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ZOOPLANKTON-CLIMATE LINKAGES IN DIFFERENT GEOGRAPHICAL REGIONS

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The inter-annual variations of total zooplankton abundance in the Gulf of Maine (1961 - 1991), the North-East Atlantic (1961 - 1994) and the North Sea (1961 - 1994) were analyzed and related to the Icelandic Low and the Azores High atmospheric pressure systems. In a similar way the variations of zooplankton biomass in the Gulf of Alaska (1956 - 1980) were related to the Aleutian Low pressure system. Cross-correlation and spectral density functions were calculated for the zooplankton and the pressure indices. Regional and global aspects of the relationship between the intensity of the zooplankton fluctuations and the atmospheric centers of action were analyzed. A discussion on possible mechanisms that may contribute to the dynamic links transferring atmospheric variation into observed changes in zooplankton abundance and biomass is included.

Key words: zooplankton, climate change, inter-annual variability, sea level pressure

The long-term (inter-annual and inter-decadal) changes in zooplankton abundance and biomass are proposed to be related to atmospheric variables and, hence, can act as the biological indicators of climate change. For example, a decline of zooplankton biomass in the California Current ecosystem in the 1950s through 1990s seem to be a response to a basin-wide warming in the north Pacific [19]. A relationship between the basin temperature and plankton inter-annual variability is evident also in the North Atlantic, where the mean temperature shows parallel trends to these of phyto- and zooplankton abundance [13].

The long-term studies of zooplankton, hydrographic and atmospheric variables have been undertaken in different geographical regions, including both sides of North America, the British Isles and the North Sea. Publications based on these data have partly provided insights into the plankton-climate relationships [1, 4, 5, 8, 17, 18, etc.].

Our aim was to compare patterns of zooplankton and climate characteristics for the Gulf of Alaska, the Gulf of Maine, the Northeastern Atlantic and the North Sea. Using a system of atmospheric indices we have attempted to provide insights into dynamic forces transferring atmospheric variations into interannual changes of the zooplankton.

Data and methods. *1. Zooplankton time series.* We will use the term zooplankton to describe changes in the total abundance of copepods, with the exception of the Gulf of Alaska where total zooplankton biomass is available.

The Gulf of Alaska data include surface temperature, salinity, and sampling of zooplankton wet-weight biomass measured at Station "P" (50°N, 145°W), from 1956 to 1980.

The Gulf of Maine plankton data were obtained with the Continuous Plankton Recorder (CPR) samplers, by the US CPR program (Northeast Fisheries Science Center, NOAA, Narragansett, RI). The CPR measurements have been made with monthly frequency on a series of transects across the Northeast U.S. Shelf since 1961. The analysis of data from the central part of the Gulf, covering the period from 1961 to 1991, is presented here.

The North-Eastern Atlantic and the North Sea plankton data were obtained with the Continuous Plankton Recorder (CPR) samplers, by the UK CPR program (SAHFOS, Plymouth, UK). The data have been collected monthly since 1948. Three subareas in the North-Eastern Atlantic and two subareas in the North Sea, for the period 1961 - 1991 were used in this work (Fig. 1).

2. Zooplankton sampling. At station “P” zooplankton sampling frequency ranged from 1 to 29 samples per month and from 8 to 12 months per year [11,12]. Daytime vertical hauls of zooplankton, 150 m to the surface, were taken by planktonic nets with 0.42 m diameter and 0.351 mm mesh size.

The CPR sampling consists of continuous (night and day) horizontal tows at 10 m depth by merchant and ocean weather ships along regular routes. Towing speeds have varied between 9 and 15 knots. Plankton enters the CPR through a 1.25 inch square opening (10 cm^2) and gets into a slowly moving graduated silk gauze of about 0.285 by 0.310 mm. Each 450 nautical miles (or less, if the route is shorter), the internal spool of the recorder is replaced by a new one. Upon data collection, the gauze is cut in segments (which constitute the samples) corresponding to 10 nautical miles (18.52 km) of towing. The volume of water filtered in 10 n-mi is approximately 3 m^3 [3].

3. Climate characteristics. The North Atlantic Oscillation (NAO) has been shown to be related to zooplankton biomass in the North East Atlantic [10]. The NAO is the see saw of atmospheric mass between two semi-permanent atmospheric pressure systems, the Azores High (AH) in the subtropical Atlantic and the Icelandic Low (IL) in the subpolar Atlantic region. AH and IL are among the large-scale pressure systems that dominate atmospheric and oceanic circulation and known as the "Centers of Action" (COAs) in meteorology.

