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# Phenological shuffling of major marine phytoplankton groups over the last six decades

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## Abstract

**Aim:** Phytoplankton form the basis of the marine food web and are responsible for approximately 50% of the world's photosynthesis. Changes to their ecology are, therefore, important: here, we examined seasonal patterns in ocean phytoplankton abundance for 45 taxa over 59 years collected from circa 410,000 km of line-transect sampling at temperate latitudes.

**Location:** The North Sea.

**Methods:** For our analysis we used plankton abundance data from the Continuous Plankton Recorder (CPR) survey, sea surface temperature measurements from the Hadley Centre, UK Meteorological Office and wind speed data from the International Comprehensive Ocean–Atmosphere Data Set, NOAA.

**Results:** We found large differences in changes in the timing of peak abundance between the major phytoplankton groups. Late-summer blooming dinoflagellates ( $n = 10$  taxa) tended to show a large seasonal advancement, the timing of peak abundance for dinoflagellates as group advancing 39 days over these six decades. By contrast diatoms ( $n = 35$ ) did not show any change as a group in their timing of peak abundance over the time series. Granger causality testing suggested a major driver of these phenological changes has been ocean warming in general but more specifically the rate of spring temperature rise as the most important factor. We also found differences in the timing of peak abundance of harmful algal bloom taxa, with some showing peak abundance earlier while others have moved later.

**Main conclusions:** There has been a fundamental transformation of the classic seasonal progression from blooms of diatoms to dinoflagellates, which lies at the heart of temperate marine food chains, as the classic bimodal diatom and dinoflagellate seasonal peaks are eroded to a more continuous, single, longer-lasting phytoplankton peak. This phenological shuffling within and between major taxonomic groups is likely to have profound implications for the transfer of energy to higher trophic levels.

## KEYWORDS

climate change, marine plankton, phytoplankton abundance, phytoplankton phenology, sea surface temperature, spring temperature rise

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## 1 | INTRODUCTION

It is widely accepted that climate change may impact the seasonal timing (phenology) of biological events such as breeding, migration and seasonal peaks in abundance (Bedford, Johns, Greenstreet, & McQuatters-Gollop, 2018; Boyce, Petrie, Frank, Worm, & Leggett, 2017; Hunter-Cevera et al., 2016; Pecl et al., 2017; Root et al., 2003; Stenseth & Mysterud, 2002; Thackeray et al., 2016). In some cases, it is suspected that different rates of phenological change within ecosystems may lead to a reshaping of trophic linkages and hence ecosystems may start to function in new ways (Thackeray et al., 2016). For example, different rates of phenological change of pollinators have impacted the match between the abundance of consumers and their resources (Thackeray et al., 2010), between plants and their pollinators (Hegland, Nielsen, Lázaro, Bjerknes, & Totland, 2009) and in juvenile diet composition of a marine top predator (Howells et al., 2017). Establishing evidence for such phenological shuffling across multiple species and trophic levels is, however, often limited by the availability of species-specific empirical data spanning long periods. As time series lengthen, so their value can grow to address new questions (Edwards, Beaugrand, Hays, Koslow, & Richardson, 2010).

To examine long-term phenological changes in ocean plankton, we used a 59-year time series from the Continuous Plankton Recorder (CPR) survey (Richardson et al., 2006), examining how the seasonal timing of peak abundance has changed over the last 59 years for a range of common diatoms and dinoflagellates. The CPR survey is unique in its length of operation, spatial coverage and taxonomic resolution and, consequently, has been used to make a series of seminal discoveries of changes in plankton abundance and distribution over the last few decades (McQuatters-Gollop et al., 2011; Richardson & Schoeman, 2004).

Marine plankton are thought to be a sensitive indicators of climate change with, for example, major changes in their range have been noted over the last 50 years (Barton, Irwin, Finkel, & Stock, 2016; Chivers, Walne, & Hays, 2017; Hinder et al., 2012). Fifteen years ago, the CPR data were used to identify major phenological changes in seasonal abundance of ocean plankton (Edwards & Richardson, 2004), leading to a series of studies that examined plankton phenology across the ocean basins (Atkinson et al., 2015; Chiba, Batten, Sasaoka, Sasaki, & Sugisaki, 2012; Schlüter, Kraberg, & Wiltshire, 2012). Often these studies have tended to focus on phytoplankton as one group or to focus only on one or a few taxa; for example, in a recent study, a 13-year time series was used to show how cell division rates for an important picophytoplankter, *Synechococcus*, was impacted by temperature so that ocean warming caused earlier blooming (Hunter-Cevera et al., 2016). In some studies patterns of phenological change in the plankton have been documented across multiple taxa, as in a notable study using data from the North Sea which reported both advances and delays in the seasonal timing of peak abundance for different plankton taxa occurring in the same area, leading to the suggestions that new trophic linkages are forming over time in the oceans (Edwards & Richardson, 2004). More recently, Hinder et al. (2012) used CPR data to show continued marked changes in phytoplankton

phenology as well as abundance. Most notably, compared to earlier work (Edwards & Richardson, 2004), earlier summer blooming of dinoflagellates had continued along with a reduced relative abundance of dinoflagellates compared diatoms (Hinder et al., 2012).

The reasons for these different phenological shifts across plankton taxa have, however, remained enigmatic. Here, we use a longer time series of plankton observations than examined previously (Edwards & Richardson, 2004) as well as a wider range of taxa (Hinder et al., 2012). We first assess whether there have been different phenological changes between diatoms and dinoflagellates over a near 60-year time series. Second, we identify environmental drivers of the observed phenological changes, examining links between plankton phenological change and sea surface temperature (SST), the rate of ocean warming in spring as well as windiness. By examining a data set that is unique in terms of its length, spatial coverage and multi-taxa composition, we considered how life history and environment change may interact to impact observed patterns of plankton phenological change.

## 2 | METHODS

### 2.1 | Plankton data collection

The plankton abundance data used in this analysis were collected by the Sir Alister Hardy Foundation for Ocean Science (SAHFOS) using Continuous Plankton Recorder (CPR) survey machines. The CPR survey is the longest-running plankton survey (Edwards & Richardson, 2004; Richardson et al., 2006) having commenced in 1931 and with continuous data from 1946.

