

Long-term responses of North Atlantic calcifying plankton to climate change

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The global increase in atmospheric carbon dioxide concentration is potentially threatening marine biodiversity in two ways. First, carbon dioxide and other greenhouse gases accumulating in the atmosphere are causing global warming¹. Second, carbon dioxide is altering sea water chemistry, making the ocean more acidic². Although temperature has a cardinal influence on all biological processes from the molecular to the ecosystem level³, acidification might impair the process of calcification or exacerbate dissolution of calcifying organisms⁴. Here, we show however that North Atlantic calcifying plankton primarily responded to climate-induced changes in temperatures during the period 1960–2009, overriding the signal from the effects of ocean acidification. We provide evidence that foraminifers, coccolithophores, both pteropod and non-pteropod molluscs and echinoderms exhibited an abrupt shift circa 1996 at a time of a substantial increase in temperature⁵ and that some taxa exhibited a poleward movement in agreement with expected biogeographical changes under sea temperature warming^{6,7}. Although acidification may become a serious threat to marine calcifying organisms, our results suggest that over the study period the primary driver of North Atlantic calcifying plankton was oceanic temperature.

Since industrialization began, the concentration of CO₂ in the atmosphere has risen from 280 ppm to ~390 ppm (ref. 8). A significant proportion of atmospheric CO₂ has been taken up by the ocean, causing the average surface ocean pH to decrease from 8.2 to 8.1 (ref. 2). This trend will continue and modelling of future scenarios suggests surface ocean pH may drop to ~7.7 by the end of the twenty-first century⁸. Many studies based on laboratory experiments have demonstrated the potential effect of acidification on various calcifying organisms^{4,9}. As a result, some studies have started to look for the current effect of acidification on marine species or taxonomic groups¹⁰, suggesting that acidification is already affecting calcifying organisms in the field. However, calcifying organisms are also controlled by multiple factors, and among the parameters that affect plankton, temperature is perhaps the most conspicuous¹¹. Temperature influences all biological processes from the molecular to the ecosystem level³ and its effects on plankton have been extensively documented^{7,12}. Here, we examined long-term changes in the spatial distribution of various calcifying planktonic groups or species recorded by the Continuous Plankton Recorder (CPR) survey¹³ in the northeast Atlantic Ocean since 1960.

Long-term spatial changes in calcifying plankton were examined by means of standardized Principal Component Analyses (PCAs) (Methods). The main advantage of applying this technique is that

normalized eigenvectors are mapped so that correlations between the frequency of occurrence (foraminifers and coccolithophores) or the abundance (molluscs and echinoderms) of a species and the principal components can be visualized at the same time for each geographical cell of a spatial domain⁷. The analyses showed that foraminifers, coccolithophores and echinoderms all increased and that both pteropod and non-pteropod molluscs decreased substantially in many areas of the northeast Atlantic in 1960–2009 (Fig. 1). Accelerating rates of changes took place in the 1990s at a time of an abrupt ecosystem shift circa 1996 in the northeast Atlantic, identified for zooplankton, fish and seabirds¹⁴ and attributed to an increase in sea surface temperature⁵.