Analogous to these centers in the northern Atlantic, are the Hawaiian High and the Aleutian Low (AL) in the northern Pacific. The see saw of atmospheric mass between these two centers of action is called the North Pacific Oscillation (NPO). Each COA influences atmospheric and oceanic currents in its own sphere of influence. In the following we will relate zooplankton fluctuations in the North Pacific to the Aleutian Low, which dominates the Subarctic Gyre. In the North Atlantic we will relate zooplankton variations to the NAO, but basically to the fluctuations of its component centers of action, the Azores High and the Icelandic Low. A relationship between zooplankton and the individual COA is more likely to be useful because it localizes the region of climatic influence on the ecosystem.

In order to make quantitative comparisons between the COAs and plankton fields, it is useful to define objective indices for the intensity, latitude and longitude of a COA at a given time. All indices are area-weighted averages. Following [14], define the intensity index I_p of sea level pressure was determined as follows:

$$I_p = \frac{\sum_{ij=1}^{IJ} (P_{ij} - P_t)\cos\phi_{ij}(-1)^M \delta_{ij}}{\sum_{ij=1}^{IJ} \cos\phi_{ij}\delta_{ij}},$$

where P_{ij} is the SLP value at grid point (i,j), P_t is a threshold SLP value for reference pressure surface (P_t = 1014 mb for AH and IL, and 1013 mb for AL). ϕ_{ij} is the latitude of grid point (i,j). M=0 for the Azores High and 1 for the Icelandic Low and Aleutian Low. δ=1 if $(-1)^M(P_{ij}-P_t)>0$ and δ=0 if $(-1)^M(P_{ij}-P_t)<0$. The intensity index is considered a measure of atmospheric mass anomaly in the studied sector (I, J).

