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LETTER

Causes and projections of abrupt climate-driven ecosystem shifts in the North Atlantic

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Abstract

Warming of the global climate is now unequivocal and its impact on Earth' functional units has become more apparent. Here, we show that marine ecosystems are not equally sensitive to climate change and reveal a critical thermal boundary where a small increase in temperature triggers abrupt ecosystem shifts seen across multiple trophic levels. This large-scale boundary is located in regions where abrupt ecosystem shifts have been reported in the North Atlantic sector and thereby allows us to link these shifts by a global common phenomenon. We show that these changes alter the biodiversity and carrying capacity of ecosystems and may, combined with fishing, precipitate the reduction of some stocks of Atlantic cod already severely impacted by exploitation. These findings offer a way to anticipate major ecosystem changes and to propose adaptive strategies for marine exploited resources such as cod in order to minimize social and economic consequences.

Keywords

Abrupt ecosystem shift, critical thermal boundary, North Atlantic Ocean, plankton, the Atlantic cod, variance.

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INTRODUCTION

Warming of the global climate is now unambiguous and its impact on Earth's functional units has become more apparent (Intergovernmental Panel on Climate Change 2007). In recent years, evidence has grown that climate variation can impact the biodiversity, structure and functioning of marine ecosystems (Beaugrand *et al.* 2002; Drinkwater *et al.* 2003; Edwards & Richardson 2004; Ottersen *et al.* 2004). Many significant covariations between changes in climate and in the abundance of marine species, ranging from plankton to fish to seabirds, have been reported (Aebischer *et al.* 1990; Beaugrand & Reid 2003). Latitudinal or biogeographical shifts have been identified and interpreted as reflecting the response of the ecosystems to rising temperature (Beaugrand *et al.* 2002; Perry *et al.* 2005). Some works have suggested that climate may also modify the timing of important developmental and behavioural events of organisms (Edwards & Richardson 2004). Such phenological shifts have been detected for some planktonic groups in the North Sea (Edwards & Richardson 2004). Generally, biological changes are species-dependent (Beaugrand *et al.* 2002; Edwards & Richardson 2004), which can involve community reassembly in time and space (Parmesan & Matthews 2006). Community reassembly is thought to be among the most worrisome consequences of climate change on ecosystems (Parmesan & Matthews 2006) because this process may unbalance the trophodynamics of ecosystems, having the potential to involve trophic mismatch or to perturb prey–predator relationships (Beaugrand *et al.* 2003; Edwards & Richardson 2004). In some regions, climate variation has been at the origin of large-scale abrupt

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ecosystem shifts (Hare & Mantua 2000; Reid *et al.* 2001; Beaugrand *et al.* 2002). Such phenomena, also called regime shifts (Hare & Mantua 2000; Reid *et al.* 2001), are characterized by a sudden and substantial change in the state of an ecosystem (Scheffer *et al.* 2001) and involve major biological modifications such as those documented above, often with implications for exploited resources (Cury *et al.* 2003). These phenomena remain generally poorly understood, and some abrupt changes (e.g. the North Pacific Ocean (Hare & Mantua 2000) and the North Sea (Reid *et al.* 2001)) have only been reported years or decades after they had actually occurred (Hare & Mantua 2000; Reid *et al.* 2001). It is likely that climate change will intensify the frequency of these phenomena (Beaugrand 2004b). However, climate also interacts with anthropogenic forces such as fishing (Cury *et al.* 2003), which has also been involved in abrupt ecosystem shifts (Frank *et al.* 2005). Some important effects of overfishing include depletion of spawning stock biomass and truncation of the age–size structure of stocks (Hsieh *et al.* 2006). These effects tend to concentrate the reproduction in time and space and reduce the quantity and the quality of eggs, which in turn decrease the resilience of stocks to environmental variability (Cury *et al.* 2003). In extreme cases, fishing makes the population dynamics almost exclusively driven by fluctuations in recruitment, which is likely to increase sensitivity of the stocks to climate variability (Hsieh *et al.* 2006). Climate and fishing interactions remain difficult to disentangle and quantify in space and time making it difficult to generalize across systems. In this report, using a new technique based on the estimation of the local variance, we first identify a large-scale ecological threshold in the North Atlantic influenced by the temperature regime and at the origin of pronounced biological changes seen across multiple trophic levels (phytoplankton to zooplankton to the Atlantic cod). Then, we investigate the long-term decadal changes in the location of this boundary and show the link between the long-term changes in its location and a major and well-documented ecosystem shift in the North Sea. We suggest that this threshold, mediated by the temperature regime, provides an improved understanding on phenomena at the origin of climate-driven ecosystem shifts. The possible link between spatial changes in the large-scale ecological threshold and other documented ecosystem shifts is also discussed. These results allow us to predict the likely location and timing of future prominent ecosystem changes (and associated shifts in the carrying capacity of the ecosystem and in cod recruitment) in the North Atlantic. In this study, climate change refers to any change in climate either due to natural variability or as a result of human activity (Intergovernmental Panel on Climate Change 2007). Marine ecosystems may already be responding to global warming, but they will do in a complex manner through existing hydro-climatic channels such as the North Atlantic Oscillation (NAO).

MATERIALS AND METHODS

Biological and physical data

Phytoplankton data

We used upper-ocean chlorophyll concentration as an indicator of the carrying capacity of the ecosystem (Longhurst 1998). This parameter has been extensively used by Longhurst (1998) to divide the marine biosphere into biomes and provinces. Data come from a monthly climatology (1997–2006) derived from the project and satellite SeaWIFS (Sea-viewing Wide Field-of-view Sensor; http://oceancolor.gsfc.nasa.gov). When long-term changes were investigated (1958–2005), we used instead the Phytoplankton Colour Index (PCI). This parameter was assessed by the Continuous Plankton Recorder (CPR) survey, an upper layer plankton community monitoring programme that has been operated on a routine monthly basis in the North Atlantic and in the North Sea since 1946 (Reid *et al.* 2003). A recent study has shown that PCI covaries well with satellite-based upper-ocean chlorophyll concentration (Raitsos *et al.* 2005).