We subsequently used the first five eigenvectors and principal components to reconstruct the decadal changes in the spatial distribution of the six species or taxonomic groups (Fig. 2). This analysis allowed us to remove a significant part of the unexplained variance, to emphasize the spatial and temporal patterns, and to interpret long-term modifications in the first principal components in greater detail¹⁵. The pteropod mollusc *Clione limacine* (more commonly known as sea angel) showed a reduction in both spatial extent and maximum abundance (Fig. 2). The other pteropod *Limacina* spp. (known as sea butterflies) exhibited the same pattern, although a biogeographical poleward movement is observed along the European continental shelf-edge, which is similar to biogeographical shifts reported for copepods⁷. Echinoderm larvae extended their spatial distribution to the northern part of the North Sea, with an increase in average abundance in the region. The increase in echinoderm larvae has previously been noted and attributed to sea surface temperature¹⁶. Bivalve larvae exhibited a pronounced reduction in spatial extent from the 1960s to the 2000s. They are now only observed in higher abundance in the northern part of the North Sea (Fig. 2). It has been conjectured that this reduction may have been caused by a rise in the thermal regime that has either directly affected the larvae through an influence on their physiology or indirectly through trophic cascade or trophic amplification¹⁷. In particular, the increase in decapods might have unbalanced species interactions in the food web¹⁷. Foraminifers increased in frequency of occurrence in all oceanic regions covered by this study. The increase was particularly evident over the north-eastern oceanic regions (Fig. 2). Coccolithophores increased strongly in the northeast Atlantic (Fig. 2). In the Southern Ocean, recent findings also found an increase in the abundance of the coccolithophore *Emiliania huxleyi*¹⁸.

We investigated whether these biological changes originated from long-term changes in annual Sea Surface Temperature (SST), large-scale hydro-climatic forcing or changes in pH or partial

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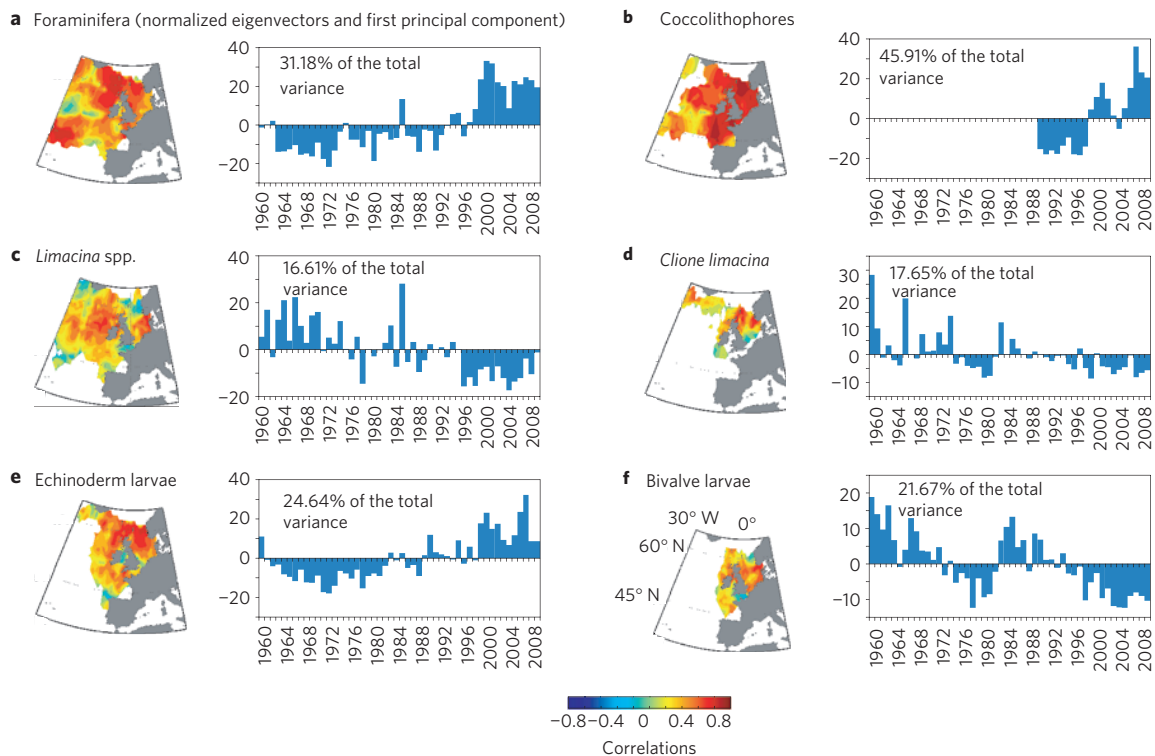