We briefly summarize the CPR survey here, it is described in detail elsewhere (Batten et al., 2003; Richardson et al., 2006; Warner & Hays, 1994). The CPR machines are towed at approximately 6–7 m depth behind "ships of opportunity": volunteer commercial shipping vessels. Plankton are collected in a slowly scrolling mesh (size 270 µm) and sandwiched by a second mesh before being rolled up in 4% formaldehyde. Some phytoplankton may escape this mesh size, but the proportions of the taxa captured are consistent and comparable between samples—the methods of analysis of these samples developed by SAHFOS have been consistent since 1958. The plankton are collected at a minimum distance of 10 km from any shoreline to avoid interference from coastal conditions. The CPR data we used were from a consistently and highly sampled area of the survey and an area with a precedent for being used for phenological analysis (Edwards & Richardson, 2004). The data collated by SAHFOS include latitude, longitude, date, time and abundance.

### 2.2 | Potential biases and limitations

The CPR survey currently records ~300 phytoplankton entities (many to species level) in routine taxonomic analysis dating back over multi-decades and more recently a large number of other organisms using

molecular techniques. Due to the mesh size of CPR silks, many phytoplankton species are only semi-quantitatively sampled owing to the small size of the organisms. There is, thus, a bias towards recording larger armoured flagellates and chain-forming diatoms and that smaller species abundance estimates from cell counts will probably be underestimated in relation to other water sampling methods. However, the proportion of the population that is retained by the CPR silk reflects the major changes in abundance, distribution and specific composition; that is, the percentage retention is roughly constant within each species even with very small-celled species (e.g., *Emiliania huxleyi*) (Edwards, Johns, Leterme, Svendsen, & Richardson, 2006). The more recent addition of an autonomous water sampler on board certain CPRs can now provide information on the whole size-spectrum of plankton using molecular techniques from bacteria and viruses to flagellates and other taxa not normally identified using standard CPR analysis.

## 2.3 | Geographic area

The plankton, SST and wind speed (WSPD) data were from the period 1958–2016 and geographic area 55–58°N, 2°W–8°E (in the North Sea). We selected this area as it corresponds with an earlier seminal study of changing phenology of plankton using a shorter CPR time series from 1960–2002 (Edwards & Richardson, 2004).

## 2.4 | Sample size and taxa

The sample size was 22,130 SAHFOS records from the chronological period and geographic area above. The taxa used were as follows: *Ceratium furca*, *C. fusus*, *C. horridum*, *C. lineatum*, *C. longipes*, *C. macroceros*, *C. tripos*, *Dinophysis* spp., *Prorocentrum* spp., *Protoperdinium* spp., *Asterionellopsis glacialis*, *Chaetoceros Hyalochaete* spp.\*, *C. Phaeoceros* spp.\*, *Cylindrotheca closterium*\*, *Ditylum brightwellii*\*, *Eucampia zodiacus*\*, *Fragilaria* spp., *Gyrosigma* spp.\*, *Navicula* spp.\*, *Odontella aurita*, *O. sinensis*, *Paralia sulcata*, *Proboscia alata*, *P. inermis*\*, *Pseudo nitzschia delicatissima complex*\*, *Pseudo nitzschia seriata complex*\*, *Rhizosolenia hebetata semispina*, *R. imbricata*, *R. styliformis*\*, *Skeletonema costatum*, *Thalassionema nitzschioides*\*, *Thalassiosira* spp. and *Thalassiothrix longissima*. These taxa were selected because (a) they were well-sampled and/or (b) they were used by Edwards and Richardson (2004). Some diatom taxa, denoted above by a star (\*), showed two distinct seasonal peaks in abundance, one in the spring and one in the autumn. For the taxa with two seasonal peaks, we calculated both the timing of the spring peak in abundance and the autumn peak in abundance.

## 2.5 | Indices of diatom and dinoflagellate seasonal peaks

Using an established methodology (Edwards & Richardson, 2004), we calculated the seasonal timing of peak abundance of each taxon as follows:

$$S_p = \frac{\sum_{i=1}^{12} M \cdot x_m}{\sum_{i=1}^{12} x_m}$$

where  $S_p$  is the seasonal peak,  $M$  is the number of the month (1–12) and  $x_m$  is the mean abundance in the month. Twelve of the diatom taxa exhibited population peaks in both spring and autumn and in some analyses these peaks were treated separately, giving 10 dinoflagellate taxa and 35 diatom taxa.

## 2.6 | Sea Surface Temperature (SST) and Wind Speed (WSPD) parameters

Monthly mean SST (°C) measurements from 1958 to 2016 for each  $1 \times 1^\circ$  grid cell were obtained from the Hadley Centre of the UK Meteorological Office (<http://www.metoffice.gov.uk/hadobs/hadisst/>) (Rayner et al., 2003). Annual SST means were calculated for the geographic area used.

Monthly mean WSPD ( $\text{ms}^{-1}$ ) data for each  $1 \times 1^\circ$  grid cell were obtained from the International Comprehensive Ocean–Atmosphere Data Set (ICOADS, <http://icoads.noaa.gov/>) (Freeman et al., 2017). Yearly scalar wind means were calculated for the geographic area used.

## 2.7 | Further analysis

A potential problem when using long-term data is that of serial autocorrelation which can result in Type I errors in correlation analysis (Yule, 1926). We controlled for such autocorrelation using a modified Chelton method to re-estimate the number of degrees of freedom, as described by Pyper and Peterman (1998).

Potential causal relationships in a time series can be further tested using a Granger test (Thurman & Fisher, 1988), a method borrowed from econometrics. In this procedure, past values of a putative causal variable (here SST or WSPD) are used in a regression model to predict future values of the dependent variable after adjusting for past values of the latter. This approach is a more rigorous measure of causality than that provided simply by past temporal correlations (Thurman & Fisher, 1988).

## 2.8 | Code and data availability

All code was written in the R statistical language (R Core Team, 2015), which is open source and freely available. Enquiries about the code used here can be directed to the corresponding author, W.J.C.

The data that support the findings of this study are publicly available:

1. The plankton population data are available from the SAHFOS CPR Survey, now part of the Marine Biological Association (MBA) of the United Kingdom: <https://www.cprsurvey.org/>.