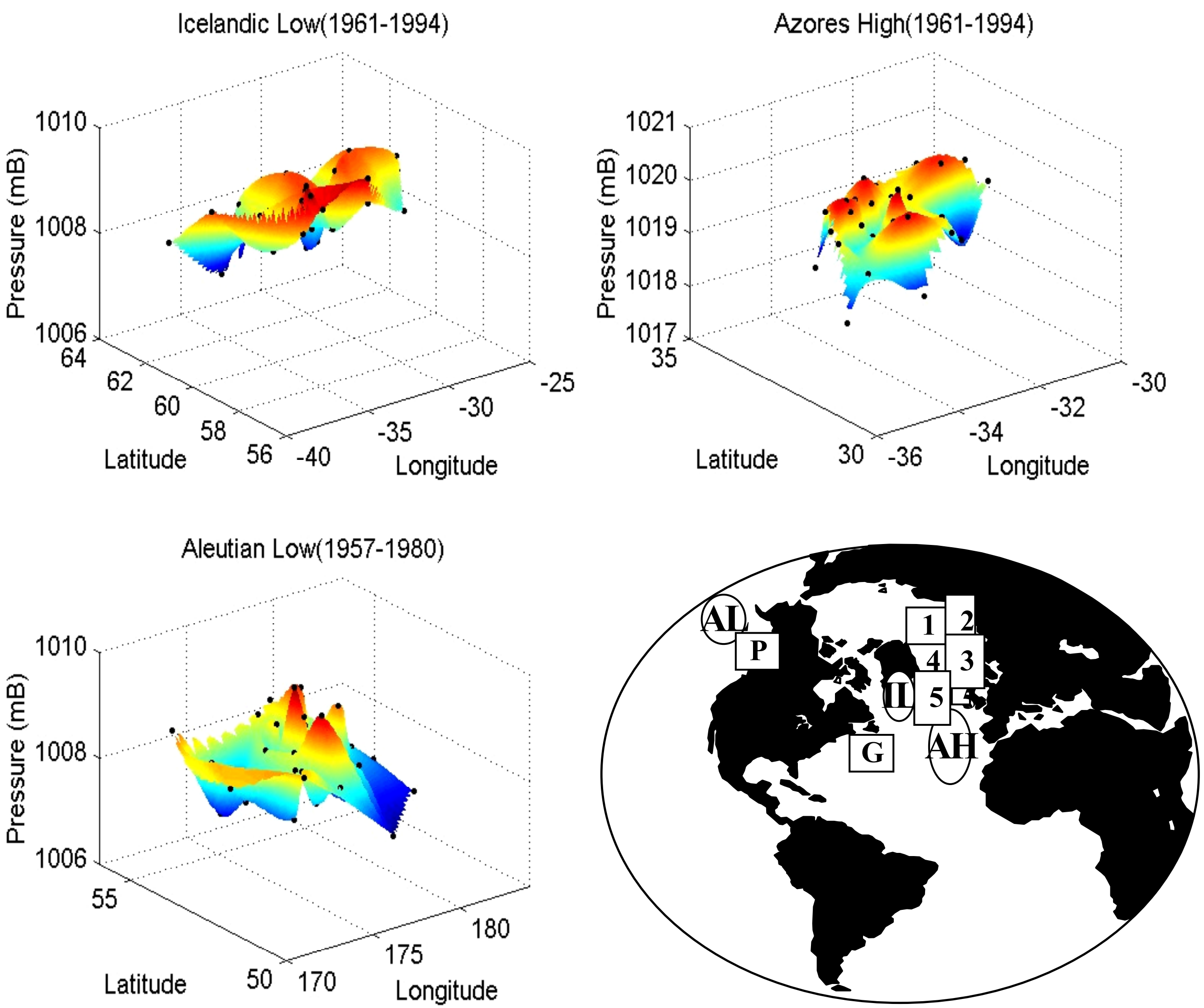

Fig. 1. Averaged spatial structures of COAs in northern hemisphere and zooplankton sampling sites. Abbreviations for the regions and COAs are the following: P, station-P; G, the Gulf of Maine, Areas 1, 4, and 5: North-Eastern Atlantic. Areas 2 and 3: North Sea. Positions of regions and COAs are given schematically

Рис. 1. Осредненные пространственные структуры центров Атмосферной активности (COAs) северного полушария и размещение зоопланктонных станций. Сокращения: P - станция «P»; G - залив Мэн, районы 1, 4. Северо-восточная Атлантика: район 5. Северное море: районы 2 и 3. Положение центров Атмосферной активности дано схематично.

The latitudinal index is determined as: $I_\phi = \dfrac{\sum_{ij=1}^{IJ}(P_{ij}-P_t)\phi_{ij}\cos\phi_{ij}(-1)^M\delta_{ij}}{\sum_{ij=1}^{IJ}(P_{ij}-P_t)\cos\phi_{ij}(-1)^M\delta_{ij}}$, and the longitudinal index I_λ is defined in an analogous manner. The location indices thus give pressure-weighted mean latitudinal and longitudinal positions of the COAs.

The areas covered by the indices are: the Aleutian Low (35°N - 70°N, 120°W - 130°E), the Icelandic Low (40°N - 75°N, 90°W - 20°E) and the Azores High (20°N - 50°N, 70°W - 10°E). Monthly sea level pressure data from NCAR were used while calculating the COA indices. The sea surface temperature data we used are from the Comprehensive Ocean-Atmosphere Data Set (2° latitude by 2° longitude).

4. Statistical analysis. Monthly time series of zooplankton, and parameters of the COAs (i.e. pressure, latitude and longitude) were annually averaged and used for the cross correlation and spectral analysis. Before averaging zooplankton time series were logarithmically transformed. The four missing years over the 30-year series for the Gulf of Maine zooplankton were estimated from the general linear trend.

The cross correlation functions and the spectral density functions (power spectra) have been applied to estimate periods and time lags in plankton and atmospheric variables. The means were subtracted and the series were detrended before calculating the power spectra, coherence, and cross-correlation functions. The squared coherence spectra were calculated to estimate the degree of concordance (correlation) in zooplankton versus atmospheric fluctuations, and phase spectra were used to estimate the phase of coherent fluctuations. A three point spectral window 0.25 - 0.5 - 0.25 was used in smoothing the spectra. Preliminary tests indicated that the coherency spectra results changed very little when changing the window, and thus that the choice of the window did not bias the results.

Results. The average annual variation of the Aleutian Low, the Icelandic Low and the Azores High pressure, latitude and longitude for the 1961 - 1994 period is shown in Figure 1. It can be observed that each COA has a distinct spatial variation during the 35-year period. Coefficients of pressure variation (cv) for each of COAs have been calculated. These are: Icelandic Low (cv=0.07), Aleutian Low (0.06), Azores High (0.04) indicating greater variability of the low pressure systems.

1. Gulf of Alaska. The dynamics of atmospheric processes in this region might be characterized by the Aleutian Low (AL). In order to verify whether cycles in the zooplankton biomass and in the Aleutian Low Indices were associated (coherent), and to understand their phase relationship, cross-spectral analysis was performed. The coherency spectra are shown in Fig. 2. Zooplankton and AL pressure are mainly related to the period of 6 years, where the coherence is 0.65 (Fig. 2a) with a lag of about 1 year (zooplankton lagging).

The latitudinal and longitudinal displacements of the Aleutian Low affect currents in the North Pacific, which in turn may affect zooplankton abundance. The cross coherency spectrum between AL longitude and zooplankton biomass shows that cycles appear to be related at 12, 6 and 4 year periods, with squared coherence r^2= 0.6, 0.8, and 0.65 respectively (Fig. 2b). No significant coherence was found between latitude of AL and zooplankton.

