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Rapid biogeographical plankton shifts in the North Atlantic Ocean

GREGORY BEAUGRAND*, CHRISTOPHE LUCZAK*† and MARTIN EDWARDS‡§

*Centre National de la Recherche Scientifique, Laboratoire d'Océanologie et de Géosciences', UMR LOG CNRS 8187, Station Marine, Université des Sciences et Technologies de Lille – Lille 1, BP 80, 62930 Wimereux, France, †Université d'Artois, IUFM Nord-Pas-de-Calais, Centre de Gravelines, 40, rue Victor Hugo, BP 129, 59820 Gravelines, France, ‡Sir Alister Hardy Foundation for Ocean Science, Citadel Hill The Hoe, Plymouth PL1 2PB, UK, §Marine Institute, University of Plymouth, Drake Circus, Plymouth PL4 8AA, UK

Abstract

Large-scale biogeographical changes in the biodiversity of a key zooplankton group (calanoid copepods) were detected in the north-eastern part of the North Atlantic Ocean and its adjacent seas over the period 1960–1999. These findings provided key empirical evidence for climate change impacts on marine ecosystems at the regional to oceanic scale. Since 1999, global temperatures have continued to rise in the region. Here, we extend the analysis to the period 1958–2005 using all calanoid copepod species assemblages (nine species assemblages based on an analysis including a total of 108 calanoid species or taxa) and show that this phenomenon has been reinforced in all regions. Our study reveals that the biodiversity of calanoid copepods are responding quickly to sea surface temperature (SST) rise by moving geographically northward at a rapid rate up to about 23.16 km yr^{-1}. Our analysis suggests that nearly half of the increase in sea temperature in the northeast Atlantic and adjacent seas is related to global temperature rises (46.35% of the total variance of temperature) while changes in both natural modes of atmospheric and oceanic circulation explain 26.45% of the total variance of temperature. Although some SST isotherms have moved northwards by an average rate of up to 21.75 km yr^{-1} (e.g. the North Sea), their movement cannot fully quantify all species assemblage shifts. Furthermore, the observed rates of biogeographical movements are far greater than those observed in the terrestrial realm. Here, we discuss the processes that may explain such a discrepancy and suggest that the differences are mainly explained by the fluid nature of the pelagic domain, the life cycle of the zooplankton and the lesser anthropogenic influence (e.g. exploitation, habitat fragmentation) on these organisms. We also hypothesize that despite changes in the path and intensity of the oceanic currents that may modify quickly and greatly pelagic zooplankton species, these organisms may reflect better the current impact of climate warming on ecosystems as terrestrial organisms are likely to significantly lag the current impact of climate change.

Keywords: biogeographical shifts, climate change, marine pelagic realm, plankton, terrestrial realm

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Introduction

Current global climate change is having large physical and biological consequences on the Earth system (Hughes, 2000; Root *et al*., 2003; Intergovernmental Panel on Climate Change, 2007a; Rosenzweig *et al*., 2008). More than 99% of organisms are ectotherms and therefore very sensitive to fluctuations in temperature (Atkinson & Sibly, 1997) and as a consequence this parameter has striking impacts on many physiological processes and controls virtually all life processes from the molecular to the cell to the regional ecosystem scale and beyond (Schmidt-Nielsen, 1990). The oceanic hydrosphere has absorbed 84% of the heat added to the climate system (oceans, atmosphere, continents and cryosphere) over the last 40 years (Levitus *et al*., 2005). However, the effect of warming on an ecosystem is not a

Correspondence: Gregory Beaugrand, e-mail: gregory.beaugrand@univ-lille1.fr

gradual process and it has been shown that, in the marine environment, critical thermal thresholds exist often manifesting themselves as abrupt ecosystem shifts (Beaugrand *et al*., 2008). Therefore, rather than a gradual change, ecosystems could experience series of sudden and stepwise shifts followed by periods of more relative stability. Temperature also modulates both directly and indirectly species interactions (i.e. competition and prey–predator interactions) leading to changes in biodiversity, structure and functioning of the whole ecosystem (Hughes, 2000; Edwards & Richardson, 2004).

At the species level, one of the first consequences of a temperature change is seen in species phenology (i.e. rhythm of species reproduction) and in a species geographical distribution (Parmesan & Yohe, 2003; Root *et al*., 2003; Beaugrand *et al*., 2002c; Edwards & Richardson, 2004). A seemingly trivial rise of just over 1 °C in the North Sea over the last 40 years has been significant enough to alter the whole ecosystem, shifting it from a once boreal into a temperate system (Beaugrand *et al*., 2008). This is because temperature continually impacts the life cycle of the species and naturally the population will respond over time, providing it is not biotically restrained (McMahon & Hayes, 2006). The optimum position is continually adjusted within its thermal envelope whether this is within a temporal niche as in seasonal succession manifested as a phenological response or in its overall biogeographical distribution manifested as a geographical movement in a population. Because species in these natural environments compete with others for resources and have to avoid predation throughout its life cycle, its actual thermal preferendum is probably much narrower than the one that would be identified in laboratory experiment (Bonnet *et al*., 2005; Helaouët & Beaugrand, 2007).

Investigating the biodiversity of calanoid copepods, Beaugrand *et al*. (2002a, b, c) reported major biogeographical shifts in the northeastern part of the North Atlantic Ocean and its adjacent seas. The studies of Beaugrand *et al*. (2002b) and Beaugrand (2005) were based on the identification of nine calanoid copepod species assemblages (Beaugrand *et al*., 2002a). They defined the species assemblages on the basis on their seasonal and diel variability, using ordination and cluster analyses and the method of indicator value created by Dufrene & Legendre (Dufrêne & Legendre, 1997). On the basis on these nine assemblages, they refined the partition of the North Atlantic Ocean proposed by Longhurst (1998). Shifts reported in Beaugrand *et al*. (2002b) were exceptional in comparison with what is generally detected in the terrestrial domain (Parmesan & Yohe, 2003).

The objectives of the present study is to update the analyses and to extend it to the nine species assemblages to encompass up to 108 species (Table 1, Fig. 1) identified in Beaugrand *et al*. (2002a) and to quantify the trends in SST in relation to climatic oscillations. The paper focuses on three main issues: (1) have the biogeographical shifts extended in other regions? (2) why are these northerly movements more pronounced in the marine than in the terrestrial realm? and (3) do the northerly movements in marine populations match surface isotherm changes? The likely consequences of these biogeographical shifts for ecosystem functioning are also outlined.