2. The temperature data are available from the Hadley Centre Sea Ice and Sea Surface Temperature data set (HadISST): <http://www.metoffice.gov.uk/hadobs/hadisst/>.
3. The wind speed data are available from the International Comprehensive Ocean-Atmosphere Data Set (ICOADS): <http://icoads.noaa.gov/>.

### 3 | RESULTS

#### 3.1 | Summary of results

Our study is unique in its six-decade analysis of 45 taxa. Our most striking result is the approximately 39 day advance of the seasonal peak of the dinoflagellates between 1958 and 2016, from mid-August moving forward to early July, while the time of peak abundance for diatoms did not move significantly (Figures 1 and 2). All individual dinoflagellate taxa exhibited large advances while the individual diatom taxa exhibited considerable variation in response.

While the sea surface temperature (SST) and wind speed (WSPD) varied over the last six decades (Figure 3a,b), only the rate of ocean warming in spring (Figure 3c) exhibited a monotonic change among these potential drivers of phenological change. Our second result is that the change in dinoflagellate phenology appears to be most strongly driven by the rate of spring SST rise, although mean spring SST and mean annual SST were also significant drivers. We found very little evidence of causal relationships between SST and diatom phenology. Similarly, interaction between WSPD and SST affected the dinoflagellates but not the diatoms, WSPD alone was not significant.

The two phytoplankton groups also differed in changes to abundance. The abundance of the diatoms fell in the first two decades but has risen since then, the dinoflagellates by contrast have exhibited a general decline in abundance over the six decades (Figure 4a,b). The abundance of the diatoms is negatively affected by WSPD whereas the dinoflagellate abundance is negatively associated with SST. These changes in abundance had little effect on the duration or rate of rise and fall of their seasonal peaks (Figure 4c,d).

Many of the individual taxa examined here are known to cause harmful blooms, including most of the dinoflagellate taxa. While all the dinoflagellate taxa have moved earlier in the year the diatom taxa have exhibited movement both earlier and later, including HAB taxa (see section 3.5).

#### 3.2 | Differences in the movement of seasonal peaks of the major phytoplankton groups and individual taxa

All individual dinoflagellate taxa exhibited advancing timing of seasonal peak abundance (Figure 2; Tables S1, S2), ranging from *Ceratium macroceros* (52.9 days earlier) to *C. longipes* (19.4 days earlier), the latter being the only dinoflagellate taxon to move less than

three weeks over the 59 years. In addition to *C. macroceros*, seven other dinoflagellate taxa (a combined 91.1% of the dinoflagellate total) exhibited movement of one month or greater.

While the diatoms as a group showed no significant phenological movement, individual diatom taxa showed a greater range of changes in the timing of peak abundance than did the individual dinoflagellate taxa (Figure 2; Tables S1, S3). Six of the 35 diatom taxa (20.9% of total) advanced approximately one month or more and five (4.7% of total) showed peak abundance delayed by a week or more. Twelve taxa (48.3% of total) exhibited movement of a week or less in either direction.

#### 3.3 | Environmental drivers of phenological changes

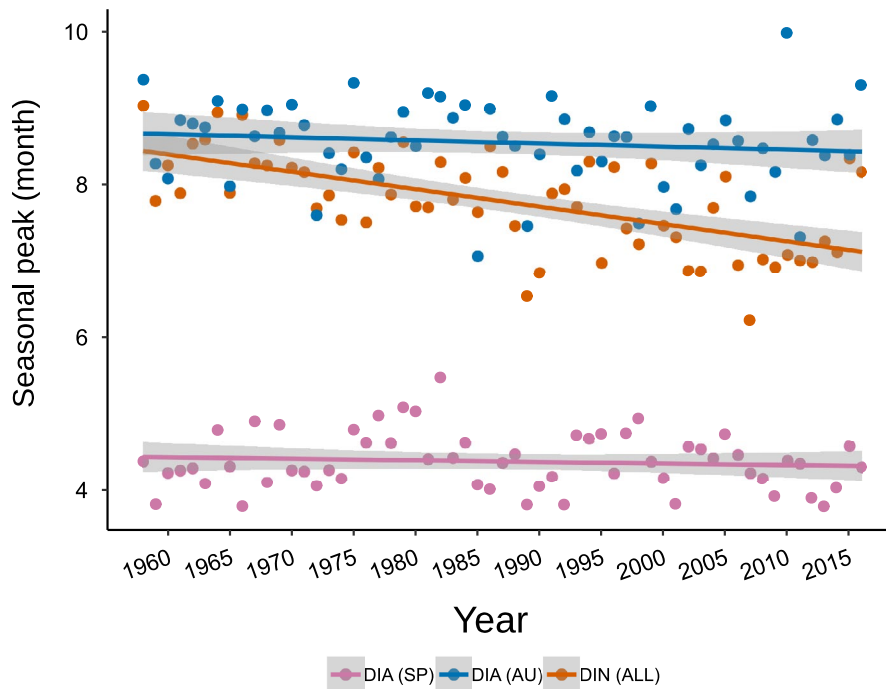
The six decades and geographic area used here exhibited periods of slight ocean cooling in the first three decades and then strong ocean warming in the latter three (Figure 3a), an increase in the annual mean wind speed in the first half of the time series and decrease in the later half (Figure 3b) and by contrast a consistent increase over the six decades in the rate of ocean warming in the months March to May (Figure 3c), the latter exhibiting the only monotonic change among these potential environmental drivers.

##### 3.3.1 | Correlations with major groups

After adjusting for serial autocorrelation using the modified Chelton method (Pyper & Peterman, 1998) we found significant correlations between the timing of the seasonal peak of the dinoflagellates and aspects of the SST: the most significant correlations were with the spring months' SSTs, the rate of temperature rise in spring and the yearly mean SST. We found no relationship between the SST and the seasonal peak of the diatoms, either spring or autumn bloomers, nor did we find any correlation between wind speed and the seasonal peaks of any group (Figures S2, S3; Tables S4, S5, S6).