Zooplankton data

Zooplankton data also originated from the CPR survey (1958–2005). We focussed on diversity and mean size of calanoid copepods. Both diversity and mean size of organisms are key properties of a pelagic ecosystem (Longhurst 1998; Beaugrand 2005). The parameters distinguish well different types of pelagic ecosystems and can potentially be used as indicators to detect a biogeographical shift (Beaugrand 2005). Both descriptors inform on the state of the ecosystem and the way it works (Brown *et al.* 2004). We assessed these two functional attributes for calanoid copepods because this group is well sampled by the CPR survey and taxonomic identification goes to the species level (Beaugrand *et al.* 2003). Diversity of calanoid copepods was assessed by the Gini coefficient (Lande 1996). It corresponds to the probability that two randomly chosen individuals from a given community are different species. It has been demonstrated that a non-biased estimator exists for this index (Lande 1996). We chose the minimum size of female as adult females or copepodite stage V to represent the majority of copepods caught in the samples (Beaugrand *et al.* 2003).

Plankton community structure in the North Sea

The CPR survey has monitored more than 400 plankton species or taxa (phytoplankton and zooplankton) since 1958 on a monthly basis. We also used this information to characterize plankton ecosystem changes that occurred in the North Sea during the period 1958–2005. We extend the index on copepod community structure proposed by (Beaugrand 2004b) to the whole plankton. An annual mean was calculated for all species or taxonomic groups using the procedure described in (Beaugrand 2004a). Then, species or taxonomic groups with an annual relative abundance > 0.001 and a presence $> 30\%$ for all years of the period 1958–2005 were selected, following the procedure described in Ibañez & Dauvin (1988). This procedure allowed the selection of 115 species or taxonomic groups (50 diatom species, 23 dinoflagellates species, 22 copepod species and 20 other zooplankton taxa including fish eggs and larvae). Abundance data in the matrix (48 years × 115 species or taxonomic group) were transformed using the function $\log_{10}(x + 1)$. Then, a principal component analysis (PCA) was performed on the correlation matrix (115 × 115 species) to identify the main pattern of long-term changes in plankton community structure (examination of principal components). We retained the first principal component as an index of plankton community structure change for the period 1958–2005.

Probability of cod occurrence and long-term changes in Atlantic cod recruitment (age 1)

To examine potential consequences of plankton changes on higher trophic levels, we selected data on the Atlantic cod (*Gadus morhua* L.). This important species is well represented in the spatial domain covered by the CPR survey and a large amount of information exists for it. We selected the species because previous studies suggest that the annual recruitment of the Atlantic cod could be linked to plankton changes, either directly through prey–predator interaction during the larval stage (Beaugrand *et al.* 2003) or indirectly if our plankton indicators reflect more than changes in plankton ecosystems. Many studies have recently provided compelling evidence of a tight benthic–pelagic coupling (e.g. Beaugrand *et al.* 2003; Frank *et al.* 2005). To the best of our knowledge, this test of a link between the Atlantic cod and plankton has not been attempted at ocean basin scale. Data of probability of cod occurrence was taken from Fishbase (http://www.fishbase.org). Probability data of cod occurrence originated from a relative habitat suitability model initially developed for mapping mammal species distribution (Kaschner *et al.* 2006) and then adapted to map the probability of occurrence of all marine organisms. A total of 62 160 data points were used to produce the probability map. No distinction was made on age but data reflect mainly the occurrence of cod ≥ 1 year (http://www.fishbase.org). Data on cod recruitment (at age 1) for the period 1963–2005 were derived from virtual population analysis and obtained from http://www.ices.dk. These data were used to examine the impact of changes in the spatial location of the large-scale ecological boundary on the North Sea ecosystem state.

Sea surface temperature

Observed sea surface temperature (SST) data (1960–2005) were extracted from the database International Comprehensive Ocean-Atmosphere Data Set (ICOADS, longitudes with a spatial resolution of 1° longitude × 1° latitude; http://icoads.noaa.gov; Woodruff *et al.* 1987). We also used ICOADS SST data with a spatial resolution of 2° longitude × 2° latitude to cover the period 1958–2005 in the North Sea.

To assess the potential impact of changes in SST on North Atlantic plankton ecosystems, data (1990–2100) from the ECHAM 4 (EC for European Centre and HAM for Hambourg) model were used. This Atmosphere-Ocean General Circulation Model (AOGCM) has a horizontal resolution of 2.8° latitude and 2.8° longitude (Roeckner *et al.* 1996). The present data were selected by the Intergovernmental Panel on Climate Change based on criteria among which are physical plausibility and consistency with global projections. Data are projections of monthly skin temperature equivalent above the sea to SST (http://ipcc-ddc.cru.uea.ac.uk). Data used here are modelled data based on scenario A2 (concentration of carbon dioxide of 856 ppmv by 2100) and B2 (concentration of carbon dioxide of 621 ppmv by 2100) (Intergovernmental Panel on Climate Change 2007). Scenario A2 supposes an increase of CO_2 with a rate similar to what is currently observed. In scenarios A2 and B2, the world population reaches 15.1 and 10.4 billion people by 2100 respectively (Intergovernmental Panel on Climate Change 2007). Data are projections of monthly skin temperature equivalent above the sea to SST (http://ipcc-ddc.cru.uea.ac.uk).

Oxygen data

Dissolved oxygen data (in mL L^{-1}) were obtained from the World Ocean Atlas (2001). This monthly climatology has a spatial resolution of 1° longitude × 1° latitude.

Analyses of the data

Analysis 1: spatial interpolation of biological data

An annual climatology was calculated for upper-ocean chlorophyll concentration (1997–2006), diversity and mean size of calanoid copepods (1958–2005), probability of cod occurrence and all environmental parameters (SST; 1960–2005). Spatial interpolation of the data was used to create a common spatial grid for all biological and physical parameters. We used the inverse squared distance interpolation technique (Beaugrand *et al.* 2002). The spatial grid (from 99.5 °W to 19.5 ° E and from 30.5 ° to 69.5 °N) had a spatial resolution of 1° latitude × 1° longitude. These data were used to evaluate how upper-ocean chlorophyll concentration, mean size and diversity of calanoid copepods and probability of cod occurrence change as a function of SST (Fig. 1).

