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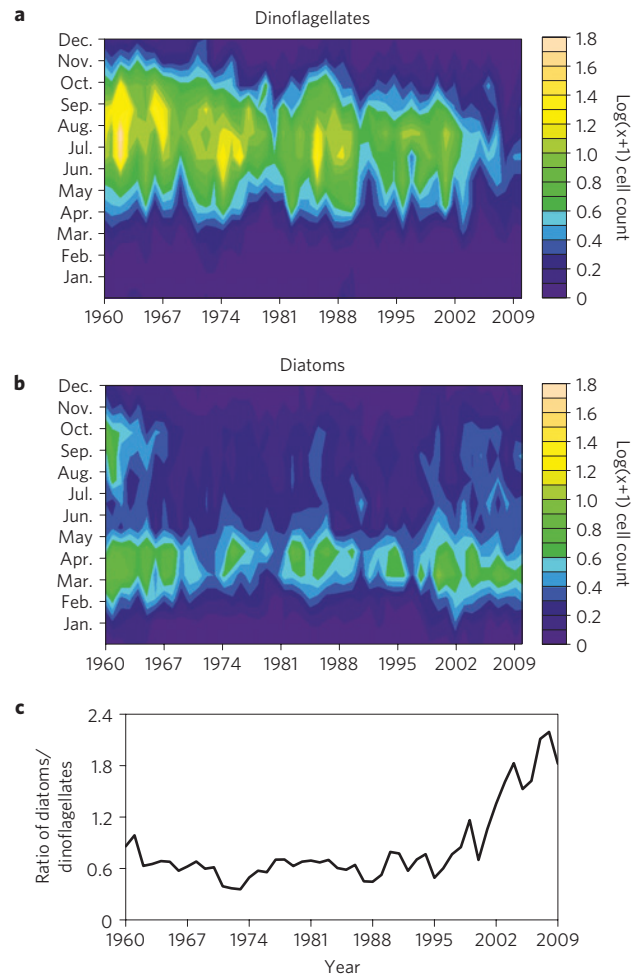
**MORAL MISFIRE**  
Psychological challenges of climate change

# Changes in marine dinoflagellate and diatom abundance under climate change

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**Marine diatoms and dinoflagellates play a variety of key ecosystem roles as important primary producers (diatoms and some dinoflagellates) and grazers (some dinoflagellates). Additionally some are harmful algal bloom (HAB) species and there is widespread concern that HAB species may be increasing accompanied by major negative socio-economic impacts, including threats to human health and marine harvesting<sup>1,2</sup>. Using 92,263 samples from the Continuous Plankton Recorder survey, we generated a 50-year (1960–2009) time series of diatom and dinoflagellate occurrence in the northeast Atlantic and North Sea. Dinoflagellates, including both HAB taxa (for example, *Prorocentrum* spp.) and non-HAB taxa (for example, *Ceratium furca*), have declined in abundance, particularly since 2006. In contrast, diatom abundance has not shown this decline with some common diatoms, including both HAB (for example, *Pseudo-nitzschia* spp.) and non-HAB (for example, *Thalassiosira* spp.) taxa, increasing in abundance. Overall these changes have led to a marked increase in the relative abundance of diatoms versus dinoflagellates. Our analyses, including Granger tests to identify criteria of causality, indicate that this switch is driven by an interaction effect of both increasing sea surface temperatures combined with increasingly windy conditions in summer.**

Changing hydrological conditions, associated with regional climate warming, are thought to underlie changes in the abundance and distribution of diatoms and dinoflagellates<sup>3</sup> and be one of the possible mechanisms for the increase in the occurrence of HAB species<sup>4,5</sup>. Other factors implicated in HAB species increases include ballast water transport, aquaculture development, transport of seed stock and eutrophication of coastal waters due to human activities<sup>1,2</sup>. Here we use data from the Continuous Plankton Recorder (CPR) survey (1,241–2,253 samples per year since 1960), which is the longest multi-decadal plankton monitoring programme in the world<sup>6</sup>, to undertake the most comprehensive analysis so far of extended spatio-temporal patterns of abundance for dinoflagellates and diatoms, including key HAB taxa, in the northeast Atlantic region. The CPR does not sample very close (<10 km) to the coast and hence will not reveal locally specific patterns of plankton change (for example, caused by local eutrophication, and local changes in circulation due to coastal development), but rather provides a view of broader-scale regional changes. As such, the CPR data reveal changes that are often caused by climate impacts operating over large areas<sup>6</sup>. Integrated abundances of twelve diatom taxa and nine dinoflagellate taxa were examined in the northeast Atlantic region (45°–60° N; 15° W–10° E;