##### 3.3.2 | Causal relationships—effect of SST and WSPD on dinoflagellates

The Granger test (Thurman & Fisher, 1988), most often used in econometrics, can be used to examine causal relationships in a time series: past values of potential causal variables are used in a regression model to predict future values of the dependent variable(s). This method provides more evidence of causal relationships than that provided by simple past temporal correlations and helps to establish a causal link. We found significant Granger causality relationships between the annual and monthly SST measures and the seasonal peak of the dinoflagellates, the most significant relationship being with the spring SST change (Figure S3; Table S7). The significant months other than the spring change for the dinoflagellates



**FIGURE 1** Timing of the seasonal peak in abundance of the major phytoplankton groups. Period 1958–2016, geographic area 55–58°N, 2°W–8°E. The spring- and autumn-blooming diatoms are shown separately. Loess smoothers were used for locally weighted polynomial regression, the grey areas indicating the 95% confidence interval. AU, autumn bloom; DIA, diatoms; DIN, dinoflagellates; SP, spring bloom

were the months of the second half of the year. Eight of the individual dinoflagellate taxa exhibited sensitivity to SST including the five most abundant taxa and representing 91.1% of the total. Six of the dinoflagellate taxa exhibited sensitivity to the rate of spring SST rise, representing 85.7% of the group and six of the dinoflagellate taxa (64.3% of the total) exhibited sensitivity to WSPD (Table S8).

### 3.3.3 | Causal relationships—effect of SST and WSPD on diatoms

The Granger test found no causal relationships between SST and the diatoms as a group with the exception of the February SST (Figure S3; Table S7). We found effects of SST on twelve of the individual diatom taxa representing 26.3% of the total and effects of the rate of spring SST rise on six of the diatom taxa representing 22.9% of the total but in neither case were the two most abundant taxa affected. The diatoms were far more affected by WSPD—Granger causality testing found significant links between twenty of the taxa and WSPD, 67% of the total and including the three most abundant taxa (Table S9).

### 3.3.4 | Interaction between SST and WSPD—effect on dinoflagellates

We looked for interactions between aspects of the SST (annual mean SST, spring SST change and fitted spring SST change) and annual mean WSPD in a regression model predicting the seasonal peaks of the phytoplankton groups (raw and weighted means)—such an interaction may indicate a collective effect of these factors on seasonal peaks. We found highly significant interaction terms between SST and WSPD for

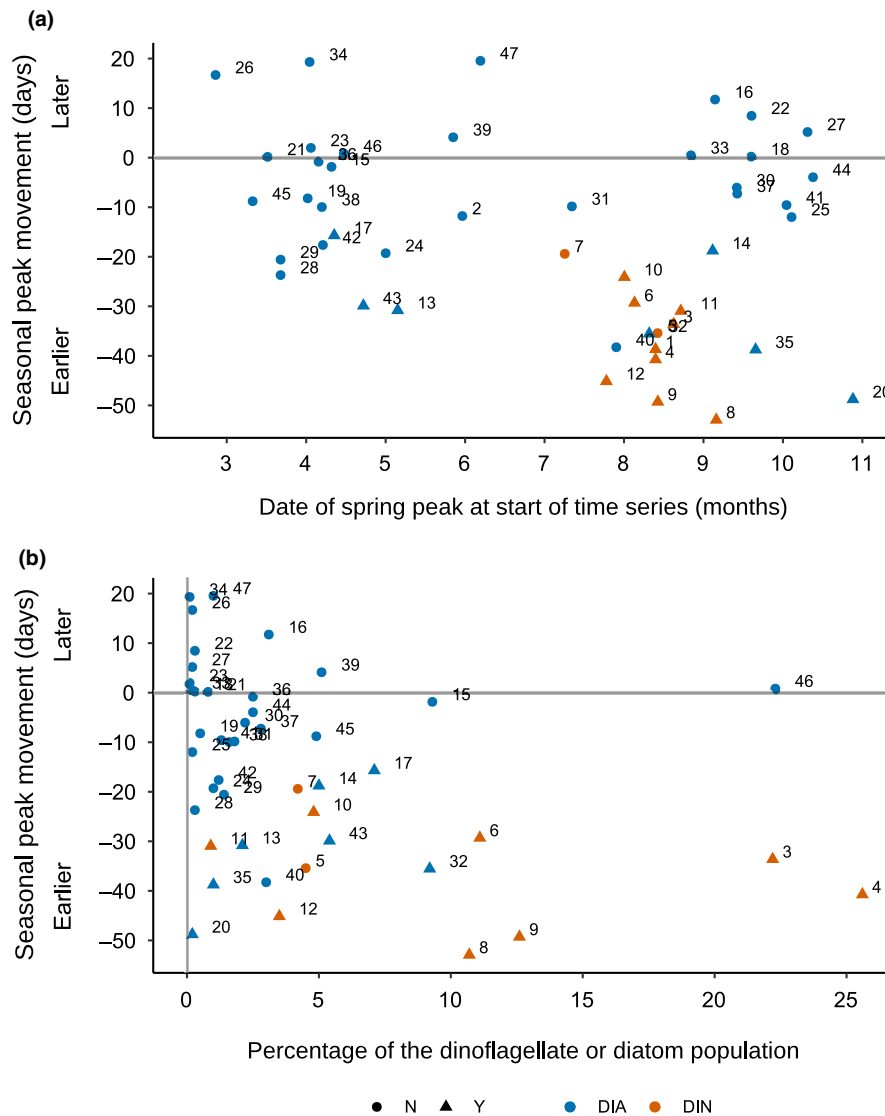
the dinoflagellates as a group ( $p$  values ranging from .0286 to <.0001) and there were significant effects of interaction between WSPD and both SST and spring SST rise on individual taxa, seven of the taxa exhibiting significant effects (90.5% of total) with the former and eight of the taxa (91.4%) with the latter SST measure. The six most abundant taxa (87% of total) exhibited effects of the interaction between WSPD and both SST measures. In all cases, the SST measures were significant while controlling for the WSPD, but the WSPD was not significant while controlling for the SST measures (Tables S10, S11).

### 3.3.5 | Interaction between SST and WSPD—effect on diatoms

The diatoms as a group exhibited no significant effects of interactions except for the diatom raw mean peak which was affected by the fitted spring SST change interacting with the mean WSPD ( $p = .0496$ ). Four of the individual taxa showed significant effects of interaction between WSPD and SST including three of the five most abundant and 36.9% overall. Seven of the individual taxa showed significant effects of interaction between WSPD and rate of spring SST rise, including five of the seven most abundant and 51.2% overall. Again, SST measures were significant while controlling for the WSPD, but the WSPD was not significant while controlling for the SST measures (Tables S10, S12).

