Reorganization of North Atlantic Marine Copepod Biodiversity and Climate

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We provide evidence of large-scale changes in the biogeography of calanoid copepod crustaceans in the eastern North Atlantic Ocean and European shelf seas. We demonstrate that strong biogeographical shifts in all copepod assemblages have occurred with a northward extension of more than 10° latitude of warm-water species associated with a decrease in the number of colder-water species. These biogeographical shifts are in agreement with recent changes in the spatial distribution and phenology detected for many taxonomic groups in terrestrial European ecosystems and are related to both the increasing trend in Northern Hemisphere temperature and the North Atlantic Oscillation.

Zooplankton play an important role in the functioning of marine ecosystems and in biogeochemical cycles (*1*). Interannual changes of their species assemblages often reflect an integrated response of the ecosystem to hydrometeorological forcing. Findings have recently suggested that augmentation of greenhouse gases in the atmosphere could be the cause of the increase in the ocean heat content observed over recent decades (*2*, *3*). However, any response of marine organisms to increasing temperature still remains poorly documented. The possibility that marine ecosystems are being modified by climatic warming (*4*) has been based on either a restricted spatial coverage of data or a narrow time window, which strongly limits unequivocal interpretation (*5*). Here, we report substantial changes during the period 1960–1999 in the biogeography of calanoid copepod assemblages at an ocean basin scale and provide evidence that this might have been influenced by the combined effect of the climatic warming of the Northern Hemisphere and the North Atlantic Oscillation (NAO). To test this hypothesis, we have compared recently proposed indicator associations of calanoid copepods (*6*) (Table 1) and sea surface temperature (SST) data against large-scale hydrometeorological parameters. The copepod assemblages are based on 176,778 samples collected by the Continuous Plankton Recorder survey (*7*, *8*), which has monitored plankton on a monthly basis in the North Atlantic since 1946.

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The number of species per association was used as an indicator (i) of change in the biogeographical range of copepod communities and (ii) of ecosystem modification (*6*). For example, in a given region, a decrease in the number of warm-temperate species (Table 1), associated with an increase in the number of cold-temperate and subarctic species, would suggest an ecosystem shift from a warm to a colder dynamical equilibrium. We spatially interpolated data for each 4-year interval from 1960 to 1999, considering both diel and seasonal variations (*8*–*10*). To quantify changes in the biogeographical ranges of copepod assemblages between the beginning and the end of the sampling period, the percentage decrease and increase in the number of species per association between the period 1960–1967 and 1992–1999 was determined (fig. S1) (*8*). An 8-year period was chosen to minimize the effects of year-to-year variability. East of 20°W in the North Atlantic Ocean and European seas, we found a significant poleward movement of warm species associated with a clear decrease in the number of subarctic and arctic species in the north. West of the mid-Atlantic ridge, especially in the Labrador Sea, the trend is opposite and the number of arctic species has clearly increased. Statistical comparisons of maps indicate that all these changes are highly significant, particularly in the southern and northern boundaries of the range of the species associations (fig. S1). A further analysis (*8*) shows an increase in the diversity of arctic species in the Labrador Sea (fig. S2A) and an increase in the mean number of subarctic species associated with a decrease of warm-water oceanic species in the Oceanic Polar Front (fig. S2B). This analysis, therefore, confirms the shift of marine ecosystems toward a colder dynamic equilibrium in the Subarctic Gyre.

In the northeastern North Atlantic and European seas, maps of the mean number of species present in an area for all species associations (Fig. 1) demonstrate that major

Table 1. Biological composition of associations and ecological characteristics.