Materials and methods

Sea surface temperature (SST) data

SST data come from the Comprehensive Ocean-Atmosphere Data Set (COADS, 1° enhanced data). They were provided by the NOAA-CIRES Climate Diagnostics Center (Boulder, CO, USA) (Woodruff *et al*., 1987). Data are organised in 1° longitude and 1° latitude box available for every month of the period 1960–2005.

The north Atlantic oscillation (NAO)

The NAO is a basin scale alternation of atmospheric mass over the North Atlantic between the high pressures centred on the subtropical Atlantic and low pressures around Iceland. This phenomenon, detected in all months of the year, is particularly strong in winter, explaining about 37% of the variability in monthly sea level pressure (SLP) from December to February (Marshall *et al*., 2001). The winter NAO index used in this study is the result of a principal component analysis performed on SLP over the North Atlantic sector for months from December to March (Hurrell *et al*., 2001) (http://www.cgd.ucar.edu/cas/jhurrell/).

Northern hemisphere temperature (NHT) anomalies

Temperature anomalies for the Northern Hemisphere from 1958 to 2005 were provided by the Hadley Centre for Climate Prediction and Research, Meteorological Office, Exeter, UK.

Index of the Atlantic subarctic gyre

We used the Atlantic Subarctic gyre originated from Hatun *et al*. (2005) to evaluate whether changes in SST could be related to the strength of the circulation within the subarctic gyre. The index is the first principal component of a PCA performed on Sea Surface High in the North Atlantic Ocean (Häkkinen & Rhines, 2004; Hatun *et al*., 2005).

Table 1 Biological composition of species assemblages and their ecological preferendum

Name of the assemblage	Species or taxa	Ecological preferendum
1. Subtropical and warm-temperate species assemblage	*Undeuchaeta major, Acartia danae, Paracandacia bispinosa, Euchaeta media, Temora stylifera, Scolecithrix danae, Euchaeta marina, Candacia ethiopica, Eucalanus attenuatus, Lucicutia* spp., *Eucalanus elongatus, Candacia pachydactyla, Rhincalanus cornutus, Euchaeta pubera, Centropages violaceus*	Oceanic and pseudo-oceanic species generally found near shelf edges and in the northward extension of the Gulf Stream
2. Warm-temperate oceanic species assemblages	*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*	Oceanic warm water species, 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
3. Warm-temperate pseudo--oceanic species assemblage	*Euchaeta gracilis, Euchaeta hebes, Ctenocalanus vanus, Calanoides carinatus*	Warm water shelf-edge species found south of about 50°N along the European shelf edge for years prior to the 1980s
4. Temperate pseudo-oceanic species assemblage	*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 until about 55°N before the 1980s
5. Shallow-water species assemblage	*Isias clavipes, Anomalocera patersoni, Labidocera wollastoni*	Species generally found above the continental shelf but mainly abundant in shallow coastal regions
6. Continental shelf species assemblage	*Centropages hamatus, Temora longicornis, Pseudocalanus* adult, *Para-Pseudocalanus* spp.	Species generally found above the continental shelf
7. Cold-temperate mixed-water species assemblage	*Aetideus armatus, Pleuromamma robusta, Acartia* spp., *Metridia lucens*	Species indicative of mixed water more usually found at the boundary between warm water and subarctic water
8. Subarctic species assemblage	*Heterorhabdus norvegicus, Scolecithricella* spp., *Euchaeta norvegica, Calanus finmarchicus*	Species indicative of subarctic water
9. Arctic species assemblage	*Calanus hyperboreus, Metridia longa, Calanus glacialis*	Species indicative of arctic water

From (Beaugrand *et al*., 2002a). The time period considered in the analyses was 1958–1999. The names of some species assemblages have been slightly modified in comparison to those used in Beaugrand *et al*. (2002b; their Table 1).

The Atlantic multidecadal oscillation (AMO)

The AMO is a large-scale oceanic phenomenon, source of a natural variability in the range of 0.4 °C in many oceanic regions (Enfield *et al*., 2001). A simple index can be constructed by calculating a running mean of Atlantic (detrended) SST anomalies north of the equator. We used the index constructed from Extended Reconstruction SST (ERSST) data and averaged in the area of 25–60°N and 7–75°W, minus regression on global mean temperature (NCDC). This index was downloaded from the website http://climexp.knmi.nl/. This oceanic oscillation has a large influence on SST changes in the region covered by this study (Enfield *et al*., 2001; Keenlyside *et al*., 2008).

The continuous plankton recorder (CPR)

The CPR survey is a plankton monitoring programme that has been operated on a routine monthly basis in the North Atlantic and in the North Sea since 1946 (Warner & Hays, 1994; Batten *et al*., 2003; Reid *et al*., 2003). Sampling is carried out by a high-speed plankton sampler (about 20 km h^{-1}) that is towed behind voluntary merchant ships at a constant depth of about 6.5 m (Hays, 1994). The CPR survey is recognised as one of the longest, richest (in terms of species information) and geographically extensive ecological surveys in the world. One CPR sample corresponds to about 3 m^3 of seawater filtered (Jonas *et al*., 2004). A total of 206 673 CPR samples was considered in the analysis.

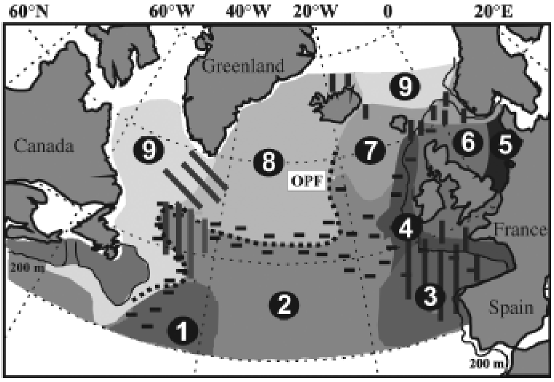

Fig. 1 Simplified distribution of the nine assemblages proposed by Beaugrand *et al*. (2002a). A number identifies each species assemblage. These numbers correspond to the ones used in Table 1 and subsequent figures. In some areas such as in the Bay of Biscay, several assemblages overlap (vertical or horizontal black bars). The thick black dotted line denotes the location of the Oceanic Polar Front (OPF). Simplified from Beaugrand *et al*. (2002b).