Figure 1 | Decadal changes (1960–2009) in northeast Atlantic calcifying plankton inferred from standardized PCAs. First normalized eigenvectors (left) showing the spatial pattern of correlations between changes in abundance (molluscs and echinoderms) or frequency of occurrence (foraminifers and coccolithophores) and the first principal component (right) for (a) foraminifers, (b) coccolithophores, (c) *Limacina* spp., (d) *Clione limacina*, (e) echinoderm larvae and (f) bivalves. Because all normalized eigenvectors were positively correlated to the first principal components, they directly reflected changes in the frequency of occurrence or abundance of the species or taxonomic groups. Note that the geographical domain varies from one taxon to another because some species or groups do not occur everywhere. For example, bivalve larvae are only found above the continental shelf. Although the percentage of variance explained by the first PCs varied among taxa, that is between 16.61% for *Limacina* spp. and 45.91% for coccolithophores, all values were above the equilibrium contribution¹⁹.

1 pressure in CO_2 (p_{CO_2}). Long-term changes in annual SST were
 2 examined by standardized PCA on the same region and the first
 3 two principal components were retained (Supplementary Fig. S1).
 4 Because data on pH and p_{CO_2} were not uniformly distributed in
 5 the northeast Atlantic, we could not apply the same technique.
 6 Rather, we produced a global three-month estimation of both
 7 pH and p_{CO_2} for the northeast Atlantic (Supplementary Fig.
 8 S2) and then estimated an annual average. To summarize into
 9 one single index the major changes observed in the calcifying
 10 plankton and to minimize the number of correlation analyses
 11 and their implications in term of multiple testing¹⁹, we combined
 12 all first and second PCs from the previous analyses (Figs 1 and
 13 2) and performed a standardized PCA on the resulting table 50
 14 years \times 12 variables (Fig. 3). All first PCs from each species or
 15 taxonomic groups were highly correlated to the first axis of the
 16 new standardized PCA (32.96% of the total variance); foraminifers:
 17 0.87, Echinoderms: 0.80, coccolithophores: 0.89, *Clione limacina*:
 18 -0.52 , *Limacina* spp.: -0.62 , bivalves: -0.69 . These results suggest
 19 that the first PC reflected well the major changes of all species or
 20 taxonomic groups. Long-term changes in the index of calcifying
 21 plankton changes paralleled decadal changes in annual SST (first
 22 PC) and large-scale hydro-climatic variables such as Northern
 23 Hemisphere Temperature (NHT) anomalies and the Atlantic
 24 Multidecadal Oscillation (AMO; Fig. 3 and Table 1). Significant
 25 correlations were detected between changes in calcifying plankton
 26 and changes in annual SST (first PC) in the North Atlantic, NHT
 27 anomalies and pH (Table 1). No correlation with the state of the
 28 North Atlantic Oscillation (NAO) was discovered. Examination
 29 of the results further indicates that changes in foraminifers,

Table 1 | Correlation analysis between changes in calcifying plankton (first principal component), changes in annual SST (as principal components) and large-scale hydro-climatic variables.

Hydro-climatic variables	Correlation between calcifying plankton changes and hydro-climatic variables	Probability of significance after adjusting for temporal autocorrelation
PC1 annual SST	0.84	0.034
PC2 annual SST	0.11	0.703
NHT anomalies	0.82	0.046
AMO index	0.67	0.068
NAO index	0.14	0.601
pH (1963–2009)	-0.71	0.047

Correlations with a probability <0.05 after adjusting for temporal autocorrelation are in bold. Correlation analysis was performed for the period 1960–2009 for all variables except pH (1963–2009) owing to the presence of missing data (see text).

echinoderms and coccolithophores were positively correlated to modifications in annual SST (first PC) and negatively correlated for pteropods and bivalves.