2. Gulf of Maine. This region is in the domain of the North Atlantic Oscillation. As mentioned above, the NAO represents a see saw effect of atmospheric pressure between two COAs, the Azores High (AH) and the Icelandic Low (IL). Both of the COAs have distinct inter-annual variations of pressure, latitude and longitude. The winter AH pressure index exhibits an upward trend over the past three decades. An upward trend is also found in *Calanus finmarchi-*

cus [7] and, although less developed (with a larger variance), in total copepod abundance.

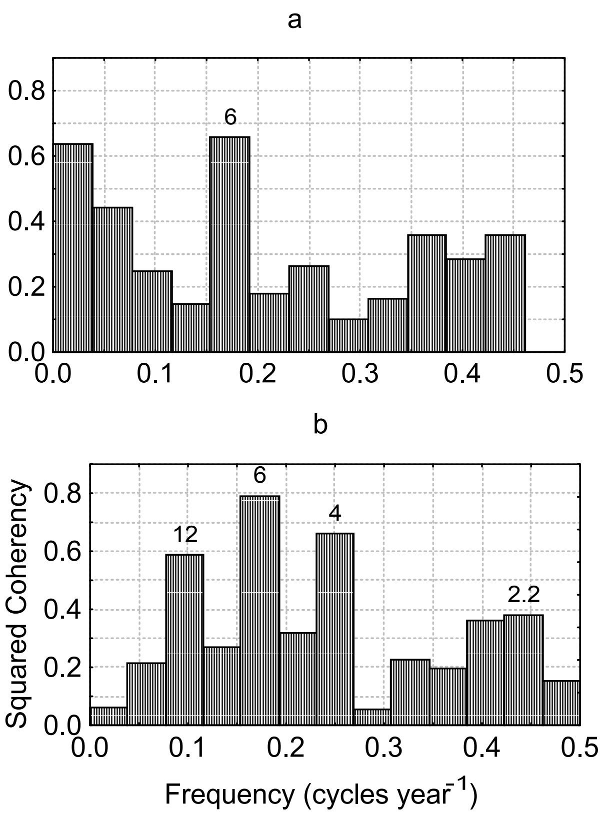

Fig. 2. Spectra of Station "P": squared coherency between AL and zooplankton (a) and coherency between AL longitudinal displacements and zooplankton (b). Numbers above bars indicate the periods (in years).

Рис. 2. Спектры для станции «Р»: спектры квадрата когерентности между Алеутским минимумом и зоопланктоном (а) и квадрата когерентности между долготными смещениями Алеутского минимума и зоопланктоном (b). Цифры над диаграммами указывают период (в годах).

With regard to zooplankton, three species - *Pseudocalanus* sp., *Centropages typicus,* and *Calanus finmarchicus,* contribute about 75 % of the total abundance in the Gulf of Maine [20]. Previous studies utilizing a time series in the central part of the Gulf of Maine show that changes of the total abundance of copepods are mostly related to fluctuations of *Pseudocalanus* sp., the most abundant species in a time series obtained for the central part of the Gulf of Maine. Fluctuations of the AH pressure and zooplankton are highly coherent at a period of 6 years (r^2=0.96).

Examination of atmospheric and zooplankton time series indicates that the series are shifted in time (Fig. 3). For instance, cross-correlation function between the yearly averaged NAO index and zooplankton points out to a three-year lag (Fig. 3b). This means that usually, zooplankton peaks occur three years after NAO extrema. The same three-year lag was found for the zooplankton and AH pressure in winter. The cross-spectral analysis confirms this lag and indicates that most likely it is dominated by the periodicity at 6 years.

3. North-East Atlantic (areas 1,4,5). Atmospheric and oceanic circulations here are again modulated by the meridional sea-level pressure gradient between Azores High and Icelandic Low. Inter-decadal decreasing trends of total copepod abundance are well known for the UK CPR and have been usually presented using the first principal component [3]. Species contribute differently to the copepod total changes in abundance in the above 3 areas. We noted for instance, that in the most northern area (1), fluctuations of the total copepod abundance are determined mostly by *Acartia clausi* followed by *Temora longicornis,* and the *Paracalanus* + *Pseudocalanus* group. In areas 4 and 5 inter-annual fluctuations of zooplankton are related mostly to the abundance of the *Paracalanus* + *Pseudocalanus* group. *Acartia, Temora, Centropages, Oithona* and *Calanus* make secondary contributions.