### 3.3.6 | Multiple regression—both groups

Stepwise multiple regression analysis was also used, we found that the spring SST change was a common factor for the seasonal peaks of both phytoplankton groups. The WSPD was also a factor for the



**FIGURE 2** Changes in the timing of the seasonal peaks over six decades for each taxon compared with (a) the initial timing of seasonal peak and (b) the proportion of the dinoflagellate or diatom population. To examine trends in seasonal peak movement either (Y) fitted values were used if the seasonal peaks exhibited a significant correlation ( $p < .05$ ) with year, or (N) the means of the first and last decades were used. Key: 1: Dinoflagellate overall mean (a only), 2: Diatom overall mean (a only), 3: *Ceratium furca*, 4: *C. fusus*, 5: *C. horridum*, 6: *C. lineatum*, 7: *C. longipes*, 8: *C. macroceros*, 9: *C. tripos*, 10: *Dinophysis* spp., 11: *Prorocentrum* spp., 12: *Protoperdinium* spp., 13: *Asterionellopsis glacialis*, 14: *Chaetoceros Hyalochaete* spp. AU, 15: *C. Hyalochaete* spp. SP, 16: *C. Phaeoceros* spp. AU, 17: *C. Phaeoceros* spp. SP, 18: *Cylindrotheca closterium* AU, 19: *C. closterium* SP, 20: *Ditylum brightwellii* AU, 21: *D. brightwellii* SP, 22: *Eucampia zodiacus* AU, 23: *E. zodiacus* SP, 24: *Fragilaria* spp., 25: *Gyrosigma* spp. AU, 26: *G. spp.* SP, 27: *Navicula* spp. AU, 28: *N. spp.* SP, 29: *Odontella aurita*, 30: *O. sinensis*, 31: *Paralia sulcata*, 32: *Proboscia alata*, 33: *P. inermis* AU, 34: *P. inermis* SP, 35: *Pseudo nitzschia delicatissima* complex AU, 36: *P. N. delicatissima* complex SP, 37: *Pseudo nitzschia seriata* complex AU, 38: *P. N. seriata* complex SP, 39: *Rhizosolenia hebetata semispina*, 40: *R. imbricata*, 41: *R. styliformis* AU, 42: *R. styliformis* SP, 43: *Skeletonema costatum*, 44: *Thalassionema nitzschioides* AU, 45: *T. nitzschioides* SP, 46: *Thalassiosira* spp., 47: *Thalassiothrix longissima*, AU, autumn bloom; SP, spring bloom

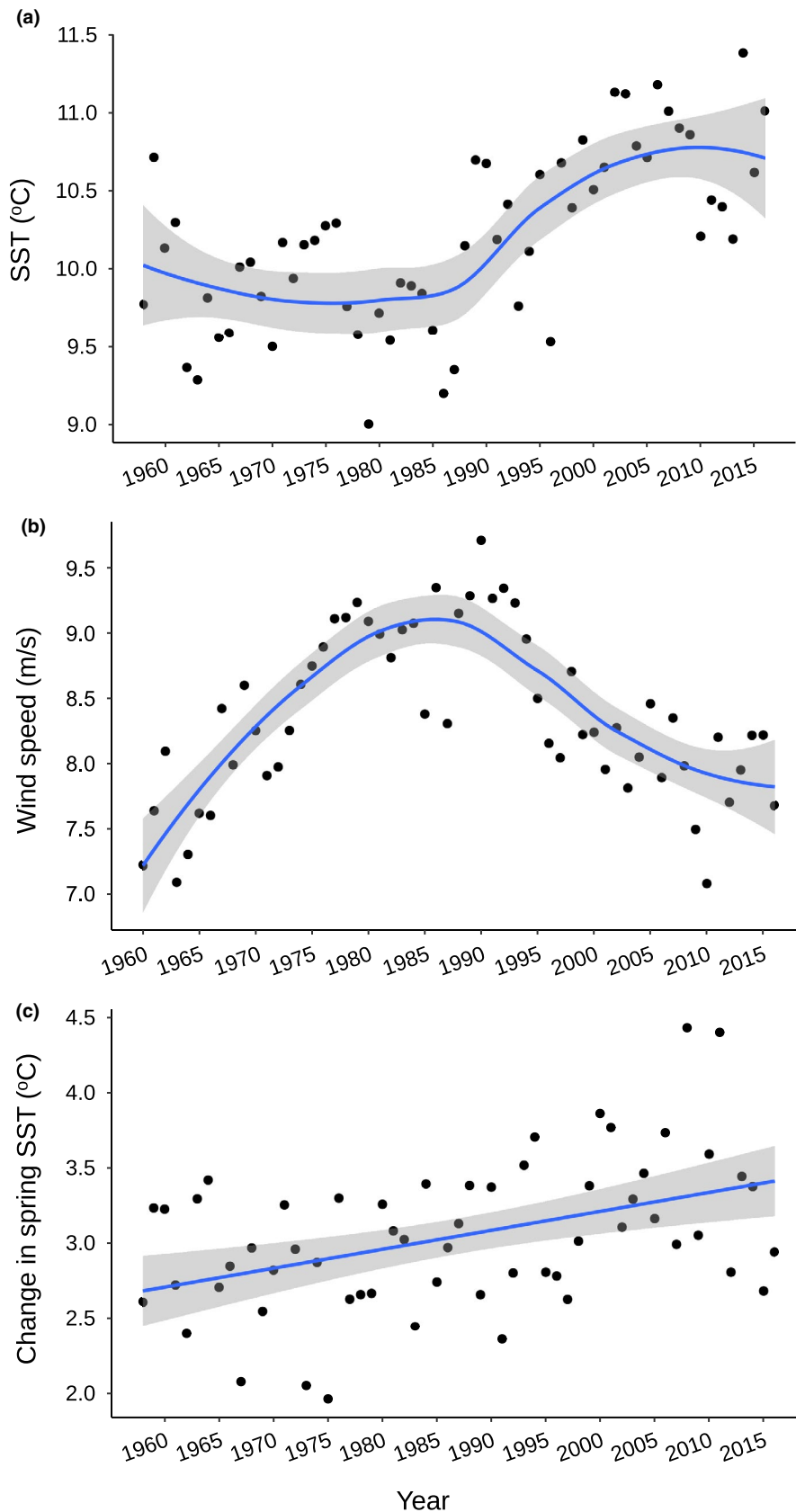
dinoflagellates but was not as significant as SST and spring SST change (Table S13).