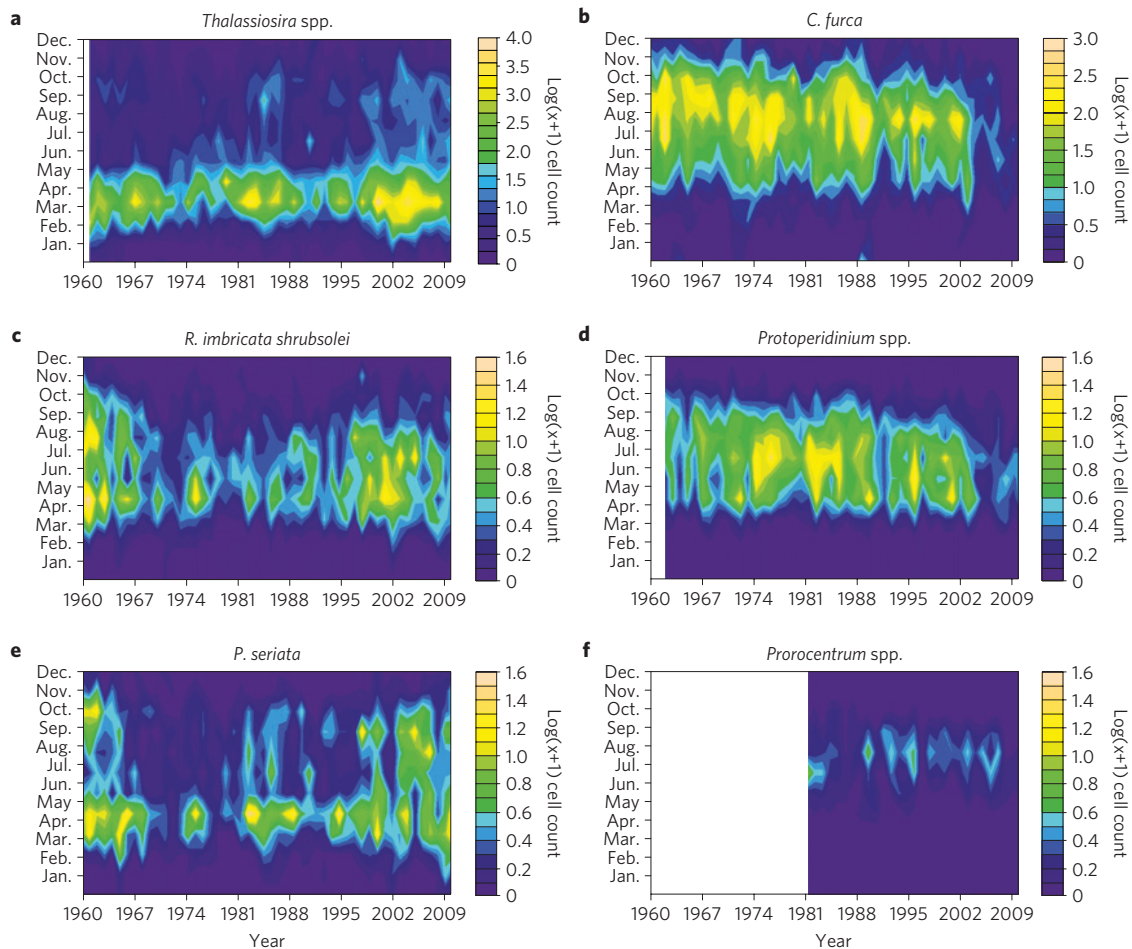


**Figure 1 | Abundance of dinoflagellates and diatoms in the northeast Atlantic region from 1960 to 2009 based on twelve diatom taxa and nine dinoflagellate taxa routinely identified in the CPR samples. a, b,** Monthly mean cell numbers per sample of dinoflagellates (a) and diatoms (b). **c,** The relative abundance of diatoms/dinoflagellates, highlighting the shift from dinoflagellates to diatoms during the past 50 years.