Analysis 1: long-term spatial changes in SST

Long-term changes in SST were investigated by means of a Principal Component Analysis [PCA, (Jolliffe, 1986)]. The PCA was performed on a correlation matrix with the double objective of identifying major long-term changes in SST (examination of principal components) and locating their geographical patterns (mapping of eigenvectors) in the north-eastern part of the North Atlantic.

Relationships between long-term changes in SST (principal component) and large-scale hydro-climatic variables (NHT anomalies, the NAO and AMO indices) were investigated by linear correlation analysis. Probabilities were calculated with consideration of temporal autocorrelation. Box–Jenkins (Box & Jenkins, 1976) autocorrelation function modified by Chatfield (1996) was assessed. The autocorrelation function was then used to adjust the degree of freedom using the Chelton's (1984) formula as applied by Pyper & Peterman (1998).

Analysis 2: long-term spatial changes in the mean number of species per assemblage

Data corresponding to the period 1958–2005 were used to investigate the long-term changes in the spatial distribution of species assemblages. Before analysis, the number of species belonging to each copepod assemblage was determined for each of the 206 673 CPR samples. As we considered nine biological assemblages, the original matrix was 206 673 × 9. Sampling by the CPR is irregular in time and space with collection taking place at any time of day or night for any month or location. To take into account this spatio-temporal heterogeneity, the number of species for each assemblage was spatially interpolated (Lam, 1983). The inverse squared distance method was used for interpolation with a constant number of six neighbours to prevent sampling-related differences between regions and with a search radius of 250 nautical miles (Beaugrand *et al*., 2002c). This was done by considering a 3-year time interval from 1958 to 2005 (48 years/3 = 16 3-year periods). This first temporal interval was selected to display the long-term variability of biological assemblages. To take into account seasonal fluctuations and diel vertical migration of calanoid copepods (Beaugrand *et al*., 2001), data were spatially interpolated for every 2-month period (six maps), considering daylight and night samples separately (two maps), for each 3-year period. The geographical cells of the 12 seasonal and day–night maps produced for each 3-year period ($16 \times 6 \times 2 = 192$ maps × 9 biological assemblages) were then averaged for each species assemblage if the number of missing data was less than four, using the same procedure described in Beaugrand *et al*. (2002c).

Analysis 3: long-term spatial changes in the species assemblages and isotherms

To determine the rate of shift, the latitudinal position of the isotherms or species assemblages were first interpolated at a given longitude corresponding to the region of interest. Then, the difference in the latitudinal position of the isotherms or the species assemblages between the beginning and the end of the period were calculated and geographical distances d were assessed as follows (Beaugrand & Ibanez, 2002):

$$d_{i,j} = R \arccos\left(\sin\varphi_i \sin\varphi_j + \cos\varphi_i \cos\varphi_j \cos g\right),$$

where $d\,(i,j)$ is the distance (in km) between i and j. φ_i is the latitude (in radian) at point i and φ_j the latitude at point j. g is the difference in longitude between i and j. R is the Earth radius in km.

Results

Long-term changes in SST show a pronounced increase around the British Isles after 1995 onwards (Fig. 2a). The period 2001–2005 was especially warm (mean annual SST of 11.21 °C) in the North Sea, exhibiting an increase of 1.11 °C in comparison with temperatures of the 1960s (mean decadal SST of 10.10 °C). Long-term changes in the first principal component are significantly positively correlated to NHT anomalies ($r_p = 0.78$, $p_{\mathrm{ACF}} = 0.0375$),

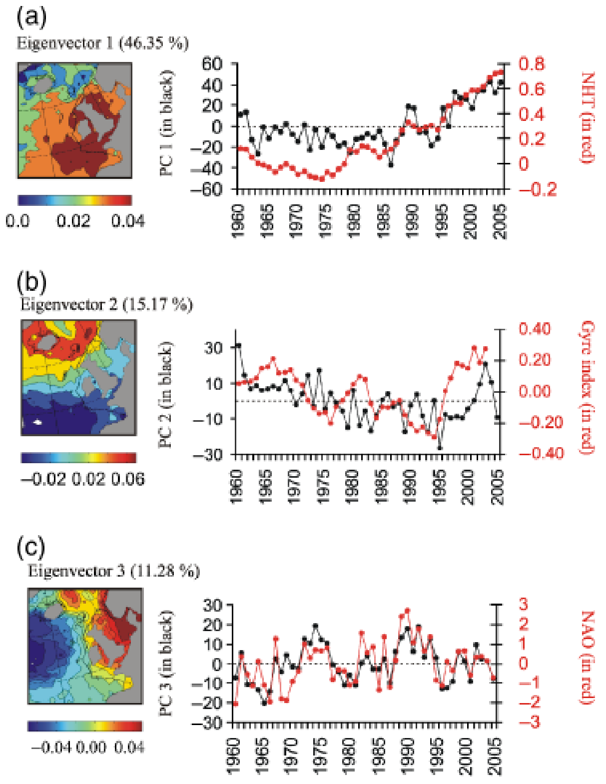

Fig. 2 Long-term changes in SST in the north-east Atlantic and adjacent seas over the period 1960–2005. (a) First eigenvector and principal component accounting for 46.35% of the total variance. NHT anomalies are superimposed in red. (b) Second eigenvector and principal component accounting for 15.17% of the total variance. The subarctic gyre index (Hatun *et al.*, 2005) is superimposed in red. (c) Third eigenvector and principal component accounting for 11.28% of the total variance. The NAO index is indicated in red.