Analysis 2: assessment of the local variance of biological parameters as a function of temperature or time

The magnitude of biological changes was assessed by calculating the local variance of biological parameters as a

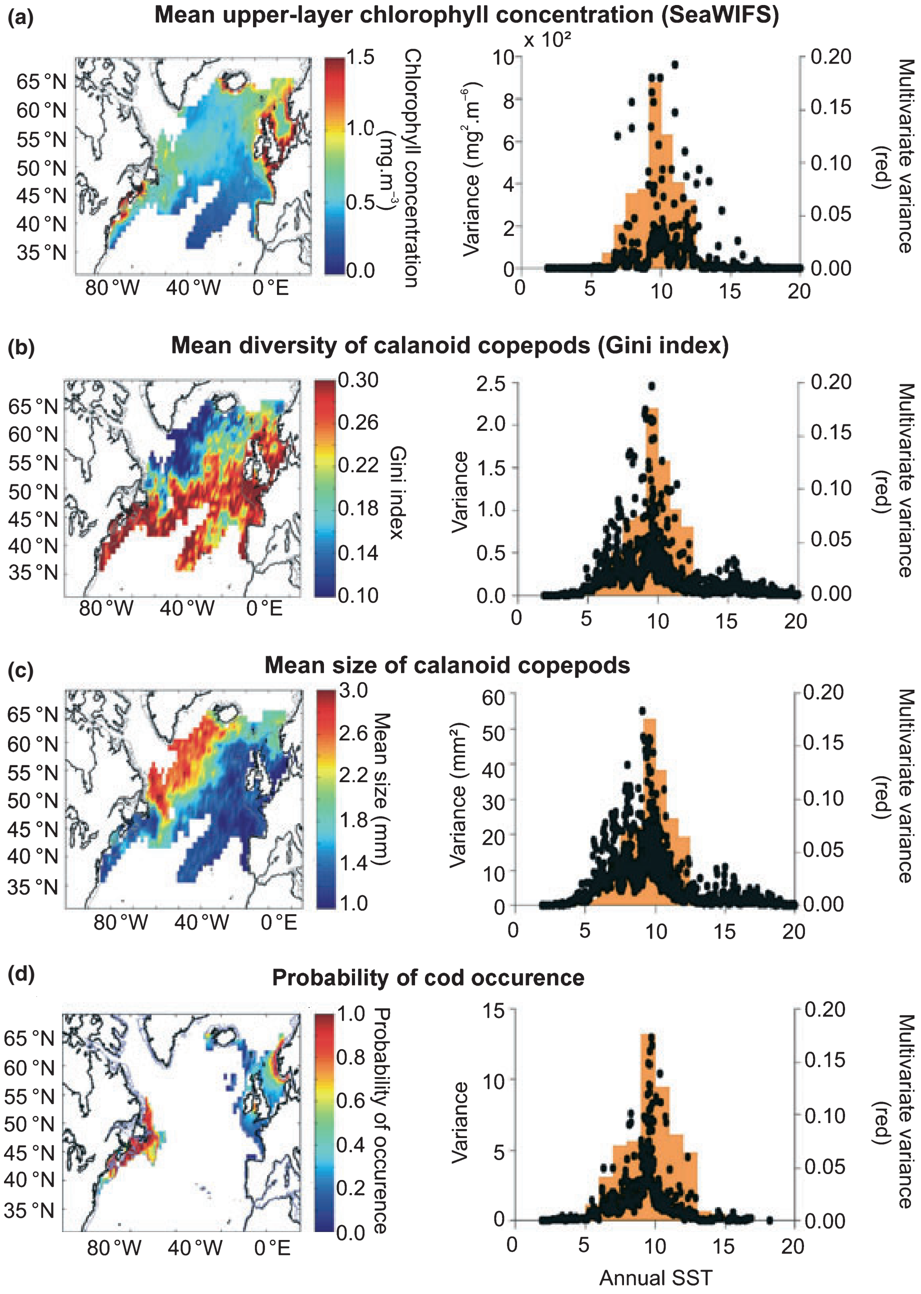

Figure 1 Climatological annual mean distribution of upper-ocean chlorophyll concentration as measured by SeaWIFS (a, left; 1997–2006); diversity (Gini index; 1958–2005) of calanoid copepods as measured by the CPR survey (b, left); mean size of female calanoid copepods (c, left; 1958–2005), mean probability of cod occurrence (d, left) and the local variance of these biological parameters as a function of sea surface temperature (right). Each point denotes a geographical pixel on the map. High values of local biological variance are mainly detected between 9 and 12 °C with a maximum between 9 and 10 °C, indicating substantial variability in these functional attributes in regions with a temperature regime of 9–10 °C. Red bars, showing the assessment of the (multivariate) variance when all three indicators are combined, confirmed that high values of variance are located between 9 and 10 °C. Grey lines denote the isobath 200 m.

function of SST (Fig. 1) or time (Fig. 3). We used a technique that we derived from the method of point cumulative semi-variogram (PCSV) proposed by Sen (1998) and recently applied and tested in the marine realm by Beaugrand & Ibañez (2002). Let $\mathbf{X}(m,p)$ be a matrix with m observations and p biological variables and $\mathbf{Y}(m,1)$ the vector of SST or time corresponding to the m observations of $\mathbf{X}$. When $P = 1$ (univariate case), the PCSV $\gamma(i)$ of $\mathbf{X}(m,1)$ at observation i ($1 \leq i \leq m$) can be calculated as follows (Sen 1998):

$$\gamma_{(i)} = \frac{1}{2}\sum_{j=1}^{m-1}\left(x_i - x_j\right)^2, \tag{1}$$

where x_i the value of $\mathbf{X}$ at observation i and x_j the value of $\mathbf{X}$ corresponding to the jth observation ($1 \leq j \leq m - 1$). In the multivariate case ($P > 1$), the p variables of the matrix $\mathbf{X}_{(m,p)}$ are first scaled to unit 1 by scaling normalization by means of the Pythagoras formula (Legendre & Legendre 1998). Each vector (variable) in $\mathbf{X}$ has a length of one and therefore contributes equally to the assessment of the local variance. We calculated the PCSV $\gamma(i)$ in the multivariate case as follows:

$$\gamma_{(i)} = \frac{1}{2}\sum_{j=1}^{m-1}\sum_{k=1}^{p}\left(x_{i,k} - x_{j,k}\right)^2, \tag{2}$$

where $x_{i,k}$ the value of the kth variable of $\mathbf{X}$ ($1 \leq k \leq p$) at observation i and $x_{j,k}$ the value of the kth variable of $\mathbf{X}$ corresponding to the jth observation ($1 \leq j \leq m - 1$). In the uni- and multivariate cases, eqn 1 or 2 leads to a matrix $\Gamma_{(m-1,m)}$ that encompasses the half-squared differences between all biological values. Simple measures of distance can then be utilized to evaluate how the local variance of $\mathbf{X}_{(m,p)}$ increased with the distance from observation i. The distance between an interval (i and j) of the physical variable or time was calculated identically in the uni- and multivariate cases:

$$d_{(i)} = \sum_{j=1}^{m-1}\left|y_i - y_j\right|, \tag{3}$$

where y_i the value of $\mathbf{Y}$ at observation i and y_j the jth value of $\mathbf{Y}$. This step leads to a matrix $\mathbf{D}_{(m-1,m)}$. Then, each column of $\mathbf{D}$ is sorted by increasing order and the corresponding variances in Γ are rearranged. For each column, variance $\gamma(i)$ of the sorted matrix Γ are progressively pooled and the cumulated local variance of $\mathbf{X}$ can be plotted as a function of the distance from observation i (Beaugrand & Ibañez 2002). Each column of the sorted and cumulated variance matrix $\Gamma^*_{(m-1,m)}$ represents a PCSV, and there are therefore as many local assessments of the variance of x as values of $\mathbf{Y}$. This analysis allows an examination of the local behaviour of the biological variable(s) $\mathbf{X}_{(m,p)}$ around observation i of the physical variable (or time). Finally, fixing a value of distance (i.e. temperature change or time difference) allows the determination of a value of local variance at observation i. It then becomes possible to plot and examine the local variance of the biological parameter(s) as a function of SST or time. In this study, all analyses were carried out by considering a difference threshold of ±0.2 °C of SST change when temperature data were used (Fig. 1) and a difference threshold of ±5 years when calculation was based on time (Fig. 3b). An average of values of variance was calculated for each degree of temperature change or each year when the analysis was based on time. If the response of the biology to change in temperature is linear, the variance should remain constant. However, if the response is nonlinear, a pronounced increase in variance allows shift or bifurcation points to be detected.

Analysis 3: mapping of changes in SST

Mean annual SST were mapped for each decade from 1960 to 1999, for the period 2000–2005 and for the period 2090–2099 to see how the ecological boundary changed from 1960 onwards and where it is expected to be located if temperature changes follow a scenario B2 (Fig. 2).

Analysis 4: long-term changes in ecosystem state and variability

A PCA was applied on the matrix 'Years (1958–2005)' × '5 ecosystem indicators' using the CPR PCI, the diversity and mean size of calanoid copepods, cod recruitments data and the index of plankton ecosystem structure to examine long-term changes in the ecosystem state in the North Sea (Fig. 3). The local variance (see Analysis 2, univariate case) was calculated directly on the first principal component to examine long-term changes in ecosystem variability.

Analysis 5: SST changes in the Eastern Scotian Shelf and the Baltic Sea

We examine the mean annual SST changes in two regions [the Eastern Scotian Shelf (Frank *et al.* 2005); the Baltic Sea (Alheit *et al.* 2005)] where ecosystem shifts have been documented (Fig. 4). We calculated the average of annual SST for two periods 1960–1979 and 1990–2005 (before and after the shifts) and the difference of mean annual SST between 1990–2005 and 1960–1979.

Analysis 6: projection of temperature changes (scenarios A2 and B2)

We used ECHAM 4 data (scenarios A2 and B2) to determine the year when the temperature regime becomes > 10 °C (Fig. 5). The threshold of 10 °C was selected because it corresponds to the establishment of the Atlantic Westerly Winds Biome. Prior to the mapping, we spatially reinterpolated the data, which were originally on 2.8° longitude × 2.8° latitude, on a grid of 1° longitude × 1° latitude.

When correlation was calculated between time series, the probability of the correlation coefficient was corrected by

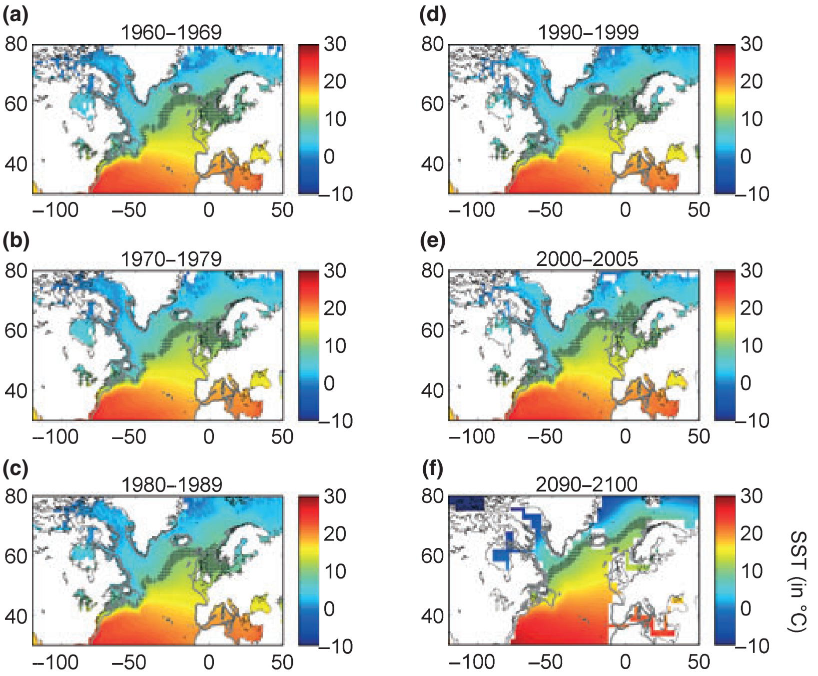

Figure 2 Decadal changes in sea surface temperature and in the isotherm 9–10 °C (observed and projected). Observed mean annual sea surface temperature in the North Atlantic Ocean in the 1960s (a), 1970s (b), 1980s (c), 1990s (d), the period 2000–2005 (e) and projected mean annual sea surface temperature for the 2090s using scenario B2 (f). The use of scenario A2 gave similar results to scenario B2 and is not shown here (Fig. 4). The location of the critical thermal boundary (9–10 °C) is indicated by '+'.

adjusting the degree of freedom to consider temporal autocorrelation (Beaugrand & Reid 2003).