In area 4 zooplankton and AH fluctuations are highly correlated at periods of 11.3 (r^2=0.95) and 2.6 years (r^2=0.70) (Fig. 4a). In area 5 coherence was observed at 17, 5.7, 4.9, 3, and 2.8 year periods (Fig. 4b). Further to the North (area 1), the cross-spectral analysis of IL pressure and zooplankton shows high coherence at 2.3 years (r^2=0.9). At this period zooplankton fluctuations are also highly coherent with the longitudinal position of IL (r^2=0.75).

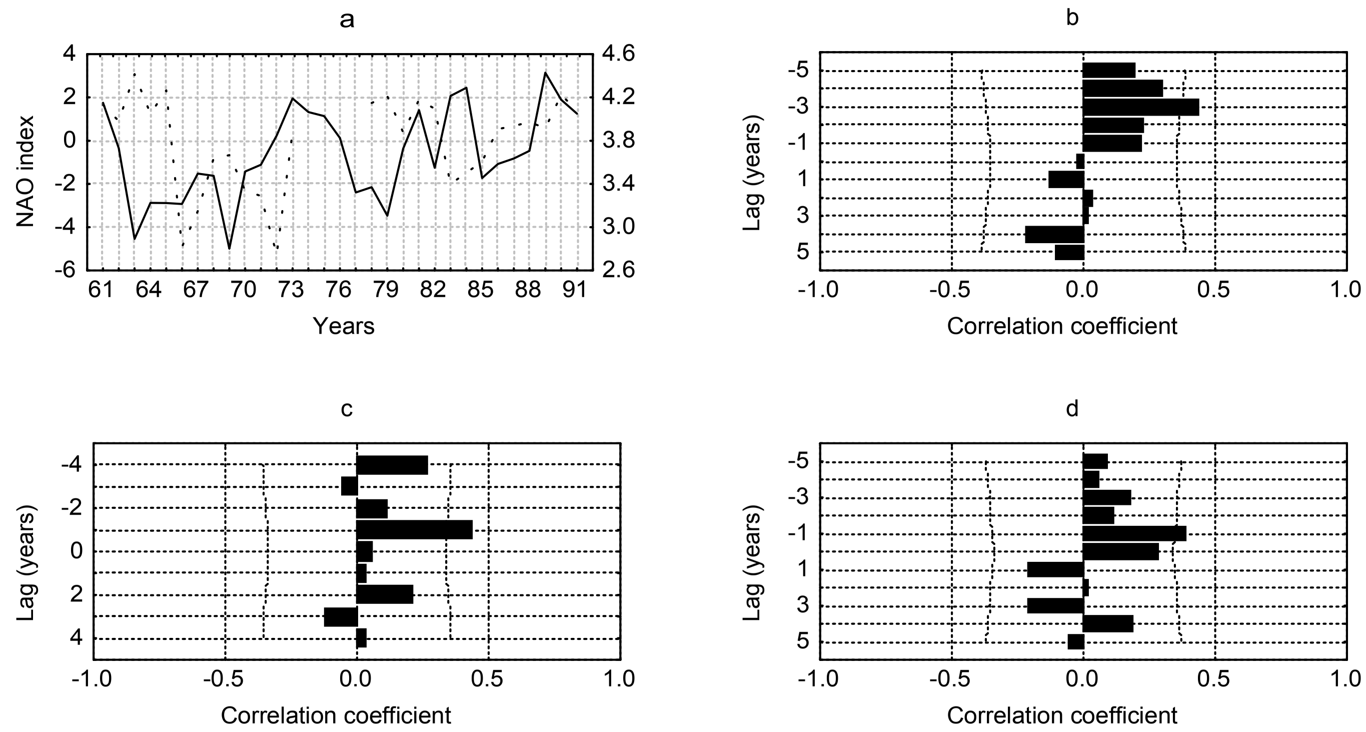

Fig. 3. Time series (a) and cross-correlation functions between zooplankton and atmospheric parameters (b - d). Dashed lines in the cross-correlation functions indicate 95% confidence interval. Negative lags indicate that zooplankton is lagged. Dashed line in figure (a) is copepod abundance in the Gulf of Maine and solid line is NAO index. Cross-correlation functions between zooplankton in the Gulf of Maine and NAO (b), zooplankton and the IL longitude (d) and latitude (c). First: IL; lagged: zooplankton; (d): area 1; (c): area 2 (see Fig. 1).