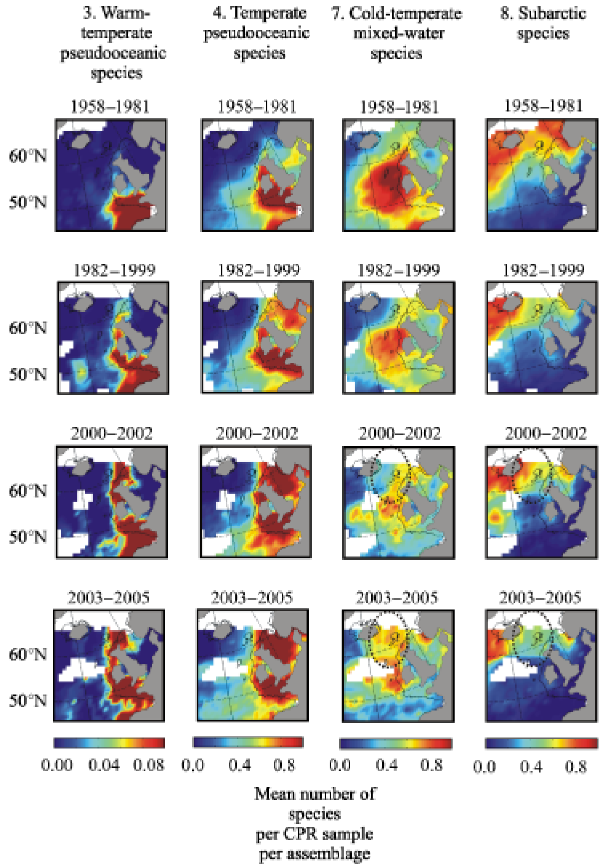

Fig. 3 Long-term changes in the mean number of species per assemblage (species assemblages 3, 4, 7 and 8) from 1958 to 2005. The period 1958–1981 was a period of relative stability and the period 1982–1999 was a period of rapid northward shifts (Beaugrand *et al.*, 2002c). These periods were selected to reduce the number of 3-year maps. Average maximum values are rarely superior to 1 because they are averages based on every 2-month and both daylight and dark periods. Many species are not found near the surface during the daylight period (e.g. *Pleuromamma robusta*) while some overwinter in deeper water (e.g. *Calanus finmarchicus*). Black dotted circle or oval denotes areas where pronounced changes have been observed.

which indicate that the temperature rise reflects an increase in global temperature observed over the Northern Hemisphere. A positive and high correlation was also observed with the AMO index ($r_p = 0.75$, $p_{\mathrm{ACF}} = 0.0032$). No significant correlation between long-term changes in SST and the state of the NAO was detected ($r_p = 0.06$, $p_{\mathrm{ACF}} = 0.77$). Long-term changes in the second principal component reflect a regular decrease in SST until the mid-1990s which reversed afterwards in regions north and west of Scotland (Fig. 2b). The second component clearly detects a recent increase in SST that occurred in regions south of Iceland and north of the North Atlantic Drift province (Longhurst, 1998; Beaugrand *et al.*, 2008). No significant correlation was detected with either the NAO index ($r_p = 0.21$, $p_{\mathrm{ACF}} = 0.22$), NHT anomalies ($r_p = 0.21$, $p_{\mathrm{ACF}} = 0.38$) or the AMO index ($r_p = -0.15$, $p_{\mathrm{ACF}} = 0.53$). However, long-term changes in the second principal component are significantly positively correlated to the subarctic gyre index ($r_p = 0.56$, $p_{\mathrm{ACF}} = 0.02$) suggesting a link between changes in SST and the oceanic subarctic circulation south of Iceland. The third principal component exhibits long-term and year-to-year variability of temperature related to the state of the NAO ($r_p = 0.70$, $p_{\mathrm{ACF}} < 0.01$). Mapping of eigenvectors shows that opposition between changes in SST in the eastern part of the subarctic gyre and regions over the North Sea. No relationship was found with either the NHT anomalies ($r_p = 0.00$, $p_{\mathrm{ACF}} = 0.98$), the subarctic gyre index ($r_p = -0.34$, $p_{\mathrm{ACF}} = 0.14$) or the AMO index ($r_p = -0.27$, $p_{\mathrm{ACF}} = 0.24$).

Northward movements of the warm-water species analysed in Beaugrand *et al.* (2002c) and Beaugrand

(2005) continued and reinforced during the period 2002–2005 (Fig. 3). Warm-temperate and temperate pseudo-oceanic (species assemblages 3 and 4, Table 1, Fig. 1) continue to progress northwards. However, due to the absence of sampling by the CPR survey above 60°N, it will become impossible to follow on a monthly basis the progression of this species group. An emerging feature has appeared during the more recent period. Cold-temperate species (species assemblage 7) have increased south of Iceland while subarctic species (species assemblage 8) have decreased, reflecting the impact of warming on the structure of plankton ecosystems. Such a result is corroborated by the increase in SST (Fig. 2).

Long-term changes of these species were not investigated in previous studies (Fig. 4). Subtropical and warm-temperate species (species assemblage 1, Table 1, Fig. 1) have increased along the southern part of the European shelf-edge since 2000. Warm-temperate oceanic species (species assemblage 2) has been replaced by warmer-water species (species assemblage 1) in the region of the Bay of Biscay. A closer examination of the North Sea indicates a northward movement of shallow-water species (species assemblage 5). The rate of the migration (about 2° of latitude) is much smaller than those found along the European shelf-edge. Continental shelf species (species assemblage 6) have moved northwards but have also decreased in the southern part of the area covered by the CPR survey (e.g. Bay of Biscay). Arctic species (species assemblage 9) have declined in regions north of the North Sea.

All these results suggest a clear movement of warm-water species associated with a decrease in colder-water species and reflect a clear response of the plankton