### 3.4 | Changes in yearly abundance

The yearly abundance of the diatoms and dinoflagellates have shown differing patterns over the last six decades. The abundance

of the diatoms fell in the first two decades of the time series but has risen since then (Figure 4a), with *Thalassiosira* spp. increasing in relative abundance in the most recent four decades (Figure S5a). The abundance of the diatoms showed significant negative correlations with wind speed (Table S14). Stepwise multiple regression analysis (Table S15) and Granger causality analysis also find significant relationships between WSPD and diatom abundance (Table S16).



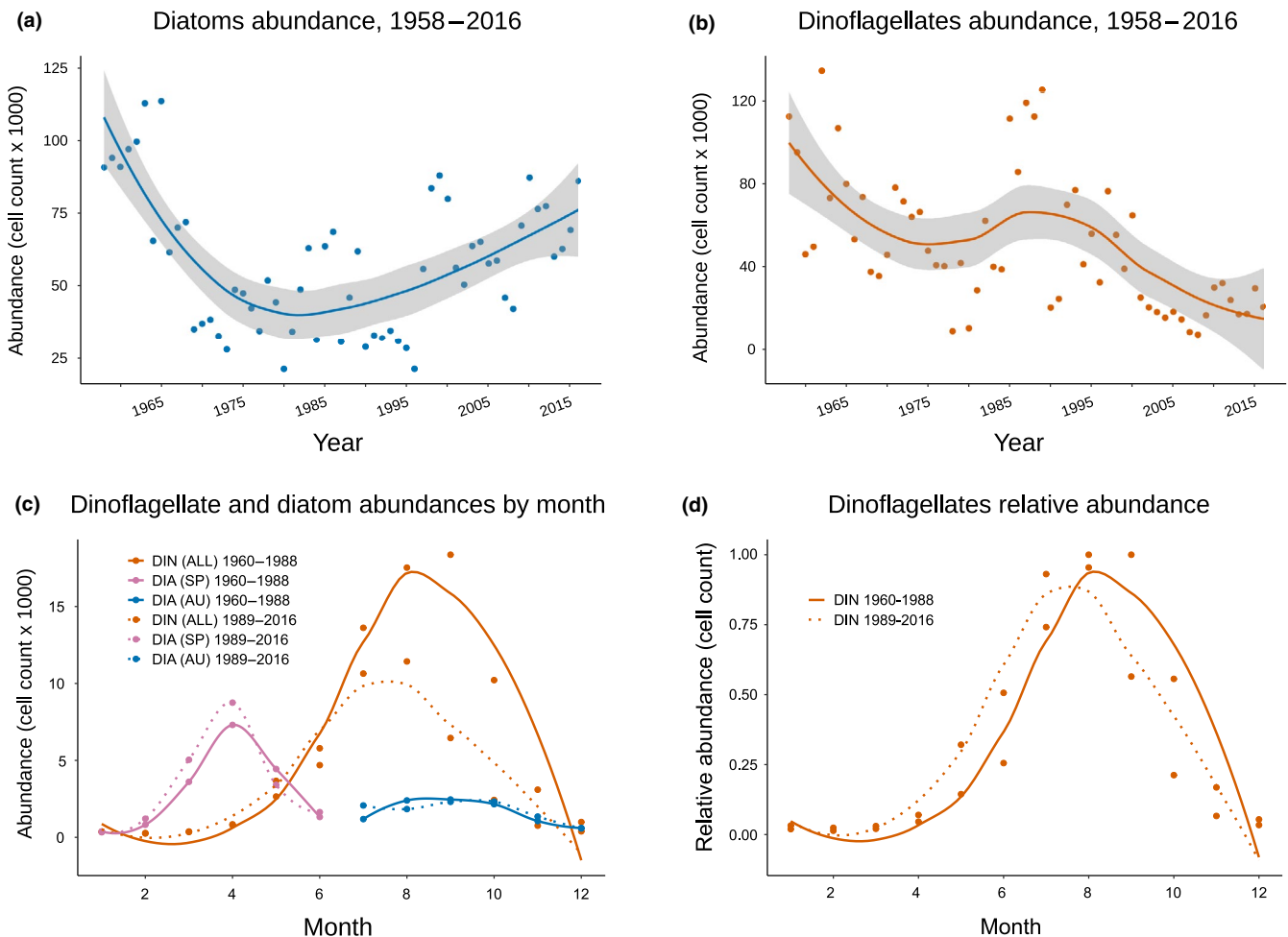


**FIGURE 3** Environmental drivers 1958–2016. (a) Annual mean sea surface temperature (SST), (b) Annual mean wind speed and (c) SST change in the spring months of March to May. Loess smoothers were used for locally weighted polynomial regression, the grey areas indicating the 95% confidence interval

The dinoflagellates by contrast have exhibited a general decline in abundance over the six decades (Figure 4b), the individual taxa generally maintaining their relative abundances (Figure S5b).

Dinoflagellate abundance showed significant negative correlations with SST and change of SST in spring (Table S14). Stepwise multiple regression analysis (Table S15) and Granger causality analysis (Table





**FIGURE 4** Abundance (total cell counts per sample) of the diatoms and dinoflagellates over six decades. (a) Yearly abundance of diatoms 1958–2016, (b) Yearly abundance of dinoflagellates 1958–2016, (c) Monthly abundances of the diatoms and dinoflagellates, (d) Relative monthly abundance of the dinoflagellates in the first and second halves of the time series. Loess smoothers were used in (a) and (b) for locally weighted polynomial regression, the grey areas indicating the 95% confidence intervals. Note that due to differences in counting protocols, direct comparison between the diatom and dinoflagellate populations cannot be made. AU, autumn bloom; DIA, diatoms; DIN, dinoflagellates; SP, spring bloom