Name of association	Species or taxa composition	Ecological characteristics
Warm-temperate oceanic species association	*Euchaeta acuta, Undeuchaeta plumosa, Euchirella rostrata, Neocalanus gracilis, Clausocalanus* spp., *Nannocalanus minor, Pleuromamma borealis, P. gracilis, P. abdominalis, P. xiphias, P. piseki, Calocalanus* spp., *Mesocalanus tenuicornis, Heterorhabdus papilliger, Centropages bradyi, Mecynocera clausi*	Warm water, generally south of 52°N but concentration associated with the path of the North Atlantic Current above 52°N east of the mid-Atlantic ridge
Southern shelf edge species association	*Euchaeta gracilis, Euchaeta hebes, Ctenocalanus vanus, Calanoides carinatus*	Warm pseudo-oceanic species generally south of about 50°N along the European shelf edge
Pseudo-oceanic temperate species association	*Rhincalanus nasutus, Eucalanus crassus, Centropages typicus, Candacia armata, Calanus helgolandicus*	Species can be found in oceanic and neritic water, but their abundance is higher along shelf edges generally until about 55°N
Cold-temperate species association	*Aetideus armatus, Pleuromamma robusta, Acartia* spp., *Metridia lucens*	Indicator species of mixed water more usually found at the boundary between warm water and subarctic water
Subarctic species association	*Heterorhabdus norvegicus, Scolecithricella* spp., *Euchaeta norvegica, Calanus finmarchicus*	Indicator species of subarctic water
Arctic species association	*Calanus hyperboreus, Metridia longa, Calanus glacialis*	Indicator species of arctic water

biogeographical shifts for all species assemblages have taken place since the early 1980s to the southwest of the British Isles and from the mid-1980s in the North Sea. The number of southern and pseudo-oceanic temperate species has increased by 10° of latitude. In contrast, the diversity of colder-temperate, subarctic and arctic species has decreased in the north. All the biological associations show consistent long-term changes, which may reflect a movement of marine ecosystems toward a warmer dynamical equilibrium. These trends are in agreement with biological modifications expected under climatic warming (*5*). In terrestrial ecosystems in west Europe, similar conclusions have been reached for butterflies (*11*), amphibians (*12*), and birds (*13*), which have either extended their range northward or have shown an earlier reproductive season. The consistent modifications of both marine and terrestrial ecosystems provide a persuasive indication that common atmospheric processes have influenced all these changes.

We used Northern Hemisphere temperature (NHT) anomalies and the NAO index to see whether the regional modifications of marine ecosystems were triggered by large-scale hydroclimatic processes (*8*). Biological data for each year were spatially reinterpolated (*8*). Then, maps of correlations between these two hydroclimatic parameters and the number of species for each association were constructed (*8*). Maps show that the poleward increase in the number of southern shelf-edge and pseudo-oceanic temperate species positively covaries with NHT anomalies (fig. S4A) and the NAO index for pseudo-oceanic temperate species in the North Sea (fig. S4B). Off southwest Europe, the relationship between the number of southern shelf edge species and both proxies becomes negative. Subarctic and arctic species are negatively correlated with both parameters in the North Sea and in the European shelf edge north of Ireland. The opposite situation occurs in the northwestern North Atlantic, where the number of arctic species is positively correlated with NHT and the NAO index in the south Labrador Sea. The patterns of correlation seen in fig. S4 accord well with the patterns of the relationships between the NAO and SST shown by Hurrell and Van Loon (*14*).