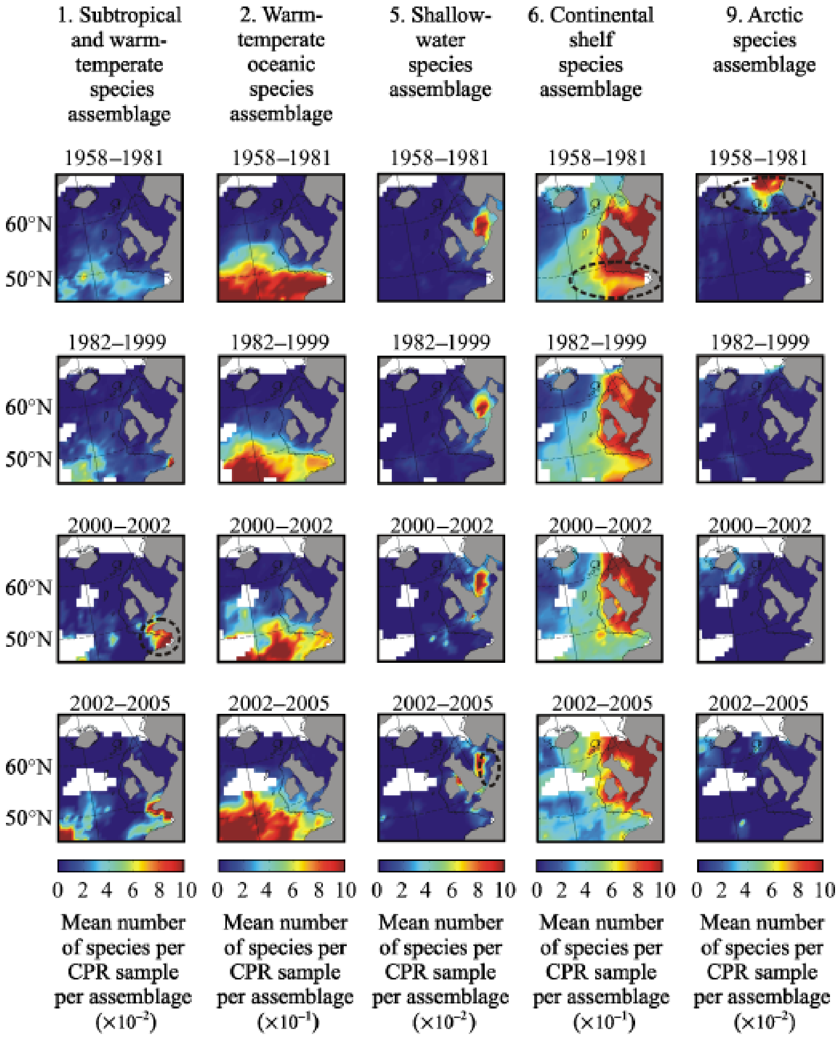

Fig. 4 Long-term changes in the mean number of species per assemblage (species assemblages 1, 2, 5, 6 and 9) from 1958 to 2005. Black dotted circle or oval denotes areas where pronounced changes have been observed. For further explanation on maps, see Fig. 3.

ecosystems to regional climate warming. However, the rate of migration of some warm-water species north does not match the movement of the isotherms (Fig. 5). This is especially conspicuous along the European shelf-edge where an apparent movement of about 10° of latitude is observed (Fig. 3).

Discussion

Rapid latitudinal shifts reported in Beaugrand *et al.* (2002a–c) and Beaugrand (2005) continued in the north-eastern part of the North Atlantic and in the North Sea during the period 2002–2005. The analyses have identified new changes in species distribution, which might reveal regional ecosystem changes. A change in species composition was detected in the southern part of Iceland in 2003 (Fig. 3). Subarctic species decreased while cold-temperate mixed water species increased. These changes might be the consequences of the increase in temperature since the mid-1990s (see Fig. 2), which was at the origin of the reversal of the Phytoplankton Colour Index, an indicator of the quantity and quality of phytoplankton inferred by the CPR survey (Reid *et al.*, 1998). Such a modification could originate from a shift from a period dominated by a positive phase of the NAO to weaker NAO patterns. Hatun *et al.* (2005) suggested that period of lower NAO indices allows the subarctic gyre to contract, enabling more warm-water species to penetrate further north and west in regions south of Iceland. Polar ecosystems, composed of rich-lipid organisms, are likely to be very sensitive to climate change (Flato *et al.*, 2000). Subarctic species have much more energy than cold-temperate species (Kattner *et al.*, 2007). It is likely that the diminution in lipid content of zooplankton may have a large effect on both lipid dynamics and the trophodynamics of biological and ecological systems. Indeed, such reduction in lipid content might reduce growth, survival and in turn affect recruitment in fish or seabirds (Wanless *et al.*, 2005; Beaugrand, 2009).

The second new biogeographical shift is found in the Bay of Biscay and over the southern part of the Celtic Sea and the English Channel after the end of 1990s. An increase in subtropical species (species assemblage 1) has paralleled a reduction in continental (species assemblage 6), warm-temperate oceanic species (species assemblage 2) and warm-temperate pseudo-oceanic species (species assemblage 3) (see Figs 3 and 4). Lindley & Daykin (2005) showed the substantial increase in the occurrence of two subtropical copepod species *Centropages chierchiae* and *Temora stylifera*. Increase in the occurrence of subtropical fish has also been documented (Quero *et al.*, 1998) and some studies have reported latitudinal movements of fish species distribution that have been mainly related to SST changes (Quero *et al.*, 1998; Brander *et al.*, 2003; Perry *et al.*, 2005).

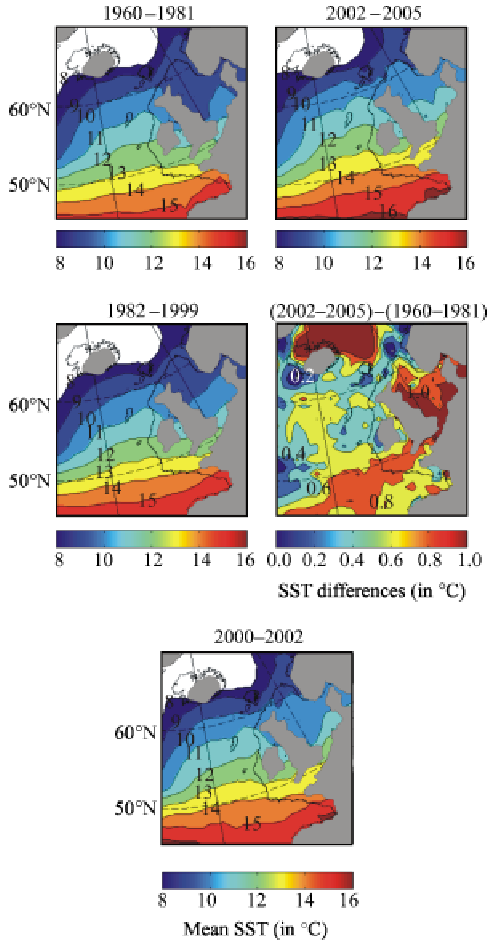

Fig. 5 Long-term changes in mean SST in the north-eastern part of the North Atlantic Ocean and adjacent seas. Differences in SST were calculated between the period 2002–2005 and the period 1960–1981.