see Methods for taxa selection and data analysis details). Included within these analyses was the spatio-temporal variability of the diatom *Pseudo-nitzschia seriata*, an important HAB taxa, and several

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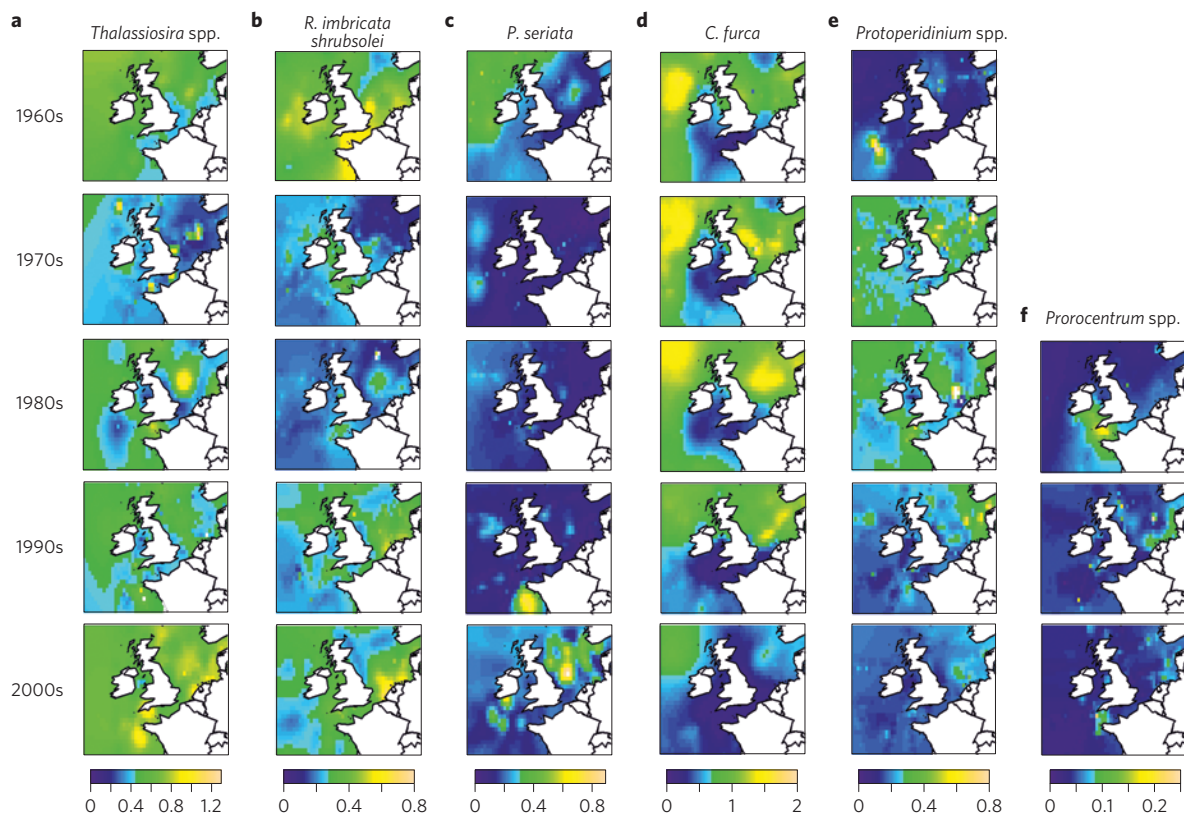
**Figure 2 | Abundance of selected taxa in the northeast Atlantic region to illustrate the shift from dinoflagellates to diatoms during the past 50 years.** **a–f.** The panels are ordered to show diatoms (left panels) and dinoflagellates (right panels). *P. seriata* and *Prorocentrum* spp. are HAB taxa (shown in bottom panels). Colour scale represents monthly mean cell numbers per sample ( $\text{Log}(x+1)$ ).