RESULTS AND DISCUSSION

We focussed on the relationships between biological variance, sea temperature and time in the North Atlantic Ocean and its adjacent seas. The variance of a population/system has been used in ecology in the past as a measure of 'temporal stability' and more recently as an indicator of an approaching major phase transition (Carpenter & Brock 2006). We assessed changes in the (local) variance of upper-ocean chlorophyll concentration (as measured by SeaWIFS), both diversity and mean size of calanoid copepods, a taxonomic group well monitored by the CPR survey and probability of cod occurrence derived from an habitat model (Kaschner *et al.* 2006) as a function of mean annual SST (Analysis 2). The plankton parameters are key indicators of a biome (Longhurst 1998) and some of them (diversity and mean size) covaried significantly to long-term changes in cod recruitment in the North Sea (Beaugrand 2003; Beaugrand *et al.* 2003). We found a pronounced nonlinearity in the response of all four biological parameters to temperature (Fig. 1), showing high local biological variance at temperatures (i.e. annual mean of SST) in the range from 9 to 12 °C with a maximum located between 9 and 10 °C. The zone of high variability is a bit larger for chlorophyll concentration because of a secondary relationships between this indicator and both the bathymetry and the proximity to the coasts. It is notable that we found the same critical thermal boundary for chlorophyll concentration (SeaWIFS), diversity and size of calanoids as well as probability of cod occurrence, data encompassing three different trophic levels and of different origin. Our results indicate that the sensitivity of ecosystems to temperature change depends on whether they are close to the critical thermal boundary of 9–10 °C, which represents a large-scale ecological threshold in the North Atlantic Ocean.

The critical thermal boundary coincided with the transitional region between the Atlantic Polar and the Atlantic Westerly Winds biome (Longhurst 1998; Fig. 2a). These results indicate that the southern edge of the spatial distribution of cod is linked to the position of the boundary between the Atlantic Polar Biome and the Atlantic Westerly Winds Biome (Longhurst 1998). The concomitant increase in variance between 9 and 10 °C of plankton indicators and cod shows that the cod distribution is tightly coupled with a system characterized by higher concentration in chlorophyll, lower diversity but copepods of greater size and obviously annual SST lower than 10 °C. Our study cannot definitively conclude on the mechanisms at work. However, three hypotheses can be formulated. First, the impact of plankton might happen through biological interactions during the larval stage (Cushing 1997; Beaugrand *et al.* 2003). Second, the plankton parameters we used might be indicators of the whole ecosystem. Indeed, strong benthic–pelagic coupling has been suggested in some ecosystems of the North Atlantic [the Eastern Scotian Shelf (Frank *et al.* 2005); the North Sea (Kirby *et al.* 2007)]. For example, the abrupt ecosystem shift reported in the North Sea has been detected