Latitudinal species shifts in response to temperature warming have become more regularly documented in both the terrestrial and the marine realm (Thomas & Lennon, 1999; Beaugrand *et al.*, 2002c; Parmesan & Yohe, 2003; Perry *et al.*, 2005). However, a comparison of the rates suggests that shifts can be more pronounced in the marine realm. Our results show that warm-temperate pseudo-oceanic species experienced an apparent movement of about 10° of latitudes (52–62°N; 10°W; 48 years; a mean poleward movement of 23.16 km yr^{-1}). The rate of change given here is a coarse indication of the shift, as it is clear (Figs 3 and 4) that these biogeographical modifications are fundamentally structured in two dimensions and have a zonal and a meridional component. Although observed latitudinal shifts were more moderate for other species assemblages (between 53°N and 62°N; 2°E; 48 years; 21.75 km yr^{-1} for temperate pseudo-oceanic; between 58°N and 62°N; 0°E; 48 years; 9.26 km yr^{-1} for subarctic species), such changes remain high in comparison with the much smaller terrestrial movements reported in the literature. Indeed, Thuiller (2007) suggests that a temperature rise of 1 °C, as approximately observed in the North Sea (see Fig. 5), moves northwards the location of ecological zones by 160 km. Examination of fossil pollen suggests that migration of trees during the post glacial warming in North America and Europe was between 100 and 1000 m yr^{-1} although recent results suggest such rates could have even been overestimated (Pearson, 2006; references therein). Thomas & Lennon (1999), investigating 59 breeding bird species over the United Kingdom, detected a northward shift of 18.9 km in 20 years, an average shift of 945 m yr^{-1}. A meta-analysis conducted on 1700 species or taxonomic groups at a global scale reported a poleward shift of 610 m yr^{-1} (Parmesan & Yohe, 2003). Parmesan *et al.* (1999) detected a maximum range shift for butterfly of 200 km over a period of 40 years, therefore, a maximal movement of 5 km yr^{-1}.

Despite the large bias towards the number of biological observations in the terrestrial realm vs. the marine, it is clear from studies that the marine response to climate change is often much faster and dramatic than those observed from terrestrial studies (Intergovernmental Panel on Climate Change, 2007a). This is also the case for phenological changes. While phenological changes of up to 6 weeks have been recorded in the North Sea, most terrestrial studies have observed changes measured in days (Edwards & Richardson, 2004; Intergovernmental Panel on Climate Change, 2007a). Therefore, the oceans are far more dynamic in their response to climate change and variability, which is reflected in the rapid biological response particularly for pelagic ecosystems.

Such a migration rate is exceptional and is much more pronounced than the rate found in other oceanic and terrestrial systems (Parmesan & Yohe, 2003). Beaugrand *et al.* (2002c) previously mentioned that other processes related to advection might have accelerated the rate of migration. Rate of northward movement in the North Sea corresponds to changes in the isotherms (Fig. 5). However, the rate is much more pronounced over the European shelf-edge in the path of the European shelf-edge current, which has recently strengthened (see Reid *et al.*, 2001b). We review processes that might have contributed to the exceptional rates of latitudinal shifts reported here (Table 2). First, marine organisms are in general stenothermal in comparison with their terrestrial counterpart (Turquier & Toulmond, 1994). Marine organisms are protected against large fluctuations in temperature thanks to the high specific heat index of water. Daily and seasonal variations in temperature are less contrasted in comparison with the terrestrial domain. Marine organisms are therefore more sensitive to change in temperature and response of plankton communities particularly rapid due to their short life-cycles (from days to months), making them ideally suited as indicators of environmental change (Beaugrand, 2005).

Second, calanoid copepods, as free-floating organisms, are able to track very quickly their bioclimate envelope contrary to terrestrial species where barriers (e.g. different substrate, presence of a lake or a town) can prevent a species to move, where dispersal is restricted to specific stages of the life cycle and where other climatic parameters become more important (e.g. precipitation, the presence of a microclimate) (Table 2). Furthermore, the presence of more other anthropogenic pressure such as habitat fragmentation and destruction is clearly a problem that limits the geographical spread of organisms (Hannah *et al.*, 2005). The majority of terrestrial organisms be its insects or mammals for example are bound to their habitat type usually dictated by the vegetation composition (Lester & Myers, 1991; Wyman, 1991). In terrestrial systems the development of these vegetative types are particularly slow moving (e.g. forest) and hence organisms that rely on this habitat will be restricted in terms of their movement. In contrast, the rapid development of marine phytoplankton with lifetimes measured in days compared with many years, photosynthetic production and herbivory that control the production are not as temporally and spatially hindered in their geographical spread. In this period of large variability in climate, it is therefore likely that terrestrial organisms might not be equilibrium with their bioclimatic envelope. This may underestimate the current impact of climate on terrestrial organisms. This is not so with plankton organisms but changes in oceanic circulation related or not to climate variability, may indeed be a confounding factor to the effects of global climate change.

Third, regions where the greatest changes were observed (Fig. 3) are generally located at the boundary between the Atlantic Westerlies Wind Biome and the Atlantic Polar Biome (*sensu* Longhurst, 1998; Beaugrand *et al.*, 2001, 2002a). Many authors have drawn attention that species and ecosystems are more influenced by climate over transitional systems (Parmesan, 2005). Recently, Beaugrand *et al.* (2008) have provided evidence that the largest rates of biological changes from phytoplankton to zooplankton to fish were concentrated between 9 °C and 10 °C, the boundary between temperate and polar biomes. Therefore, the region of

Table 2 Comparison of both physical and biological processes and characteristics in the pelagic and terrestrial realm that might explain the quicker response of marine zooplankton to climate change

