stephens, 1998; Taylor *et al.*, 1998) and eastern Atlantic (Stephens *et al.*, 1998) in different ways. While an east–west response was not evident in total community biomass or abundance time series, responses at the species level may be fairly different. It is already known that *Calanus helgolandicus* and *C. finmarchicus* exhibit opposite behavior in relation to the NAO, due to different life cycles, thermal preferences and reactions to other environmental factors (Fromentin and Planque, 1996; Planque and Taylor, 1998).

An interesting feature found in most of the zooplankton–NAO correlations was a time lag between the NAO and zooplankton, which might span several years (Table I). Comparing the correlations, we found that the time lag depends more upon the scale of the basin than on the distance from the atmospheric pressure systems [e.g. Icelandic Low (IL) and Azores High (AH)] composing the NAO. A 3-year time lag was reported for Iceland, on the far outskirts of the pressure systems, as well as within 'the NAO central region' (northwestern Gulf of Maine, northeastern Atlantic Ocean) (Garrod and Colebrook, 1978; Reid *et al.*, 1998), eastern Atlantic (UK-L4, Helgoland Roads) and the tropical latitudes (PETAO). This is in contrast to the smaller basins, still influenced by the NAO (like the Aral Sea and Adriatic Sea), where little or no time lag was found. This implies that the scale of basins and their advective processes, as well as the inertial scale of these processes, play a significant role in their interannual dynamics and response to the NAO.

A number of key physical variables, with known inter-relationships within the plankton, exhibit well-pronounced linkages to the NAO. For instance, in the Gulf of Maine, the NAO index was positively correlated with the winter sea surface temperature, leading it by 2 years. Sea surface temperature (SST) on the other hand was positively correlated with *C. finmarchicus,* leading it by 2 years (Conversi *et al.*, 2001). In the Mediterranean Sea, a sea-level trend reflects the NAO trend between 1960s

and 1990s (Tsimplis and Baker, 2000). Correlations between NAO and sea level, as well as NAO and sea surface temperature changes, were reported for the Black Sea (Stanev and Peneva, 2002; Ginzburg *et al.*, 2004). For the Caspian Sea, an upper level atmospheric tele-connection between grid points in the North Sea and northern Caspian was identified. This teleconnection referred as the North Sea–Caspian Pattern was evident at the 500-hPa level (Kutiel and Benaroch, 2002). In the Aral Sea region, changes in aridity were reported to be linked to fluctuations in the NAO index (Small *et al.*, 1999).

To explain the mechanisms and factors underlying the correlation between zooplankton and NAO, researchers assume a number of basic hypotheses. For instance, Fromentin and Planque (Fromentin and Planque, 1996) hypothesized that in the northeast Atlantic a high NAO reinforces the west wind stress, which generates strong mixing of the surface layer. This delays the phytoplankton bloom and reduces primary production, which might be one of the causes of the diminished abundance of *C. finmarchicus*. They also suggested a direct, negative effect of increasing sea surface temperature on this cold-water species.

Direct temperature effects mediated by NAO through interannual fluctuations are known for the zooplankton communities of European lakes. The most important factor affecting the over-wintering zooplankton populations was water temperature, influenced by the NAO. A significant positive correlation was found between the NAO index and the number of over-wintering *Eudiaptomus* (George and Hewitt, 1999). In Esthwaite Water in Cumbria, UK, high abundances of the genus *Daphnia* were found in cold, calm winters when small flagellates were also abundant. In contrast, the highest numbers of *Eudiaptomus* were in mild, windy winters when phytoplankton was dominated by colonial diatoms. Interannual changes in the winter abundance of *Eudiaptomus* had no effect on their subsequent development, but the abundance of the overwintering *Daphnia* population had a significant effect on the size of the spring 'cohort'.

Another hypothesis deals with the mechanisms of advection, driven by the wind stress and the NAO, which drives the large-scale spatial displacement of the water masses. For instance, in the Gulf of Maine, which is considerably influenced by Scotian Shelf currents, copepod populations are subjected to advective transport over the seasonal cycle (Miller *et al.*, 1998; MERCINA, 2001, 2003). The scale of this transport is poorly known, but some estimates have been made for the eastern side of the ocean. Bryant *et al.* (Bryant *et al.*, 1998) incorporated *C. finmarchicus* into particle-tracking circulation models in the northeastern Atlantic and found that even over an annual cycle the distance between beginning-of-year and end-of-year positions of organisms can be thousands of kilometers apart.

In the tropical Atlantic, the AH (the atmospheric pressure system impacting the tropical zone from the north, a component of the NAO) affects interannual changes in copepod species diversity. Fluctuations in annual mean pressure as well as the longitudes of the AH and South Atlantic High explain 74% of total inter-annual variability of the copepod species diversity index at the scale of the tropical zone, in which low-frequency latitudinal displacements of the current system could result in interannual variations of species diversity across the region (Piontkovski and Landry, 2003). Reports on dominant advective effects from the other regions are the CALCOFI time series, where interannual fluctuations of zooplankton biomass in the California Current mirror advective mass transport of water from the north (Chelton *et al.*, 1982).

For some regions, we noticed that the correlation between zooplankton and the NAO might be higher when the NAO is substituted by its components: the AH and the IL atmospheric pressure systems. For instance, in the northern latitudes (e.g. the Icelandic time series), substituting the NAO index with the IL pressure index gives a higher correlation level: $r = 0.53$ at $P_{0.05}$ (zooplankton-IL) versus $r = 0.49$ at $P_{0.05}$ (zooplankton-NAO). The same was noticed for the Gulf of Maine zooplankton time series (Piontkovski and Hameed, 2002). In this case, we found the correlation $r = 0.7$ ($P < 0.002$) for interannual changes in observed versus predicted copepod abundance, when the total copepod abundance (N) is represented as the function of just two independent variables.

$\text{Ln}\,N = 152.4 - 0.51(\text{IL with a lag of 3 years}) + 0.33$ (sea surface temperature with the lag of 2 years). This suggests that in some cases, the decomposition of the NAO into its major components (AH and IL) might enhance the sensitivity of the analysis of biological time series with regard to climate change.

ACKNOWLEDGEMENTS

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