Modifications in calcifying plankton were also correlated to changes in pH (negatively for foraminifers, coccolithophores and echinoderms and positively for pteropods and bivalve larvae). Correlation between long-term changes in p_{CO_2} (Supplementary Fig. S2a) and in calcifying plankton (Fig. 3a) was positive

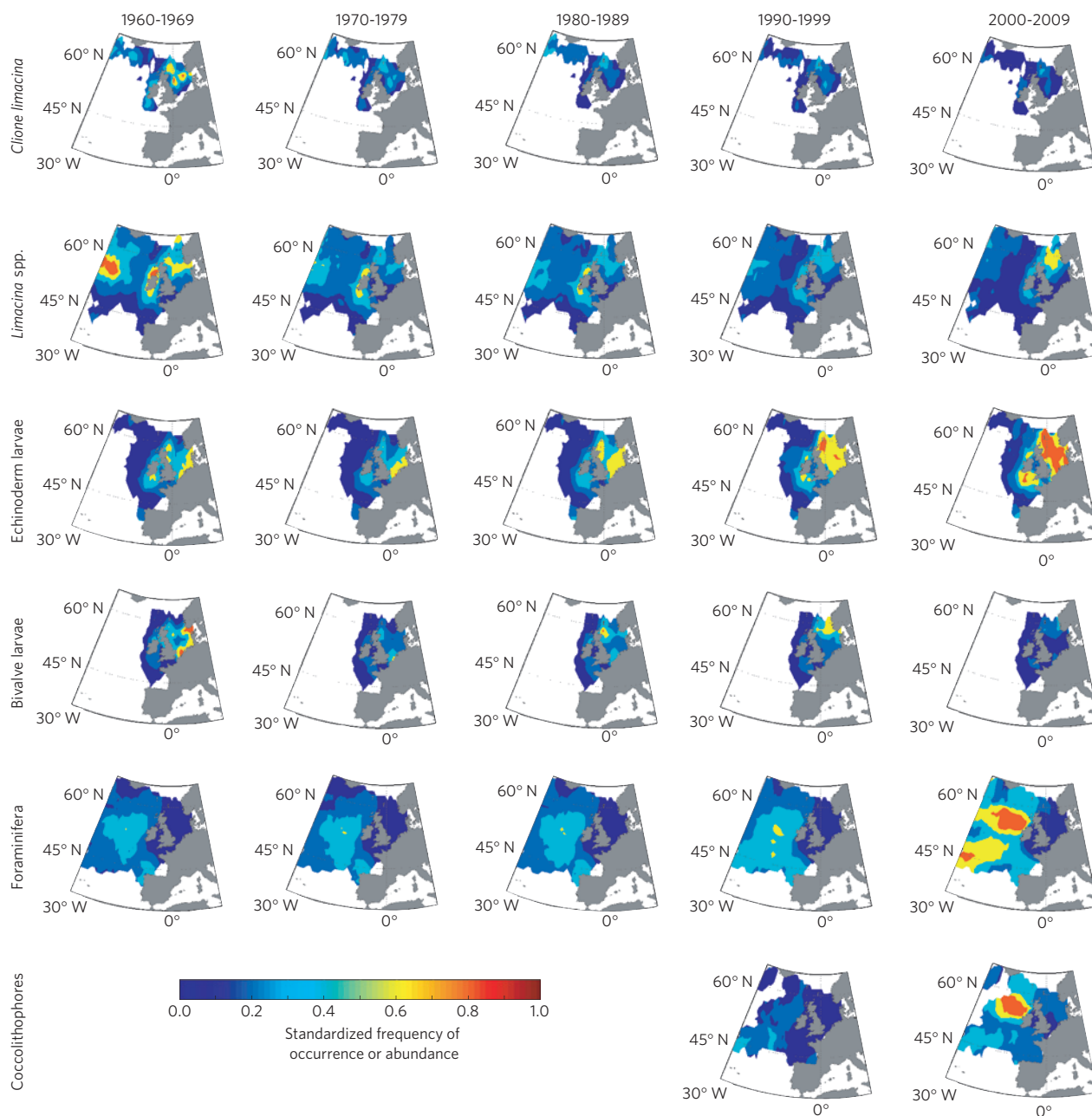


Figure 2 | Decadal changes in the modelled spatial distribution of calcifying plankton in the northeast Atlantic. The abundance or the frequency of occurrence of calcifying plankton were modelled by multiplying the first five principal components and eigenvectors calculated from standardized PCA. Frequency of occurrence (coccolithophores and foraminifers) or abundance (pteropod and non-pteropod mollusks and echinoderm larvae) were standardized between 0 and 1.