Processes	Terrestrial realm	Pelagic realm (plankton)
Habitat		
Main climatological limiting factor	Temperature, precipitation, atmospheric circulation	Temperature, atmospheric circulation
Secondary factors	Sunlight, topography, geology, soil type, microclimate	Current, sunlight, stratification, ocean, bathymetry
Physical barriers	High	Smaller (oceanic currents and frontal structures such as the Oceanic Polar Front)
Predictability	Less predictable	More predictable
Interactions with the climate system		
Type of interaction	More complex (e.g. microrefugia)	More simple although indirect effect of climate through oceanic circulation might make it more difficult projections (no microrefugia)
Variation in climate	Higher short-term (daily or monthly) variance making parameters such as minimum or maximum temperature very important	Buffered domain. Extreme in climate are less important
Synergistic effect		
Anthropogenic interaction	High to very high (habitat fragmentation, exploitation, human infrastructure)	Much smaller in general at a large scale (existence of more indirect relationships through fishing)
Capacity to track climate change		
Sensitivity to temperature change	Lower (eurytherm)	Higher (stenotherm)
Reproductive characteristics		
Size of offsprings	Smaller	Larger
Age at maturity	Older	Younger
r/K selection	Stronger interaction between r-and K-selected species	Lesser interaction between r-and K-selected species
Reproductive rate (advantage to high reproductive rates)	Slower (e.g. Months to several decades for plants; weeks to several months to years for insects)	Quicker (e.g. Phytoplankton: days; zooplankton from weeks to several months)
Dispersal (advantage to efficient dispersers)	Low/medium (often constrained by their interspecific relationships with plants)	Higher as biotic interactions are smaller. Domain more constrained by the physical environment
Interspecific interactions (Advantage to community with smaller biotic interactions)	Greater. Many species of insects are specific to a type of vegetal community. Co-shifts	Smaller Species shift

References are indicated in the discussion.

interest here is expected to witness the most prominent latitudinal shifts. However alone, this biogeographical propriety cannot explain the substantial shift of warm-temperate pseudo-oceanic species.

Fourth, the biogeographical shifts observed for warm-temperate pseudo-oceanic species do not match the mean annual rate of the isotherms (e.g. the isotherm 13 °C changes by 7.25 km yr^{-1}; 50°N–53°N; 10°W; 1960–2005) along the European shelf-edge (see Figs 3 and 5). However, a study of latitudinal changes in the isotherms, performed on a monthly basis, could reveal more intense changes. For example, McMahon & Hayes (2006), using AVHRR satellite images, detected a northward shift of 330 km in the position of the 15 °C surface isotherm in August between 1985 and 2000. Such a shift corresponds to a northward migration of 20.62 km yr^{-1}, a rate close to the one observed for the warm-temperate pseudo-oceanic species assemblage (23.16 km yr^{-1}). Hobson *et al*. (2008) have recently shown that the position of the 12 °C, 15 °C and 18 °C surface isotherms were more commonly found northwards in the recent years and could play a role in influencing the observed changes in the spatial distribution of pelagic species (e.g. Quero *et al*., 1998; Beaugrand *et al*., 2002b; McMahon & Hayes, 2006). Other processes could also contribute to the poleward movement. Contrary to the terrestrial realm, the pelagic biotope is composed of two components: a stable-biotope component (e.g. bathymetric characteristics) and a substrate-biotope component (e.g. water masses; Van Der Spoel, 1994). Previously mentioned in Beaugrand *et al*. (2002c), the increased intensity of the European shelf-edge current may have played an important role in advecting more warm-water species faster northwards (Reid *et al*., 2001b). There are clear indications of a sustained change in the characteristics of the water masses along the European shelf-edge. A deep reduction in the amount of the Norwegian Sea Deep Water (deep polar water mass) in regions to the north-west of the North Sea has been observed (Heath *et al*., 1999). This cold and deep body mass used to be the overwintering habitat of the subarctic species *Calanus finmarchicus*. Some authors hypothesised that the substantial reduction of this subarctic species was related to the decrease in Norwegian Sea Deep Water (Planque & Taylor, 1998; Heath *et al*., 1999). The reduction in the abundance of *C. finmarchicus* might allow warm-temperate pseudo-oceanic species, composed of species (e.g. *Euchaeta hebes*, *Calanoides carinatus*) that diapause in deep environment to overwinter. This process might have largely contributed to the substantial rate of shift observed in this study.

Finally, the apparent shift of 10 °C of warm-water pseudo-oceanic species might be considered as another example of the Reid's paradox, named after the difficulties of a botanist Clement Reid who were attempting to understand the relatively rapid spread of oaks across the United Kingdom during the warming post-glacial period (Pearson, 2006). While several hypotheses have been proposed to explain this anomaly, a theory could be relevant here. The theory states that colonisation could propagate from local population, persisting in a microclimate (microhabitats, Mcglone & Clark, 2005). The relatively low density could explain why palynological studies were unable to detect the presence of the pollen. Transposing this hypothesis to the marine pelagic realm, migration rates could appear very high as colonisation could have propagated from several local points already above the observed limited boundary but not detected because of the coarse sampling of the pelagic realm. Although being the most extensive marine monitoring program of the world, the CPR survey has collected 206 673 samples (1946–2005), an average collect of 3445 samples per year, mainly over a region (the North Atlantic sector) of about 16 million of km^2, therefore, an approximate density of 2.2 samples per geographical square of 100 km side per year. This represents a spatial resolution much smaller to what is normally achievable in many terrestrial studies (e.g. Huntley *et al*., 2008).

Long-term changes in SST is highly correlated positively to NHT anomalies, suggesting that global temperatures has the greatest influence (Fig. 2; 46.35% of the total variance) although high correlation with the AMO index suggests that part of this variance might also be attributable to longer frequency variability (Enfield *et al*., 2001; Keenlyside *et al*., 2008). The covariation between NHT anomalies and SST reinforced after approximately 1980 (Beaugrand, 2009). Beaugrand (2009) also shows that this strengthening in the covariation between SST changes and NHT anomalies in the North Atlantic Ocean (especially in the northern part of the North Atlantic) during the period 1960–2006. A large part of the variance of sea temperature in the north-eastern part of the North Atlantic Ocean is also attributable to changes in both oceanic (subpolar gyre index; 15.17% of the total variance) and atmospheric (NAO; 11.28% of the total variance) forcing. However, interaction between climate warming and natural pattern of atmospheric variability is complex (Intergovernmental Panel on Climate Change, 2007b). Using atmospheric-ocean general circulation modelled data, Paeth *et al*. (1999) found that anthropogenic global warming had a significant influence on the simulated variability of the state of the NAO. Another study has recently confirmed this result (Stephenson *et al*., 2006). It seems indeed that anthropogenic climate change will manifest itself through existing climatological processes such as the NAO although the strength of this influence is difficult to predict (Stephenson *et al*., 2006). Therefore, the separation is quite simple and the synergistic influence makes the issue quite complex.