Рис. 3. Временные серии (a) и кросс-корреляционные функции между зоопланктоном и атмосферными параметрами (b - d). Пунктирные линии на кросс-корреляционных функциях указывают 95% доверительные интервалы. Отрицательные значения смещений означают, что зоопланктон «запаздывает». Рис. (a): прерывистая кривая - численность зоопланктона в зал. Мэн; сплошная кривая - индекс Североатлантического колебания (NAO). Рис. (b): кросс-корреляционные функции между зоопланктоном зал. Мэн и Североатлантическим колебанием. Рис. (c): зоопланктон и широта Исландского минимума. Рис. (d): зоопланктон и долгота Исландского минимума. На всех рисунках «запаздывает» зоопланктон. Рисунок (d): район 1, (c): район 2 (см. рис. 1).

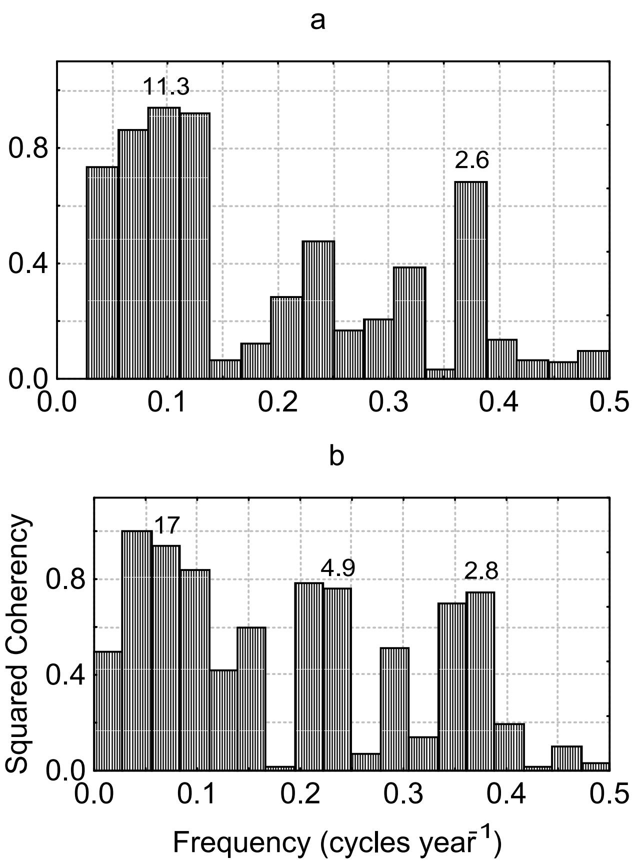

Fig. 4. Spectra of squared coherency between zooplankton and the Azores High pressure in the North-Eastern Atlantic. Numbers above bars indicate the periods (in years); (a): area 4; (b): area 5 (see Fig. 1).

Рис. 4. Спектры квадрата когерентности между зоопланктоном и давлением в Азорском минимуме в Северо-восточной Атлантике. Цифры над диаграммами указывают период (в годах). Рис. (a): район 4, (b): район 5 (см. Рис. 1).

In terms of cross correlations of annually averaged data, one year time lag between IL longitude and zooplankton (lagged) was found for area 1 (Fig. 3d). There were no statistically significant lags for areas 4 and 5.

4. North Sea (areas 2 and 3). The Azores High and Icelandic Low are the dominant COAs altering the atmospheric circulation in this region. *C. finmarchicus*, together with the *Paracalanus* + *Pseudocalanus* group contribute mostly to the total copepod abundance in area 2. In area 3 the average contributions to abundance were, in decreasing order, *Paracalanus* + *Pseudocalanus, Acartia, Temora, Oithona, Centropages* and *C. finmarchicus.*

In area 2 (which is the northern part of the sea), the squared coherence spectrum of zooplankton and AH pressure has peaks at 5.7, 4.9 and 3.8 years (Fig. 5a).

In area 3, the domain where zooplankton and AH pressure fluctuations were highly coherent (r^2= 0.7-0.85) was observed the high frequency range (i.e. periods from 2.6 to 2.1 years, see Fig. 5b).

The one year lag was also noted in the cross correlation of zooplankton and the latitudinal displacements of the Icelandic Low in area 2 (Fig. 3c). The same type of link was evaluated between zooplankton and the NAO index.