abundant non-HAB taxa including the diatom *Thalassiosira* spp. and the dinoflagellate *Protoperdinium* spp. In addition to these 21 diatom and dinoflagellate taxa, for some other taxa for which there were shorter time series, we also examined more recent trends in abundance. These shorter time series were produced because the taxa were not identified in the earlier years of the CPR survey. These taxa were selected because they have been shown to be HAB species: the dinoflagellates *Prorocentrum* spp. (identified since 1981) and *Dinophysis* spp. (a mixotrophic species identified since 1971). *Noctiluca scintillans* was selected as an example of a heterotrophic species (identified since 1997) that is not typically considered a HAB species, but may act as a vector for toxigenic phytoplankton<sup>7</sup> and have other harmful effects<sup>8</sup>. In these ways we addressed the questions of how diatom and dinoflagellate abundance has changed over the past 50 years and whether HAB species have been increasing.

To examine long-term changes in distribution, we examined detailed spatial trends for six abundant taxa every 5 years by ordinary kriging, using R (ref. 9) and packages sp (ref. 10) and gstat (ref. 11). Our results reveal a pronounced change in the relative abundance of diatoms versus dinoflagellates (Fig. 1). For example, in the 1960s–1980s, dinoflagellates were relatively more abundant than diatoms in the CPR samples, but this pattern has been reversed in the past decade. These broad taxonomic changes are also reflected within individual taxa, albeit with some level of variability in patterns across taxa. As such our results challenge the view that HAB species have increased in frequency and intensity and have become more widespread in recent decades<sup>2,12</sup>

and instead point to a broader switch from dinoflagellate to diatom dominance. For example, previously abundant dinoflagellates such as *C. furca* and *Protoperdinium* spp. are now increasingly rare when compared with previous levels (Figs 2 and 3) and similarly the HAB dinoflagellate *Prorocentrum* spp. has been very rare since 2007 (Fig. 2). Conversely, both non-HAB (for example, *Thalassiosira* spp.) and HAB diatoms (for example, *P. seriata*) have become more abundant and widespread in the past decade (Figs 2 and 3). In some cases this increase in diatom abundance extends back through the 50-year times series (for example, *Thalassiosira* spp.) whereas for others the present increase spans only two or three decades (for example, *R. imbricata shrubsolei* and *P. seriata*; Fig. 3). In addition, some diatoms (such as *P. seriata*) also now show extended high abundance throughout the summer in-between the spring and autumn peaks (Fig. 2e). This increase in *Pseudo-nitzschia* is already having a profound effect within UK waters. Since 1999, there have been frequent closures of shellfish harvesting sites around the Scottish west coast and islands due to *Pseudo-nitzschia*<sup>13,14</sup>. Our results support those from experimentation with *P. seriata* in Scottish waters, where enhanced growth rates and toxin production occur when temperatures reach 15 °C and there is a long photoperiod<sup>13,15</sup>. A caveat of our study is that changes in coastal ecosystems might be taking place in ways that are not observed by the CPR sampling (that is, areas within 10 km of land).

The present warming of the northeast Atlantic region is favouring warmer-water species at the expense of cold-water species, with consequent range extensions and contractions



**Figure 3 | Decadal spatio-temporal changes in abundances of selected dinoflagellates and diatoms in the northeast Atlantic. a–c,** Diatoms (*Thalassiosira* spp., *R. imbricata shrubsolei* and *P. seriata*). **d–f,** Dinoflagellates (*C. furca*, *Protoperidinium* spp. and *Procoentrum* spp.). Colour scale represents decadal mean cell numbers per sample ( $\text{Log}(x+1)$ ).