1 ($r = 0.66, p < 0.001$). However, we could not correct for temporal
 2 autocorrelation and stress that fewer years (25 years) were
 3 considered in comparison to the analysis using pH data (47 years)
 4 because the number of missing data was too large. To investigate the
 5 statistical causality of the relationship between changes in the degree
 6 of acidification, annual SSTs and our index of changes in calcifying
 7 plankton (first PC), we therefore focused on pH data, which were
 8 nevertheless correlated negatively to p_{CO_2} ($r = -0.61, p = 0.001$,
 9 25 years). The first-order partial correlation between pH and
 10 calcifying plankton (first PC), keeping the linear effect of annual
 11 SSTs (first PC) constant, was smaller ($r_{\text{pH, pk, SST}} = -0.31, p = 0.01$,
 12 1963–2009; pk, plankton; SST, first PC on annual SST) than the
 13 first-order partial correlation calculated between annual SST
 14 (first PC) and calcifying plankton (first PC) removing the linear

effect of the pH ($r_{\text{SST, pk, pH}} = 0.72, p < 0.001$, 1963–2009). These
 results suggest that annual SSTs had a more direct (statistical)
 effect on calcifying organisms than the pH (or p_{CO_2}) during the
 period 1960–2009.

Many laboratory studies have revealed the potential effect of
 ocean acidification on marine species. Pronounced acidification
 will have an influence on organism physiology (for example,
 calcification, dissolution, photosynthesis) and biology (for ex-
 ample, reproduction) with potential strong ramification at the
 community level (for example, resistance to diseases, imbalance
 of predator–prey interaction), with consequences for ecosystem
 functioning and some global biogeochemical cycles (for example,
 the oceanic carbon cycle)⁴. However, although the effects are
 clearly obvious for a high atmospheric concentration of CO_2 ,