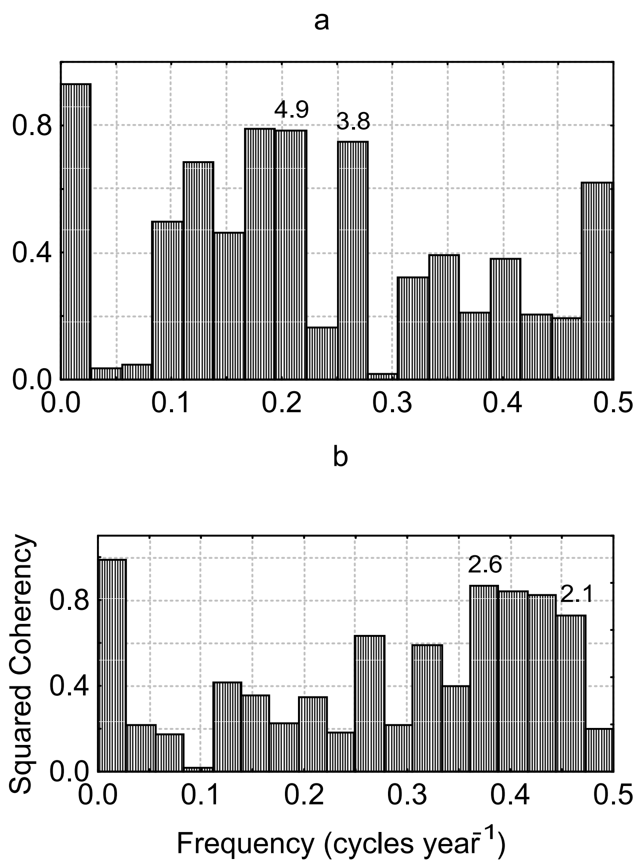

Fig. 5. Spectra of squared coherency between zooplankton and the Azores High pressure in the North Sea; (a): area 2, (b): area 3.

Рис. 5. Спектры квадрата когерентности между зоопланктоном и давлением в Азорском максимуме для Северного моря. Рисунок (a): район 2, (b): район 3.

Discussion. Analyzing long-term changes of zooplankton and climate from the viewpoint of geographical comparisons we attempted to differentiate the trends and periodicities. Our linear trends analysis for the zooplankton in the Gulf of Maine and the North-Eastern Atlantic, areas 4 and 1 confirms previous results [3,17,20], showing a tendency of the zooplankton to decline in the North-Eastern Atlantic, and to increase in the Gulf of Maine. On the background of these trends, a period of 5 to 6 year is found in the zooplankton spectra at a number of regions (the Gulf of Alaska, the Gulf of Maine, and the North-East Atlantic). This periodicity contributes from 7 to 16 % of the total variance of zooplankton. An oscillation of nearly 6 years is also noticed for the Southern Oscillation Index and NAO index [16] and a 5-7 year period is also found in movements of anomausly warm or cold surface water in the North pacific gyre [9]. Conversi and Hameed [6] reviewed several oceanic, atmospheric and environmental variables showing this periodicity. Here we find high coherence of this periodicity between atmospheric parameters and zooplankton at all three areas studied, in every case with zooplankton lagging (but with different lags in different areas).

Fromentin and Planque [10] reported the correlation between *Calanus* species and the NAO for the northeastern Atlantic. Describing possible mechanism of linkage they hypothesized that a high NAO reinforces the wind stress, which generates strong mixing of the surface layer. This delays the phytoplankton bloom and reduces primary production, which leads to the diminished abundance of the *C.finmarchicus*. One the other hand, the enhanced (at high NAO) sea surface temperature also impact negatively on the *Calanus* abundance known to be a cold-temperature water species.

The above two circumstances are likely to be responsible for about 44% of abundance variation (from low to high NAO years). We have taken the NAO index and related it to zooplankton fluctuations in the north Atlantic (Fig. 3b). The cross-correlation function shows that NAO is related with zooplankton of both sides of the Atlantic, but with different lag, preceeding zooplankton by one year in the North Sea and three years in the Gulf of Maine. Time lags in zooplankton-climate relationships have been reported earlier by Garrod and Colebrook [13] who compared a time series of the first principal component of 18 zooplankton taxa and index of atmospheric pressure (i.e. the number of days of westerly weather over the British Isles per year). They suggested positively correlated trends between westerly weather and zooplankton and negatively correlated quasi-cyclical fluctuations with a period of about 3 years. The correlations between the 3-year cycles were the highest when zooplankton was two years lagged behind the weather index.

It would be difficult to explain the 1-to-3 year lagged response of zooplankton abundance to atmospheric processes in the framework of the Fromentin-Planque's hypothesis exclusively. Perhaps the mechanisms linking atmospheric processes and zooplankton fluctuations are more complicated, and may involve macroscale horizontal shift of the water masses. This shift could be related to the temporal fluctuations of the atmospheric centers of action, the Icelandic Low and Azores High, which dominate the atmospheric and oceanic circulation in the North Atlantic. Using the same CPR data we treat the above correlation between zooplankton abundance and NAO as part of a mechanism of large-scale water mass spatial displacements caused by variations in COAs. Naturally, the planktonic field has a certain degree of macroscale spatial heterogeneity. This heterogeneity differs over the geographical regions above. Probably, this is why one and the same COA (say, AH) has different coherence spectra with zooplankton even in relatively neighboring regions, such as area 2 and 3 (see Fig. 5).