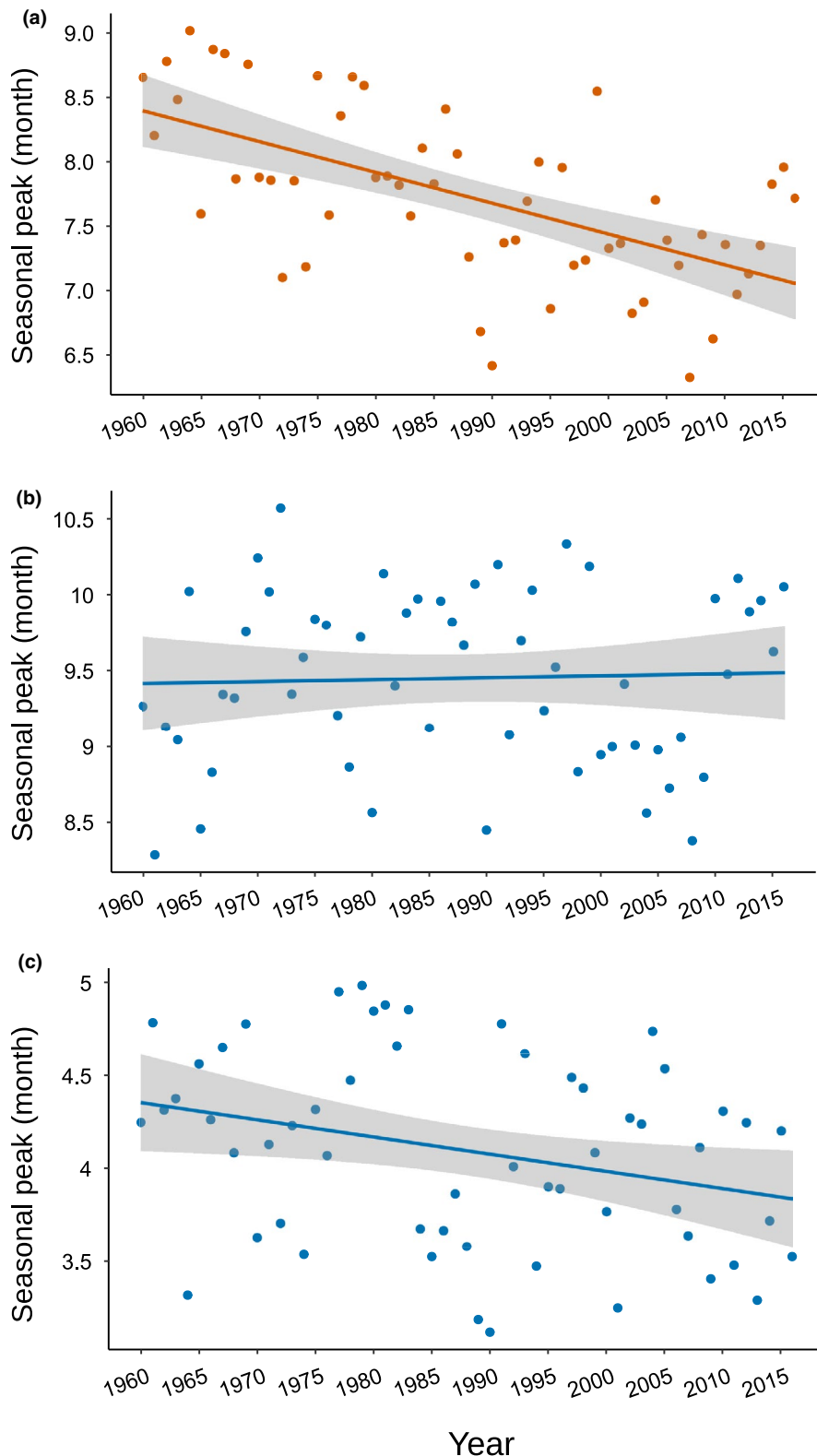
S16) also find significant relationships between SST and dinoflagellate abundance.

The changes in abundance of the two groups have had little effect on the duration or rate of rise and fall of their seasonal peaks (Figure 4c). Adjusting for the difference in abundance of the dinoflagellates, the similarity of the shape of the seasonal peak in the first and last three decades of this time series and its 39-day advancement is evident (Figure 4d).

### 3.5 | Differences between HAB taxa

Many of the individual taxa examined here are known to cause harmful blooms, including most of the dinoflagellate taxa. While all the dinoflagellate taxa have moved earlier in the year the diatom taxa have exhibited movement both earlier and later, including HAB taxa. Of the more abundant diatoms examined here the *Chaetoceros* taxa move in both directions and *Skeletonema costatum*

moves a month earlier, both genera known to cause HABs (Rensel & Whyte, 2003; Taylor, Fukuyo, Larsen, & Hallegraeff, 2003). The only diatom exhibiting a change in relative abundance, *Thalassiosira* spp., is a non-HAB taxon. Less abundant but among the diatom taxa exhibiting the largest shifts in seasonal peaks, *Pseudo nitzschia delicatissima* complex has moved nearly 40 days earlier, *Eucampia zodiacus* nine days later and *Proboscia inermis* 19 days later, these taxa are also being HAB taxa (Baek, Shimode, Han, & Kikuchi, 2008; Jiang et al., 2014; Nishikawa, Hori, Tanida, & Imai, 2007; Tang, Koch, & Gobler, 2010; Trainer et al., 2012). The majority of the dinoflagellate taxa examined here cause HABs (Baek et al., 2008; Taylor et al., 2003)—all these taxa have moved earlier in the year. Figure 5 illustrates the movement of three representative individual taxa known to cause HABs; the dinoflagellate *Ceratium fusus* has moved 41 days earlier (Figure 5a), the autumn bloom of the diatom *Chaetoceros Phaeoceros* spp. has moved 12 days later (Figure 5b) and the spring bloom of the same diatom has moved 16 days earlier (Figure 5c).