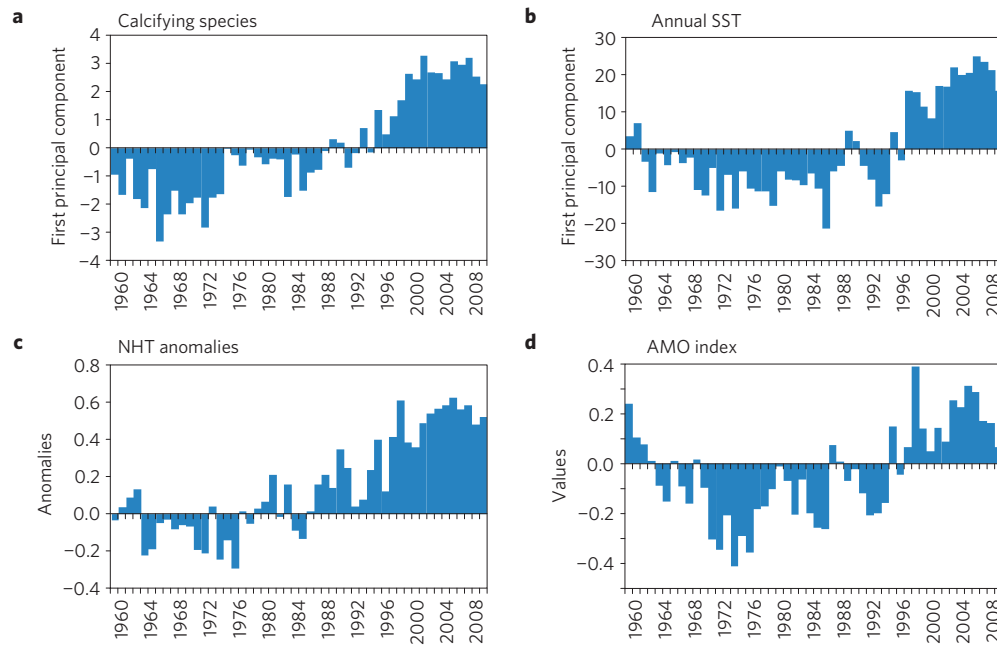


Figure 3 | Decadal changes (1960–2009) in North Atlantic calcifying plankton in relation to large-scale hydro-climatological forcing. a, Long-term changes in the first principal component reflecting the abundance or frequency of calcifying plankton. **b**, Long-term changes in annual North Atlantic SST. **c**, Long-term changes in NHT anomalies. **d**, Long-term changes in the AMO index. The index of the abundance or the frequency of calcifying plankton was calculated using a standardized PCA on the first principal components reflecting the long-term changes in foraminifers, coccolithophores, *Limacina* spp., *Clione limacina*, echinoderm larvae and bivalves inferred from the CPR survey.

1 some corresponding to the concentration expected for the end
 2 of this century, most studies to date have relied on acute and
 3 short-term exposure in CO₂ (ref. 20). The effects of ocean acid-
 4 ification are more difficult to detect at the current atmospheric
 5 concentration of CO₂, or even at concentration expected in the
 6 next decades. Although some species will be adversely affected
 7 by ocean acidification, recent studies showed that others (for
 8 example, crustaceans) may benefit from a higher concentration
 9 of atmospheric CO₂ (ref. 21). Therefore, as with global warming,
 10 some species might benefit from the increase in dissolved CO₂
 11 in the ocean²¹. Some species may also be more resistant than
 12 previously assumed (for example, the role of a protective organic
 13 layer) and others may adapt to ocean acidification²². The reduc-
 14 tion in calcification might have pronounced effects on ecosystem
 15 functioning and both carbon and calcium carbonate exports. How-
 16 ever, we should be cautious in the attribution of current changes
 17 in calcifying plankton¹⁰ to ocean acidification because plankton
 18 are also highly sensitive to temperature as well as other physical
 19 and chemical factors.

20 Attributing the effect of ocean acidification in the field is
 21 complicated by the multifaceted effects of global change on
 22 marine ecosystems²³. Calcifying plankton are being influenced
 23 by ocean acidification at the same time as they are being
 24 affected by global climate change^{7,12}. Whereas much emphasis has
 25 been made on projecting the responses of calcifying organisms
 26 to ocean acidification, our study provides evidence that these
 27 organisms can also be strongly affected by climate-induced changes
 28 in sea temperatures. In the northeast Atlantic, all calcifying
 29 planktonic groups showed accelerating rates of change between
 30 the mid-1990s and the end of the 1990s, which paralleled
 31 pronounced modifications in large-scale hydro-climatic forcing
 32 and sea temperatures.

33 Methods

34 **Hydro-climatic data.** Annual SST originated from the data set ERSST_V3
 35 (ref. 24). The data set is derived from a reanalysis on a 2° × 2° spatial grid based

on the most recently available International Comprehensive Ocean-Atmosphere
 Data Set (ICOADS). 36

We used NHT anomalies, provided by the Hadley Centre for Climate
 Prediction and Research, as proxy for the effect of global change in temperatures. 37
 We also used the AMO and the winter NAO index²⁵. The AMO is an index of 38
 long-term (50–80 years) ocean/atmosphere variability in the range of 0.4 °C in 39
 many oceanic regions²⁶. The winter NAO index describes the basin-scale gradient 40
 of atmospheric pressure over the North Atlantic, between the high pressure centred 41
 on the subtropical Atlantic and low pressure around Iceland²⁷. 42
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pH and p_{CO2} data. Partial pressure of CO₂ (p_{CO2}) was assessed using the
 Lamont-Doherty Earth Observatory database²⁸. Increasing p_{CO2} concentrations 45
 in the surface ocean could induce alterations in seawater chemistry, leading to a 46
 decrease in pH (ref. 29). 47