Good examples of dominant advective effects are the CALCOFI time series, where inter-annual fluctuations of zooplankton biomass in the California Current mirror advective mass transport of water from the North [1].

Hays et al [15] have also emphasized that spatial heterogeneity introduces considerable noise into the inter-annual fluctuations of copepod abundance in the UK CPR time series in the North-East Atlantic.

Other indications of impact of the horizontal spatial heterogeneity on zooplankton temporal cycles in the regions are the variations of the seasonal cycles. For instance, in the Gulf of Maine, these are different for *Calanus finmarchicus* and *Pseudocalanus* sp. abundance, in connection to low and high NAO years [7]. One of the reasons is that the intensity, directions and patterns of macroscale water mass transport through the Gulf of Maine vary considerably with the state of the NAO, which affects the characteristics of zooplankton seasonal cycles.

The IL and AH indices act as indicators of atmospheric forces driving the large-scale spatial displacement of the northern Atlantic water masses. An example of linkages between zooplankton and AH pressure index was given for the North-East Atlantic.

The same zooplankton fluctuations are also related with the latitude of the AH position in winter. The latitudinal and longitudinal position of the IL should also alter zooplankton fluctuations in the North-East Atlantic, which is reflected by their cross-correlation functions (see Fig. 3). This is a new interesting fact that zooplankton fluctuations seem to be sensitive to the macroscale longitudinal and latitudinal displacements of COAs. This means that in fact three major characteristics of COAs, the pressure gradient, the latitude and longitude could be ecologically meaningful factors affecting indirectly inter-annual fluctuations of zooplankton.

Summary. 1. Changes of climate lead to changes in the plankton population dynamic rates, through the direct impact of temperature on stratification and mixing of the upper layer that affects nutrient supply and the stress of predators. **2.** Changes of climate lead to pressure and spatial shifts of the atmospheric centers of action that results in changes in ocean current velocities bringing changes into the intensity of transport of water masses inhabited by structurally and functionally different planktonic communities. This is what is mirrored in the time series obtained at spatially fixed ("anchored") stations or regions. If transport of the water mass is the major factor in this scheme, the correlation we observe between zooplankton and COAs would depend considerably upon the characteristics of the macroscale spatial heterogeneity of the zooplankton field. Further assessments of the two-dimensional spatial autocorrelation functions and spectra of zooplanktonic fields would enable to test this hypothesis.

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Связи планктона и климата в различных географических регионах. С. А. Пионтковский, С. Хамид. Межгодовые колебания суммарной численности зоопланктона в заливе Мэн (1961 - 1991), северо-восточной Атлантике (1961 - 1994) и Северном море (1961 - 1994) проанализированы и связаны с системами атмосферного давления: Исландским минимумом и Азорским максимумом. Сходным образом колебания биомассы зоопланктона в заливе Аляски (1956 - 1980) были связаны с системой давления Алеутского минимума. Для зоопланктона и индексов давления рассчитаны кросс-корреляции и функции спектральной плотности. Проанализированы региональные и глобальные аспекты связи между интенсивностью флуктуаций зоопланктона и центров атмосферного давления. Приводится обсуждение возможных механизмов, которые могут вносить вклад в динамику связей, трансформирующих атмосферные колебания в наблюдаемые изменения численности и биомассы зоопланктона.

Ключевые слова: зоопланктон, изменение климата, межгодовая изменчивость, давление над уровнем моря

Зв'язки планктону і клімату в різних географічних регіонах. С. О. Піонтковський, С. Хамід. Міжрічні коливання сумарної чисельності зоопланктону в затоці Мен (1961 – 1991) в північно-східній Атлантиці (1961- - 1994) та в Північному морі (1961 - 1994) проаналізовані і пов'язані з системами атмосферного тиску: Ісландським мінімумом і Азорським максимумом. Подібним чином коливання біомаси зоопланктону в затоці Аляски (1956 - 1980) було пов'язано з системою тиску Алеутського мінімуму. Для зоопланктону та індексів тиску розраховано крос-кореляції і функції спектральної густини. Проаналізовано регіональні і глобальні аспекти зв'язку між інтенсивністю флуктуацій зоопланктону і центрів атмосферного тиску. Проводиться обговорення можливих механізмів, які можуть вносити внесок у динаміку зв'язків, що трансформують атмосферні коливання в спостережені зміни чисельності і біомаси планктону.

Ключові слова: зоопланктон, зміни клімату, міжрічна мінливість, тиск над рівнем моря