respectively<sup>16</sup>. We investigated the links with climate by analysing sea surface temperature (SST; data supplied by Hadley Centre of the UK Met Office) and summer surface scalar wind speed (SSWS; data supplied by The International Comprehensive Ocean–Atmospheric Data Set) in the northeast Atlantic from 1960 to 2009. We employed a range of statistical methods to address issues of potential spurious correlation (correcting for non-stationarity by de-trending and correcting for serial autocorrelation) and to highlight potential causal and modifying mechanisms (examining Granger causality criteria and regression interaction terms). We examined the observed yearly average abundances for all of the abundant diatom taxa ( $n = 12$ ) and dinoflagellate taxa ( $n = 9$ ) for which long time series existed (see Methods) as well as integrated diatom and dinoflagellate abundance. In addition we considered *Dinophysis* spp. as an example of a mixotrophic HAB dinoflagellate and *N. scintillans* as an example of a heterotrophic dinoflagellate even though shorter time series existed for these taxa. After adjusting for serial autocorrelation using the modified Chelton method<sup>17</sup>, we found significant correlations between mean annual abundance for many taxa against either SST or SSWS (or both; Table 1). For the dinoflagellate taxa, abundance tended to decrease with increasing temperature and/or wind. This effect was seen for 10 of the 12 individual dinoflagellate taxa, with the reverse pattern tending to be found for diatoms. In addition the integrated dinoflagellate abundance showed a significant negative correlation with both SST and SSWS (Table 1 and Supplementary Fig S1). The pattern of long-term change was therefore more consistent across dinoflagellates, which have largely showed a long-term decline, and more variable across diatoms, many of which have shown a long-term increase although this pattern is not present across all taxa (Supplementary Figs S2 and S3).

Potential causal pathways in a time series can be further investigated with a Granger test<sup>18</sup>, where past values of a putative causal environmental variable (SST or SSWS) are used in a regression model to predict future values of plankton abundance, after adjusting for past values of plankton abundance (and de-trending for stationarity). This approach therefore represents a measure of forecasting over and above that provided simply by past temporal correlations, and helps point towards a causal link<sup>18</sup>. We found evidence for significant Granger causality in the relationship between either SST or SSWS for five of the dinoflagellate taxa (*Protoperidinium* spp., *C. furca*, *C. tripos*, *Dinophysis* spp. and *N. scintillans*), and for five of the diatom taxa (*Thalassiothrix longissima*, *Skeletonema costatum*, *Pseudo-nitzschia delicatissima*, *R. hebetata semispina* and *P. seriata*) as well as the combined ‘diatom’ group (at 10% level), with the effect of SST appearing over a lag of 1–3 years and the effect of SSWS appearing over a lag of 1–2 years (Supplementary Table S1).

Last, we investigated whether there was any interaction between the two climate variables in a regression model predicting the abundance of our diatom and dinoflagellate taxa, which would indicate a more complex relationship between abundance and climate change, and shed any light on the possible mechanisms involved. We focused on the North Sea (51°–60° N; 3° W–10° E), which has shown the largest regional change in plankton abundance. Highly significant interaction terms, between SST and SSWS, were found in the linear regression models for several taxa. For diatoms, the significant interaction terms were all showing a synergistic positive effect on abundance (*P. seriata*,  $p = 0.003$ ; *Ditylum brightwellii*,  $p = 0.0002$ , *P. delicatissima*,  $p = 0.0004$ ; *S. costatum*,  $p = 0.0002$ ; integrated diatom abundance,  $p = 0.01$ ). For dinoflagellates, the significant interaction terms were negatively correlated with abundance (*C. furca*,  $p = 0.02$ ; *C. macroceros*,  $p = 0.02$ ; with two species significant at the 10% level). This means that the effect of each