To examine changes in pH and estimate their potential impacts on ecosystems,
 we also considered pH values. The data set consisted of surface pH values (top 48
 10 m of water column) compiled from both the International Council for the 49
 Exploration of the Sea (<http://www.ices.dk/ocean/>) and the World Ocean Database 50
 (<http://www.nodc.noaa.gov/OC5/SELECT/dbsearch/dbsearch.html>). Both p_{CO2} 51
 and pH annual time series were calculated for the period 1960–2009 in the spatial 52
 domain from 30° W to 10° E and from 40° N to 67° N. 53
 54
 55

Biological data. Biological data used in this study were collected by the CPR survey. 56

Spatial interpolation of biological data. Data were spatially interpolated by 57
 applying the inverse squared distance interpolation procedure with a search radius 58
 of 250 km (ref. 7). The spatial grid had a resolution of 1° latitude × 1° longitude 59
 and ranged from 30° W to 10° E and from 40° N to 67° N. Interpolation was carried 60
 out for each year and two-month period of the period 1960–2009. Although 61
 abundance distribution maps were created for *Clione limacina*, *Limacina* spp., 62
 echinoderm and bivalve larvae, maps were calculated as percentage of frequency 63
 of occurrence for coccolithophores and foraminifers owing to the method of 64
 enumeration of these taxa. 65

Standardized principal component analysis. A standardized PCA was performed 66
 to examine long-term changes in annual SST in the area where biological changes 67
 were examined (30° W–10° E and 40° N–67° N; ref. 7). This technique applies an 68
 orthogonal linear transformation to reorganize the total variance of the data in 69
 such a way that the first component contains the highest amount of variance¹⁹. 70
 The representativity of the principal components is measured by the eigenvalues. 71
 Here, the first principal component reflected the main long-term changes observed 72
 in the data and the normalized eigenvectors represented the correlation between 73

changes in annual SSTs observed in each geographical cell and the corresponding principal component.

Standardized PCAs were also applied to examine long-term changes in the annual abundance or frequency of occurrence of each calcareous plankton (30° W–10° E and 40° N–67° N). Long-term decadal changes were then re-estimated by using the first two eigenvectors and principal components.

Correlation analyses. Relationships between changes in calcareous plankton and both annual SST and large-scale hydro-climatic changes were investigated by correlation analyses. Probabilities of significance of correlation coefficients were calculated, taking into consideration the temporal autocorrelation¹¹. The autocorrelation function was used to assess the temporal dependence of years. When data were autocorrelated, we adjusted the degree of freedom and re-estimated the probability of significance¹¹.

Partial correlation analyses. First-order partial coefficients of correlation were calculated to examine the statistical causal influence of SST and pH on calcifying species. The partial correlation coefficients allow the relationship between two variables to be measured, after removing the effect of a third variable while keeping its mean constant. The partial correlation coefficient between the variables 1 and 2, removing the linear effect of variable 3 (denoted $r_{12,3}$), was calculated as follows¹⁹:

$$r_{12,3} = \frac{r_{12} - r_{13} \cdot r_{23}}{\sqrt{1 - r_{13}^2} \sqrt{1 - r_{23}^2}}$$

where r_{12} , r_{13} and r_{23} are simple linear coefficients of correlation between 1 and 2, 1 and 3, and 2 and 3, respectively.

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Author contributions

G.B. and A.M.-G. conceived the study; G.B., A.M.-G. and E.G. compiled the data; G.B. and E.G. analysed the data. G.B., A.M.-G., M.E. and E.G. wrote the paper.

Additional information

Supplementary information is available in the online version of the paper. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to G.B.

Competing financial interests

The authors declare no competing financial interests.