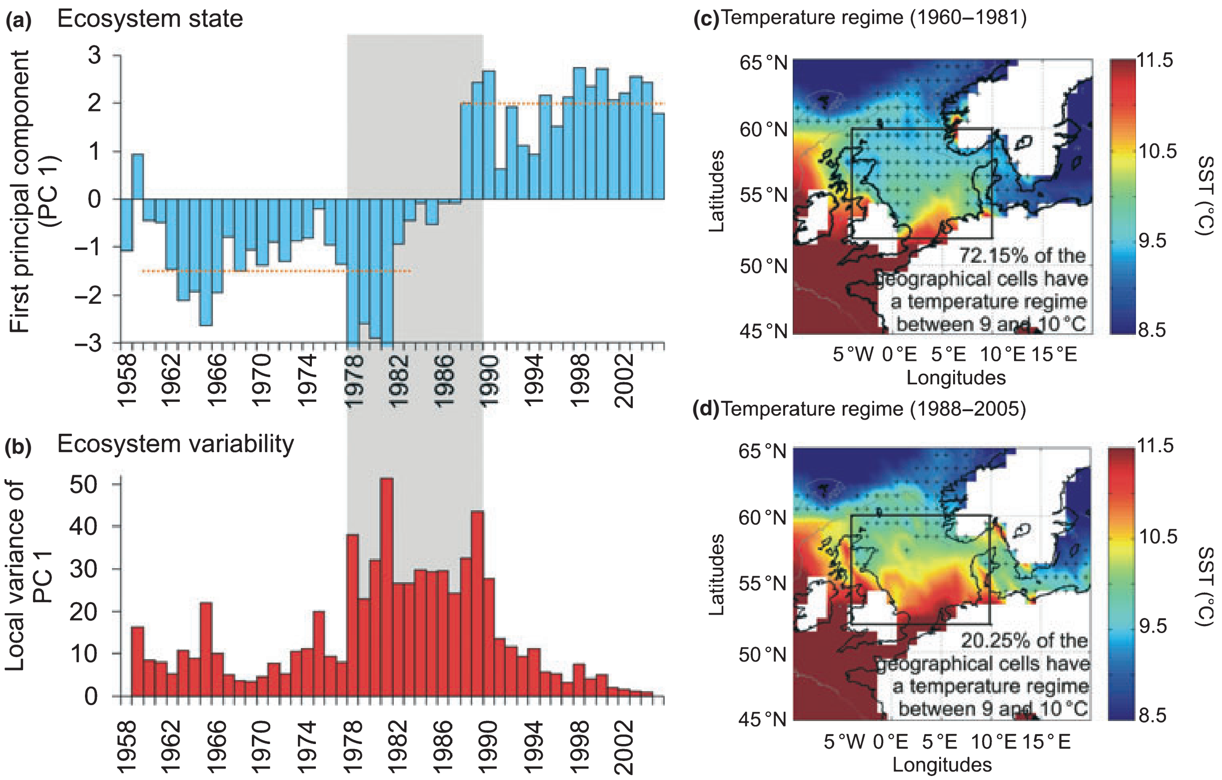

Figure 3 (a) Long-term changes in the state of the ecosystem (in blue, first principal component, 65.24% of the total variance) calculated by applying a PCA on five biological parameters [phytoplankton colour index: correlation *r* with first principal component: 0.91; mean size of calanoids: *r* = 0.84; mean calanoid diversity (Gini index): 0.82; plankton change index: 0.76; cod recruitment: −0.69]. (b) Long-term changes in ecosystem variability (in red). The light grey rectangle shows the unstable period (1980–1989). (c) Observed mean annual sea surface temperature in the North Sea during 1960–1981. (d) Observed mean annual sea surface temperature in the North Sea during 1988–2005. The location of the critical thermal boundary (9–10 °C) is indicated by '+'. The periods 1960–1981 and 1988–2005 were selected on the basis of Fig. 3a,b.

in both pelagic and benthic ecosystems (Kroncke *et al.* 1998; Reid *et al.* 2001). Using a large number of both biological (benthic and pelagic organisms) and physical parameters, Weijerman *et al.* (2005) also found a clear indication of a regime shift in the North Sea. Third, as already stated, our plankton parameters are good indicators of the ecosystem state and have quite different value in the Atlantic Westerly Winds and Atlantic Arctic biomes. It is possible that no direct functional link exists between our plankton indicators and cod. However, the results are interesting because they reflect on the capacity of the system to support the fish. If the boundary moves northwards with climate warming, it is likely that the cod will have to move northwards. Such a pattern of change has been detected in the North Sea (Perry *et al.* 2005; Rindorf & Lewy 2006) and likely mechanisms proposed (Beaugrand *et al.* 2003). However, a debate remains on whether the species will be able to acclimatize or whether variability in prey has implications for survival at the larval stage (e.g. Brander *et al.* 2006; Neat & Righton 2007).

Our analysis revealed that biome boundaries are highly sensitive to climate change and that a climate-driven modification in their geographical locations may be at the origin of pronounced ecosystem shifts. Examination of the long-term changes in its position showed a northward shift with a rate of propagation more rapid in the north-eastern side of the Atlantic, especially in the North Sea (Fig. 2a–e). Using forecast temperature data from the coupled AOGCM ECHAM 4, the critical thermal boundary could move northwards up to 10° in latitude by 2100 (Fig. 2f). The threshold coincides with the maximum upper lethal temperature of polar species (Peck & Conway 2000). For example, the upper critical temperature limit of the Antarctic eelpout (*Pachycara brachycephalum*) is *c.* 9 °C (Dick van *et al.* 1999). Heat-induced hyperglycaemia was observed in this species at both temperatures of 9 and 10 °C. The cause invoked by the authors to explain final death was a respiratory possibly associated with a circulation failure. Our results therefore indicate a possible link between the critical thermal boundary detected at a macroecological scale and

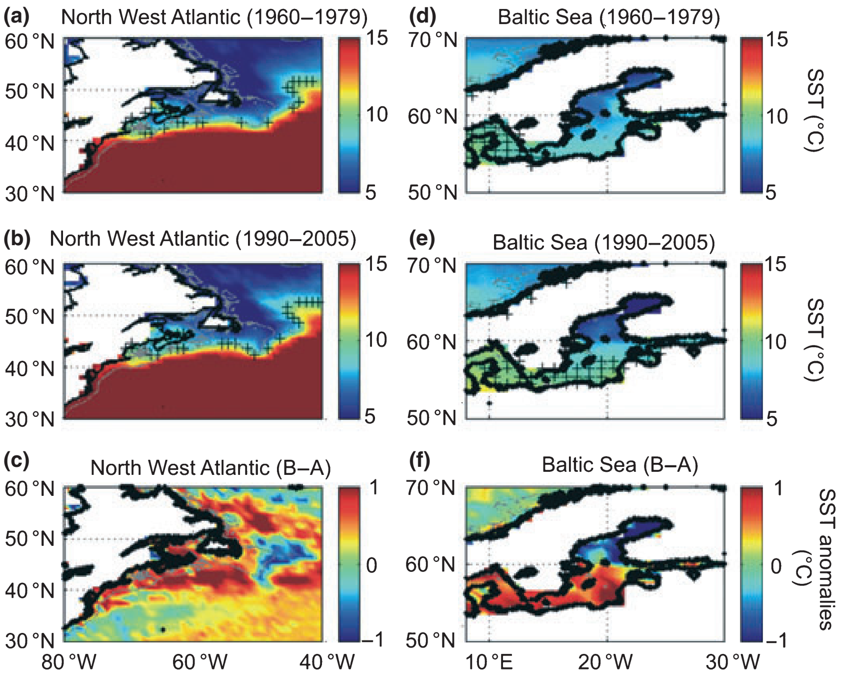

Figure 4 Long-term changes in sea surface temperature over the North West Atlantic and the Baltic Sea, regions where regime shifts have been reported. Mean sea surface temperature over the North West Atlantic for the period 1960–1979 (a) and 1990–2005 (b). The differences between these periods are indicated in (c). Mean sea surface temperature over the Baltic Sea for the period 1960–1979 (d) and 1990–2005 (e). The differences between these periods are indicated in (f). Red colour denotes an increase in temperature and blue colour a decrease. Note that temperature anomalies are concentrated along the critical thermal boundary. Grey lines denote the isobath 200 m. The location of the critical thermal boundary (9–10 °C) is indicated by '+'.