**Table 1 | The significance of modified Chelton correlation for diatoms and dinoflagellates against SST and SSSWS.**

	Modified Chelton <i>p</i> value for correlation coefficient			
	SST		SSWS	
Integrated diatoms	0.12		0.4	
<i>P. seriata</i>	0.008*	+	0.02*	+
<i>Thalassiosira</i> spp.	0.005*	+	0.02*	+
<i>R. imbricata shrubsolei</i>	0.009*	+	0.5	
<i>T. longissima</i>	0.56		0.005*	–
<i>T. nitzschioides</i>	0.07		0.06	
<i>E. zodiacus</i>	0.12		0.63	
<i>D. brightwellii</i>	0.005*	+	0.006*	+
<i>S. costatum</i>	0.2		0.33	
<i>P. delicatissima</i>	0.39		0.5	
<i>R. styliformis</i>	0.001*	–	0.42	
<i>R. hebetata semispina</i>	0.03*	–	0.02*	–
<i>R. alata indica</i>	0.19		0.02*	–
Integrated dinoflagellates	0.001*	–	0.001*	–
<i>Prorocentrum</i> spp.	0.81		0.03*	–
<i>Protoperdinium</i> spp.	0.006*	–	0.007*	–
<i>C. furca</i>	0.002*	–	0.002*	–
<i>C. fusus</i>	0.0004*	–	0.004*	–
<i>C. lineatum</i>	0.0002*	–	0.005*	–
<i>C. tripos</i>	0.001*	–	0.01*	–
<i>C. macroceros</i>	0.11		0.003*	–
<i>C. longipes</i>	0.005*	–	0.0005*	–
<i>C. minutum</i>	0.02*	+	0.48	
<i>C. hexacanthum</i>	0.06		0.002*	+
<i>Dinophysis</i> spp.	0.02*	–	0.01*	–
<i>N. scintillans</i>	0.87		0.008*	–

The sign of the affect of SST or SSSWS on abundance is indicated (+ or –). \**p* < 0.05.

climate variable cannot be considered in isolation. For example, the diatom *P. seriata* shows high abundance only when both SST and SSSWS are at a high level (Supplementary Fig. S4). When either SST or SSSWS levels are low, *P. seriata* occurs at low abundance. In clear contrast, the opposite interaction effect was evident in the dinoflagellate taxa where low abundance occurred at high SST, but only when accompanied by high SSSWS conditions. Such interactions could explain why dinoflagellates have become relatively less abundant when compared with diatoms.

Since 1960, there has been both a 1°C rise in SST and a significant increase in SSSWS in the northeast Atlantic region (Supplementary Fig. S1). This increase in wind introduces surface kinetic energy, which will stimulate vertical mixing leading to increased turbulence<sup>19</sup>. As turbulent environments are associated with diatoms<sup>18</sup> and calm conditions with dinoflagellates<sup>20</sup>, the recent switch from dinoflagellate to diatom dominance with increasing SSSWS is perhaps not surprising. What is less clear cut are the precise mechanisms behind this relationship. For those species that are either entirely or mainly dependent on photosynthesis to obtain energy, diatoms are generally considered superior competitors to dinoflagellates<sup>21</sup>. Diatoms have numerous physiological advantages over dinoflagellates, including higher growth rates, higher photosynthetic rates and an improved ability to compete for nitrogen at low concentrations<sup>21</sup>. As a consequence, providing there is sufficient turbulence to enable diatoms to remain suspended within the surface mixed layer, diatoms typically outcompete dinoflagellates. Interestingly, we found that the recent increased windiness has caused a decline in abundance of all dinoflagellates regardless of trophic status (that is, phototrophic, mixotrophic and heterotrophic species), even including heterotrophic species that predominantly feed on

diatoms (for example, *Protoperdinium*), indicating that additional mechanisms are at play. Both field and laboratory studies indicate that dinoflagellates are especially sensitive to small-scale turbulence<sup>22</sup>. Although species-specific differences exist, in general, small-scale turbulence seems to impact negatively on dinoflagellate cell-division and life-cycle processes<sup>22</sup>. The ability of some common, cosmopolitan dinoflagellate species to bloom in turbulent upwelling regions provides an exception to this rule<sup>23</sup> and indicates that further research is required to explain large-scale shifts in plankton composition presented within this study. The interactive effect of temperature is presumably linked to the general impact of higher temperatures leading to increased vital rates such as cell division and photosynthesis.