An important point should be stressed. The isotherm 10 °C in the North Sea moved northwards by an approximate rate of 21.75 km yr $^{-1}$ (53°N–62°N; 2°E; 1960–2005; Figs 2 and 5). This is of the same magnitude that the shift reported along the European Shelf-edge and may explain totally the biogeographical shifts (Figs 3 and 4), as well as the abrupt ecosystem shift observed in the North Sea (Reid *et al*., 2001a; Beaugrand & Ibanez, 2004; Weijerman *et al*., 2005). Beaugrand *et al*. (2008) linked the movement of the isotherms 9–10 °C to the abrupt ecosystem shift observed in this region. The whole ecosystem change as a result of the shift in the location of the isotherm (indicator of the boundary between polar and temperate systems) and changes have been detected from phytoplankton to zooplankton to fish in the pelagos (Beaugrand & Reid, 2003) and the benthos (Kroncke *et al*., 1998), affecting also benthic-pelagic coupling (Kirby *et al*., 2008). From our study, it is clear that a global quantification of the distance of migration can lead to very coarse assessment and we think it is preferable to provide directly (when possible) observed maps of change (Figs 3–5) that give a more complete understanding of the biogeographical shifts. This stepwise change in temperature (see Fig. 5) might have strong consequences on North Sea ecosystems. Species characterising warm-water oceanic and pseudo-oceanic species are increasing, replacing subarctic species that are richer in energy (Kattner *et al*., 2007). This inevitably leads to trophic mismatch with higher trophic level (Durant *et al*., 2005). Beaugrand *et al*. (2003) drew attention on potential mechanisms that could influence larval cod survival in the North Sea. They found that the replacement of *C. finmarchicus* by its congeneric warmer-water species *C. helgolandicus* involved a mismatch between the timing of presence of potential preys and the occurrence of larval cod. Furthermore, prey biomass decreased and some important zooplankton prey such as euphausiids also diminished. The authors hypothesised that the thermal regime and its implications on species composition reduce the capacity of the ecosystem to support a high level of cod. These results have recently been confirmed in another analysis, which has established at the scale of the North Atlantic Ocean a link between changes in phytoplankton concentration (SeaWIFS and CPR data set), zooplankton diversity and size (CPR data set) and the Atlantic cod (Fishbase data set) (Beaugrand *et al*., 2008). An increase in the variance of all trophic levels was detected for a thermal regime between 9 °C and 10 °C. This regime characterises the boundary between the Atlantic Westerlies Wind and the Atlantic Polar biomes (*sensu* Longhurst, 1998). The link between plankton ecosystem state and cod was very high (see Beaugrand *et al*., 2003; their Fig. 1). These results suggest that the Atlantic cod will not be able to return to level of abundance observed during the gadoid outburst (mid-1960s and 1970s) if sea temperature continues to warm.

This study shows that temperature is a key driver of marine ecosystems and that marine pelagic species are highly sensitive to temperature changes. All biogeographical shifts observed in this study are consistent and reflect the response of the ecosystems to a warmer hydro-climatic regime. As a result, an increase in species diversity, associated with a decrease in the mean size of organisms, has been observed (Beaugrand, 2009). This study reinforces laboratory experiments which have provided evidence that temperature is a key parameter to explain the spatial distribution of a species (Parmesan, 2005). The strong dependency of copepods to temperature makes it possible to propose projections of future changes in species distribution and to anticipate abrupt ecosystem shift. Faced with a modified set of environmental conditions, local genetic adaptation and/or physiological changes could occur (Spicer & Gaston, 1999). However, it seems unlikely that this would happen on such a short-time scale. Providing that the thermal preferendum of a species is identified (Helaouët & Beaugrand, 2007; Beaugrand & Helaouët, 2008), forecasting might become possible. The impact of anthropogenic greenhouse effect on temperature could be expected to be gradual. However, anthropogenic climate change also acts on hydro-climatic processes such as the NAO and the Atlantic Overturning Meridional Circulation. These types of indirect effects, by essence nonlinear (e.g. Paillard, 2001; Keenlyside *et al*., 2008), are much more difficult to predict.

Large-scale biogeographical shifts observed in Beaugrand *et al*. (2002a, b, c) are still ongoing. Other shifts occurred more recently in the Bay of Biscay and south of Iceland at the end of the 1990s. The most conspicuous driving factors appear to be temperature, forced mainly by NHT anomalies but some relationships indicate an influence of other hydro-climatological types of forcing linked to the NAO, the AMO and the oceanic circulation (i.e. the circulation of the subpolar gyre). Plankton movements do not match changes in temperature everywhere. While changes in copepod assemblages are well explained by the northward shift in the 10 °C isotherm, this is not so in other regions and especially along the European shelf-edge where the shift in the isotherms are three times less pronounced than changes observed in some plankton assemblages. Regional processes related to ocean circulation changes (i.e. contraction of the subpolar gyre, increase in the European shelf-edge current) might be of importance. They are in large part driven by atmospheric forcing (e.g. the NAO influence on the subpolar gyre). A monthly examination of changes in isotherms might also reveal more intense northward shifts that could explain the plankton movements reported here. Another process, called the Reid's paradox, could also be of relative importance to explain the apparent rapid shift observed in copepods along the European shelf-edge.

Shifts observed for copepods are much more intense that those observed in the terrestrial realm. We believe that changes observed in the plankton reflect better the adjustment of biological systems to current warming than in the terrestrial realm. Factors related to the presence of natural or artificial barriers and the characteristics of the life cycle of species (generation time of trees) might mask the impact of climate warming on terrestrial ecosystems. It is therefore possible that the current impact of warming on terrestrial systems could be actually far more pronounced than previously documented.

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[Correction added after online publication 29 April 2009: Figs 2, 3 and 4 captions and order were corrected].