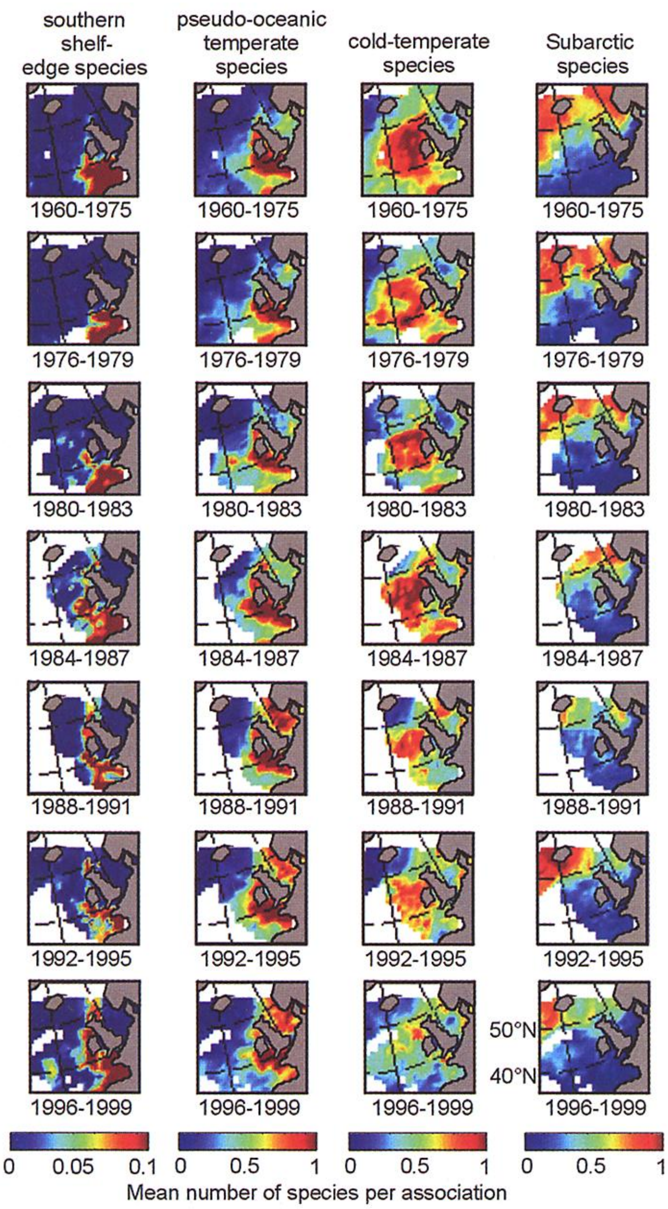

Fig. 1. Long-term changes in the mean number of species per association from 1960 to 1999. The mean of the 4-year periods from 1960 to 1975 was calculated to reduce the number of maps. This previous period shows spatial patterns consistent with the following period, 1976–1979. The arctic association has been replaced by the cold-temperate association, which is more common in the area. However, the former also shows a clear decrease in the extreme northern part of the east North Atlantic (fig. S3). Average maximum values were not superior to 1. This can be explained by the fact that for all the 4-year periods, every month was considered for daylight and dark periods. A number of species are not found near the surface during the daylight period (such as *Pleuromamma robusta* and *Metridia lucens*) whereas others overwinter in deep water (such as *Calanus helgolandicus*).

Using a standardized principal component analysis, long-term changes in SST were investigated from 1960 to 1997 (*8*) to understand how these large-scale hydrometeorological parameters have influenced the biogeographical shifts observed in the studied area. The first two eigenvectors and principal components represent 40.9% of the total variability (Fig. 2). The region south of a line from 40°N, 45°W to 60°N, 5°E, especially in the west European Basin, is characterized by a decrease in SST from 1960 to about 1975 and then a strong continuous increase until 1997. Long-term changes in this signal are correlated positively with NHT anomalies. In the Subarctic Gyre, the second principal component, which exhibits a decrease until 1993 and then an increase, is negatively correlated with the NAO.

This analysis suggests that the shift in northeast Atlantic marine ecosystems toward a warmer dynamic equilibrium has been influenced by the increasing trend in NHT. However, the positive influence of the NAO on SST in the North Sea (*15*) must have played a synergistic role with NHT anomalies. Our results are concordant with other biological changes reported for the European region in the terrestrial environment (*11–13*) and in the marine environment to include the increase in tropical fish reported in the Bay of Biscay area (*16*). In the Subarctic Gyre, the shift in northwest Atlantic marine ecosystems toward a colder dynamic equilibrium tends to be more related to the influence of the NAO.

Ecosystems of the northeast North Atlantic have changed toward a warmer dynamical equilibrium. The ecological regime shift recently reported in the North Sea (*17*) has been attributed to an increase in the flow of the European slope current. The significance of the role of this current is reinforced by this study (Fig. 1, southern shelf-edge species) and the changes seen there could be part of a larger scale event triggered by the increasing trend in NHT.