Our study shows a fundamental shift in the relative abundance of diatoms versus dinoflagellates in the northeast Atlantic and North Sea, with a marked decline in dinoflagellates in recent years. Using a range of statistical treatments we have shown that both sea temperature and summer windiness are important climate drivers of the biological changes and we highlight the key synergistic effects of these climate variables. Given the many potential changes in climate variables, it is unlikely that simple linear relationships will exist with species abundance. Synergistic effects, such as those described here, must be considered to help develop our understanding of the mechanistic processes underlying biological changes in the oceans.

## Methods

**Integrated indices of diatom and dinoflagellate abundance.** To create integrated indices of diatom and dinoflagellate abundance, from the CPR database 12 diatom taxa (*Thalassiothrix longissima*, *Thalassionema nitzschioides*, *Eucampia zodiacus*, *Ditylum brightwellii*, *Skeletonema costatum*, *Pseudo-nitzschia delicatissima*, *P. seriata*, *Thalassiosira* spp., *Rhizosolenia imbricata shrubsolei*, *R. styliformis*, *R. hebetata semispina* and *R. alata indica*) and nine dinoflagellate taxa (*Ceratium*

*furca*, *C. fusus*, *C. lineatum*, *C. tripos*, *C. macroceros*, *C. longipes*, *C. hexacanthum*, *C. minutum* and *Protoperdinium* spp.) were selected on the basis of three criteria. First, only taxa abundant enough to reach a threshold maximum abundance value were included so that rarer taxa were excluded. Second, species needed to be present on >4% of all samples. Third, we included only taxa that were first identified between 1960–1963 and were persistently present until 2009; that is, we included only taxa for which there was a long time-series.

***P. seriata* (complex).** Identification of *P. seriata* complex is achieved using a previously published method<sup>24</sup>, splitting *P. seriata* complex and *P. delicatissima* complex on the basis of their cell transapical axis. However, accurate identification of *P. seriata* complex at the species level is not possible in routine CPR analysis and requires further investigation<sup>6</sup>. In this paper we refer to the complex as *P. seriata*.

**Large-scale hydro climatic parameters.** Monthly mean gridded ( $1^\circ \times 1^\circ$ ) SSTs, from 1960 to 2009, were taken from the Hadley Centre of the UK Met Office. Annual SST means were calculated for the northeast Atlantic region ( $45^\circ\text{--}60^\circ\text{N}$ ;  $15^\circ\text{W--}10^\circ\text{E}$ ), and a subset of this region corresponding to the North Sea ( $51^\circ\text{--}60^\circ\text{N}$ ;  $3^\circ\text{W--}10^\circ\text{E}$ ) for the months May, June, July and August.

Monthly mean SSSWS ( $\text{m s}^{-1}$ ) was obtained from The International Comprehensive Ocean–Atmosphere Data Set for 1960–2009 (<http://www.ncdc.noaa.gov/oa/climate/coads/>). Data are summarized for a given latitude and longitude. Yearly scalar wind was averaged over the months May, June, July and August for the northeast Atlantic region ( $45^\circ\text{--}60^\circ\text{N}$ ;  $15^\circ\text{W--}10^\circ\text{E}$ ) and a subset of this region corresponding to the North Sea ( $51^\circ\text{--}60^\circ\text{N}$ ;  $3^\circ\text{W--}10^\circ\text{E}$ ).

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## Author contributions

G.C.H. and M.B.G. conceived the study; S.L.H. and A.W.W. compiled the data; S.L.H., M.B.G. and G.C.H. led the data analyses and interpretation with contributions from all authors. S.L.H. and G.C.H. wrote the paper with contributions from all authors.

## Additional information

The authors declare no competing financial interests. Supplementary information accompanies this paper on [www.nature.com/natureclimatechange](http://www.nature.com/natureclimatechange). Reprints and permissions information is available online at [www.nature.com/reprints](http://www.nature.com/reprints). Correspondence and requests for materials should be addressed to G.C.H.