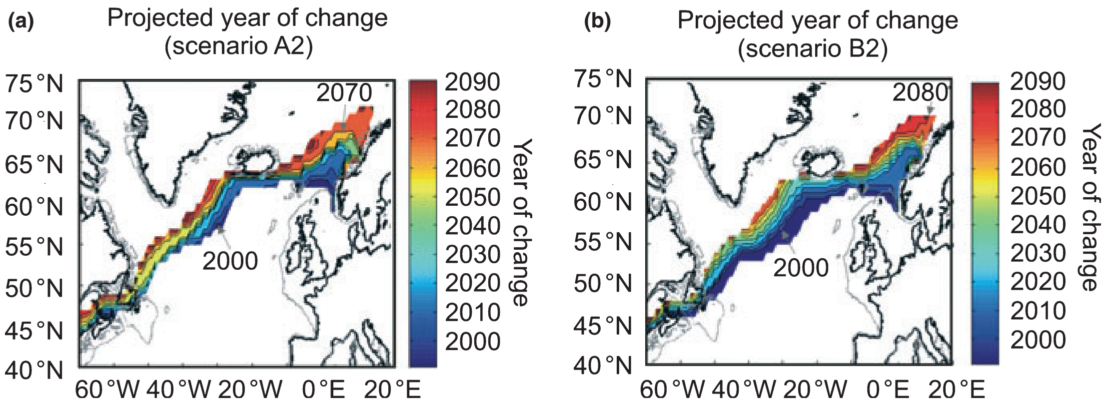

Figure 5 Projected changes in the isotherm 9–10 °C in the North Atlantic. (a) Projected year when sea surface temperature becomes > 10 °C using scenario A2. (b) Projected year when sea surface temperature becomes > 10 °C using scenario B2. The threshold of 10 °C was selected because it corresponds to the establishment of the Atlantic Westerly Winds Biome.

limits detected at the physiological level. Recent studies have demonstrated that thermal constraints exist on oxygen transport (Peck & Conway 2000; Pörtner & Knust 2007). Spatial changes in annual mean SST and surface oxygen concentration are evidently related negatively ($r = -0.98$; $P < 0.0001$; $n = 37055$ using data from a grid of 1° × 1° for the whole of the oceanic hydrosphere). Given the excellent relationships between mean annual SST and mean annual concentration in oxygen, the critical thermal boundary detected between 9 and 10 °C means that substantial changes in the ecosystem state arise when a concentration of oxygen of between 6.45 and 6.60 mg L^{-1} is crossed (Fig. S1). The ecological threshold we identified could reflect an abrupt change in oxygen limitation, which could impact organism physiology through mechanisms such as the capacity of organisms to perform aerobically (Pörtner & Knust 2007).

Annual wind intensity, mainly driven by the North Atlantic Oscillation (Dickson *et al.* 1996), increased from the beginning of the 1980s, reinforced in the 1990s and then decreased from 2000 onwards (Fig. S2). This increase in wind intensity, with a strong positive meridional component (west-southwesterly wind), is likely to have amplified the progression of the critical thermal boundary polewards in the north-eastern part of the North Atlantic and may have well contributed to the northward biogeographical movements of some planktonic groups reported in this region (Beaugrand *et al.* 2002). The smaller changes observed in the western side are probably related to greater hydrological forcing (Krauss *et al.* 1990) and weaker and westerly winds, thereby limiting northward advection over the Canadian shelf.

The North Sea is among the most biologically productive ecosystems in the world and supports important fisheries (Reid & Edwards 2001). Major changes, called regime shift (Reid *et al.* 2001), have been reported in this region (Beaugrand 2004b). We examined whether the large-scale northward movements in the location of the critical thermal boundary (Fig. 2) could be at the origin of the shift. We compiled data from the CPR survey for the period 1958–2005 using for the first time all available species or taxonomic groups. An index of the ecosystem state was created by applying a standardized PCA on five biological parameters [index of the plankton community structure (first principal component, representing a significant part of total variance of 18.95%, from a PCA performed on 115 plankton species, see Supplementary material), mean size and diversity of calanoids, PCI, cod recruitment at age 1, Fig. S3] for the period 1958–2005 (Fig. 3a). This analysis combined with the assessment of local temporal variance of the first principal component revealed that the 1980s is overall a period of high variability (Fig. 3b). All five biological parameters considered in the analysis were highly correlated to the first principal component (PCI: correlation r with first principal component: 0.91; mean size of calanoids: $r = 0.84$; mean calanoid diversity (Gini index): 0.82; plankton change index: 0.76; cod recruitment: −0.69; $P < 0.05$ for all parameters after adjusting for temporal autocorrelation), explaining 65.24% of the total variance. Changes in the ecosystem state and variability coincided with the northward shift in the biome boundary linked to temperature changes (Fig. 3c–d, Fig. S4). It is important to remember that the northward shift has probably been exacerbated by the increase in west-southwesterly winds linked to a prolonged positive phase of the North Atlantic Oscillation. As expected, the coefficient of variation (CV) of the first principal component (index of the ecosystem state representing 18% of the total variance, see Fig. 3c) for the first period (1960–1981; CV = 36.98%) was greater than during the second period (1988–2005; CV = 10.26%) and this despite the higher variability in the temperature regime in 1988–2005 (mean annual SST = 9.86 °C and CV in annual SST = 3.33% for 1960–1981 and mean annual SST = 10.50 °C and CV in annual SST = 3.86% for 1988–2005).

It is interesting to note that the critical thermal boundary links two other regions (the Baltic Sea and the North West Atlantic) where abrupt ecosystem shifts have been reported (Alheit *et al.* 2005; Frank *et al.* 2005). Strong increases in temperature were detected in the two regions (Fig. 4, Fig. S5). The pronounced change in the dynamic regime of the Eastern Scotian Shelf ecosystem (and adjacent systems) has been primarily driven by overfishing but it has also been suggested that climate could have played a role (Frank *et al.* 2005). No such ecosystem shift has been reported in other regions covered by this study, which seems to indicate that shifts are likely to occur over vulnerability hot spots (regional discontinuities characterized by high biological variance) represented here by the isotherm 9–10 °C. The Southern Gulf of St Lawrence, Grand Banks and Flemish Cap are also crossed by the critical thermal boundary. Although we present evidence for the effect of the boundary shift on ecosystems and on cod populations, there are of course many areas in which this explanation does not apply. Cod populations have declined in most areas due to fishing pressure and where they have also been subject to adverse environmental change (e.g. West Greenland, South Labrador; Brander *et al.* 2006), the populations collapsed, which may have resulted in increases in their prey populations and in major ecosystem changes. We did not evaluate the impact of fishing on cod. Future work could use the proposed technique to identify and quantify potential tipping point, which might differ from a region to another depending upon the carrying capacity of the ecosystem. In this study, we think we provide compelling evidence to explain ecosystem shifts associated with the movement of a biogeographical boundary represented by the isotherm of 9–10 °C and mediated by climate, not changes related fishing pressure or the direct effects of adverse environmental changes on cod.