The observed biogeographical shifts may have serious consequences for exploited resources in the North Sea, especially fisheries. If these changes continue, they could lead to substantial modifications in the abundance of fish, with a decline or even a collapse in the stock of boreal species such as cod, which is

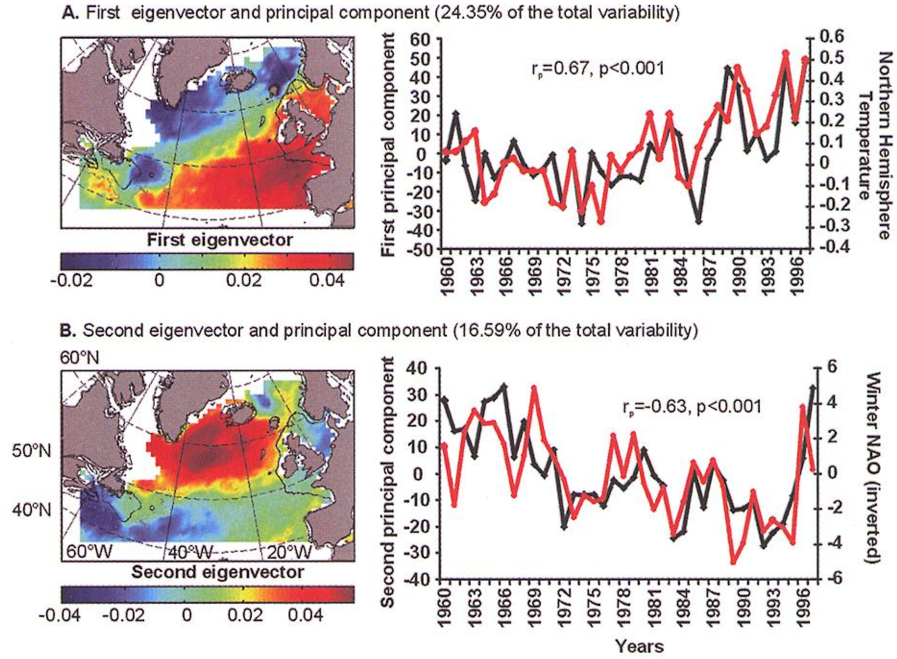

Fig. 2. Principal component analysis of long-term changes in SST in the North Atlantic Ocean. (**A**) First eigenvector and principal component (PC) (in black). Long-term changes in NHT anomalies (in red) and the Pearson correlation coefficient between the first PC and NHT anomalies are indicated. (**B**) Second eigenvector and PC (in black). The long-term changes in the winter NAO (in red) and the Pearson correlation coefficient between the second PC and the NAO index are indicated. The signal displayed by the first PC is highly correlated positively with NHT anomalies [Pearson correlation coefficient (r_P) = 0.67, $P < 0.001$]. In the Subarctic Gyre, the values of the second PC decreased until about 1993 and then increased. The long-term change in the second PC is highly correlated negatively with the NAO index ($r_p = -0.63$, $P < 0.001$). Probability was corrected to account for temporal autocorrelation with the method recommended by Pyper *et al.* (*20*).

already weakened by overfishing (*18*). Possible mechanisms by which such changes may be manifest are reviewed by Sundby (*19*). Because changes in community structure reflect the adjustment of pelagic ecosystems to modifications in water masses, currents, and/or atmospheric forcing, it is clearly important to continue to monitor plankton associations, which provide us with a valuable means of checking the well-being of marine ecosystems in the North Atlantic Ocean and possibly in other oceanic regions.

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Supporting Online Material

www.sciencemag.org/cgi/content/full/296/5573/1692/DC1
Materials and Methods
Figs. S1 to S4
References

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Soil Fertility and Biodiversity in Organic Farming

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An understanding of agroecosystems is key to determining effective farming systems. Here we report results from a 21-year study of agronomic and ecological performance of biodynamic, bioorganic, and conventional farming systems in Central Europe. We found crop yields to be 20% lower in the organic systems, although input of fertilizer and energy was reduced by 34 to 53% and pesticide input by 97%. Enhanced soil fertility and higher biodiversity found in organic plots may render these systems less dependent on external inputs.

Intensive agriculture has increased crop yields but also posed severe environmental problems (*1*). Sustainable agriculture would ideally produce good crop yields with minimal impact on ecological factors such as soil fertility (*2*, *3*). A fertile soil provides essential nutrients for crop plant growth, supports a diverse and active biotic community, exhibits a typical soil structure, and allows for an undisturbed decomposition.

Organic farming systems are one alternative to conventional agriculture. In some European countries up to 8% of the agricultural area is managed organically according to European Union Regulation (EEC) No. 2092/91 (*4*). But how sustainable is this production method really? The limited number of long-term trials show some benefits for the environment (*5*, *6*). Here, we present results from

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