We believe that ecosystem changes observed in this study are mainly related to temperatures as this is the only parameter that links the western to the eastern part of the North Atlantic, the North Sea and the Baltic Sea. However, the critical thermal boundary found in this study is a proxy for many environmental conditions. For example, annual mean and seasonal variability (assessed here by the calculation of the CV) in SST are significantly correlated negatively ($r = -0.70$, $P = 0.0003$, $n = 29\,523$; period 1960–2005 using data from a grid of 1° × 1° for the whole of the oceanic hydrosphere). Therefore, seasonal stability increases when temperature rises. Such factors are among the most important candidates to explain the ecogeographical pattern in species richness observed between the poles and the tropics (Rohde 1992). This increase in temperature (and seasonal stability) could explain the augmentation in North Sea calanoid copepod diversity observed in this study as temperature rose by *c.* 1 °C. These changes in diversity was temporally synchronous with a reduction in the mean size of copepods ($r = -0.75$, $P = 0.0021$; Fig. S2). Such modifications are expected from the large-scale distribution of these parameters (Fig. 1). The increase in diversity should not be interpreted either as an indication of an improved stability of North Sea ecosystems or being positive for ecosystem resilience but rather as an adaptation of the ecosystem to temperature rise (and less seasonality) or a fingerprint of a climate-induced biome shift.

Using ECHAM 4 modelled temperature data, we show the time from when SST is expected to become > 10 °C in the North Atlantic (i.e. when the system develops into a full temperate biome; Fig. 5a,b). Before performing the analyses, we compared observed and modelled data for the period 1990–2005 (Fig. S6). Modelled and observed data on annual SST were highly positively correlated in the area covered by this study (Fig. S5; $r = 0.95$, $P < 0.0001$, $n = 1809$), showing that the model captures relatively well the complexity of the hydro-climatic environment of the region at a decadal scale. However, it should be noted that the North Atlantic Ocean is a region where natural hydro-climatological variability is large (Keenlyside *et al.* 2008). Although the correlation between modelled and observed SST data on a year-to-year basis is also significantly high ($r = 0.93$, $P < 0.0001$, $n = 29527$) for the period of reference 1990–2005, the difference between observed and modelled SST data is greater than when averaged at a decadal scale, indicating that the projections are sensitive to large-scale natural variability at a year-to-year scale. Scenarios of changes in SST, in addition to observed sea temperature changes (Fig. 2), suggest that an increase in cod stock to pre-1980s conditions in the North Sea is extremely improbable (even with a substantial decrease in fishing pressure). This region is now well above the critical thermal boundary (Fig. 2) and recruitment is likely to remain low in comparison with other periods (e.g. the gadoid outburst) because the physiological stress related to temperature rise (e.g. increase in larval metabolism and its effect on energetic demand) has been accompanied by a reduction in the quantity and quality of prey as well as a mismatch between the timing of prey and larval occurrence (and therefore a decrease in energetic gain) (Beaugrand *et al.* 2003). The coarse spatial resolution of most AOGCM models (e.g. ECHAM 4) makes the projections of the isotherm 9–10 °C more difficult to achieve near the coast and above continental shelves. This potential caveat does not seem to affect strongly our results but it is clear that future studies will benefit from improved spatial resolution of the AOGCM models.

Abrupt shifts are expected to proliferate northwards during the next century in the south-western part of Norway (Fig. 5a,b). The boundary propagates quickly but perpendicularly to Norwegian coasts. The migration is more limited off Canadian coasts but is orientated towards the continent. This will progressively restrict cod habitat up to the South Labrador region. There, the interplay between fishing and climate is likely to be maximal. The ecosystems can exhibit local stability but are globally unstable (Begon *et al.* 2006). Overfishing in these transitional areas could precipitate collapses of fish stocks, possibly many decades before they would be expected to occur by the action of climate alone. Because of the direction of temperature change, the system is likely to be impossible to reverse once it has shifted (Scheffer *et al.* 2001). It is thereby important to adopt a precautionary approach limiting fishing mortality. This should, however, remain compatible with social and economical constraints and new management strategies, which anticipate the characteristics of the changing ecosystem, should also be prepared. Our projection of temperature changes are scenarios and should not be considered as exact prediction, but rather as general guidelines on what could happen and as an aid in conceptualizing a broad strategy on future climate and fishing interaction.

Our study shows that regions in which a biome boundary shift occurs appear to be the areas most vulnerable to climate change impacts in the North Atlantic while other regions spatially embedded deeply within a major biome can remain relatively ecologically stable over long periods. The speed and magnitude of climate warming is expected to be elevated (Intergovernmental Panel on Climate Change 2007). It will lead to abrupt ecosystem shifts and interact with fishing on exploited resources. Rising variance gives an early warning for ecosystem managers of an impending abrupt shift. Our results suggest that we should abandon the paradigm of relative stability of marine ecosystems and implement a proactive, dynamic and flexible management strategy, based on a large-scale ecosystem approach and regular monitoring (Hughes *et al.* 2005).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article.

Figure S1 Relationship between mean annual SST and the mean annual concentration in oxygen for the whole ocean.

Figure S2 Observed mean annual wind intensity and direction in the North Atlantic Ocean in the 1960–70s (a), 1980s (b), 1990s (c) and the period 2000–2005 (d).

Figure S3 Long-term biological changes in the North Sea (1958–2005).

Figure S4 Observed mean annual sea surface temperature in the North Sea for the period 1980–1989.

Figure S5 Differences in sea surface temperature and wind intensity between the 1980s and the period 1960–1979 (a, d), the 1990s and the period 1960–1979 (b, e), and the period 2000–2005 and the period 1960–1979 (c, f).

Figure S6 Relationships between annual observed (COADS) and modelled (ECHAM 4) SST for the period 1990–2005 in the North Atlantic (40–80 °N, 80 °W–30 °E).

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