**FIGURE 5** Timing of the seasonal peak in abundance of the dinoflagellate *Ceratium fusus* (a) and the diatom *Chaetoceros* *Phaeoceros* spp. autumn bloom (b) and spring bloom (c). Loess smoothers were used for locally weighted polynomial regression, the grey areas indicating the 95% confidence interval for each line

## 4 | DISCUSSION

A systematic change is occurring in temperate ocean systems in the classically described seasonal phytoplankton progression from diatom to dinoflagellate abundance. Our results suggest that the classic bimodal phytoplankton abundance pattern of a diatom peak in abundance in

spring followed by a dinoflagellate peak in autumn with a drop in all phytoplankton abundance between peaks is being replaced by a single, long-lasting peak and that this change is driven by a major shift in the timing of peak abundance for dinoflagellates. Our work shows that changes in plankton phenology, noted by Edwards and Richardson (2004), have continued. Importantly, our analysis shows that there are

major differences in the phenological shifts between diatoms and dinoflagellates driven by environmental change. Furthermore, our results show a continued decline in the abundance of dinoflagellates that has been noted previously (Hinder et al., 2012). Hinder et al. (2012) reported that dinoflagellate abundance decreased across five decades with increasing temperature and windiness, although the mechanisms behind this relationship are unclear. Here, a key challenge is the disjunct between typically short duration laboratory experiments that examine phytoplankton responses to environmental conditions versus the much longer time-scales climate change operates across (Duarte, 2014).

The greater phenological change exhibited by dinoflagellates compared to diatoms may be linked to their different life histories. In temperate regions, the general seasonal pattern of plankton abundance has been well described (Boyce et al., 2017; Mann & Lazier, 2013). Typically diatoms bloom in spring and early summer when an increase in solar radiation and a reduction in wind-driven winter mixing lead to the development of stratification which, combined with increased illumination, means that diatoms can remain in the well-lit near-surface zones and propagate (Mann & Lazier, 2013). As summer progresses, stratification intensifies and near-surface nutrients become depleted, diatom abundance subsides and the dinoflagellates increasingly dominate using their mobility and mixotrophy to secure nutrients. The smaller autumn diatom bloom occurs as reducing solar heating weakens the thermocline and late-summer storms combine to increase vertical mixing, renewing the nutrients available to diatoms in the euphotic zone. In addition to the effects of nutrient stoichiometry, increasing heterotrophic pressure and parasitism may also be significant in the early diatom decline (Baker, Alegado, & Kemp, 2016; Brussaard, Kempers, Kop, Riegman, & Heldal, 1996; Guinder et al., 2018; Ji, Edwards, Mackas, Runge, & Thomas, 2010; Larsen et al., 2004). Given the importance of solar heating and reduced wind-driven mixing in the development of stratification, it is not unexpected that climate change may have profound implications for the phenology of plankton although often the specific links between environmental drivers and plankton abundance are opaque (Edwards & Richardson, 2004). Our analysis suggests that the most important environmental drivers of dinoflagellate phenology were the rate of spring SST rise, the absolute spring SST and interaction between SST and WSPD. The warming winter and spring SSTs that extend throughout the time series might be expected to lead to earlier spring stratification and promote earlier diatom blooms; however, this effect may have been counteracted by the increase in windiness that occurred in the first three decades of the time series which is also linked with the falling diatom numbers. Key to the finding that the spring diatom bloom has not advanced may be that at this time of year light levels may be limiting so diatoms can, generally, not bloom any earlier both because light intensities are too low and day length is too short. So compared to dinoflagellates, spring blooming diatoms may be more dependent on day length or light intensity rather than on temperature-mediated physiology, a view supported by observation in the East China Sea (Liu et al., 2016).

The importance of the rate of ocean warming occurring over a few weeks in spring has received little attention, especially

compared with the focus on absolute temperatures; yet, the rate of spring warming is presumably a good index of the likely development and strength of spring stratification and the resulting levels of both near-surface nutrients and light available for phytoplankton (García-Corral, Martínez-Ayala, Duarte, & Agustí, 2015; García-Martín et al., 2017; Smyth et al., 2014). Changes in environmental conditions are not impacting the timing of the diatom bloom but are causing the seasonal switch to dinoflagellates to occur earlier, which may be due to a more intense spring thermocline, hence limiting nutrient re-supply to near-surface waters as the spring and summer progress and so promote earlier removal of near-surface nutrients by diatoms. Of note here is that the increase in windiness evident in the first part of the time series largely occurs in winter and spring (Figure S4b), while in the summer windiness is much lower and hence may not have counteracted the effect of rising SSTs on summer stratification. Furthermore, it is possible that the increasing abundance of diatoms over the last three decades has resulted in a faster depletion of nutrients, leading to an earlier dinoflagellate bloom as suggested by Chiba et al. (2012). While it is well known that many areas of the ocean are warming, it is also often predicted that climate change will cause changes in storm occurrence and windiness, although these features of climate change receive less attention. The interplay we observed between windiness and SST highlights the importance of considering wind in future climate change scenarios.

We also observed differences in abundance between the two groups over the six decades. The consistent fall in dinoflagellate abundance may be due to the dinoflagellate peak moving earlier into warmer months. Boyce et al. (2017) found that phytoplankton phenocycle amplitude was negatively related to mean SST, especially at latitudes  $>30^{\circ}\text{N}$ , and Gittings, Raitsos, Krokos, and Hoteit (2018) found the same effect in a tropical system. This could be due to increased heterotrophic production in warmer conditions leading to increased grazing pressure (Boyce et al., 2017; Ji et al., 2010; Wasmund, Nausch, & Feistel, 2013). Similarly, Barton, Lozier, and Williams (2015) have highlighted the potentially important role of grazing in driving long-term phytoplankton variability. Long-term changes in the relative abundance of diatoms and dinoflagellates linked to temperature and nutrient levels have also been noted elsewhere (Cloern & Jassby, 2012; Xiao et al., 2018). Alternatively, the declining abundance of dinoflagellates in warmer temperatures could be due to parasitic infections such as fungal infections, which can accelerate the termination of a bloom and result in a lower peak population (Frenken et al., 2016). Serranito, Jamet, Rossi, and Jamet (2019) also noted long-term changes in the size of dinoflagellates at a site in the Mediterranean, linked to changing nutrient levels. The complexity of understanding the mechanisms underpinning long-term changes in phytoplankton populations is further complicated by the fact that, even among a group such as dinoflagellates, we recorded major differences in the trends of both phenology and abundance across individual taxa.

Harmful algal blooms (HAB) are well known as a threat to the health of humans, marine taxa and fisheries (Jiang et al., 2014; Trainer et al., 2012). Their frequency and geographic range has increased in

the last few decades (Anderson, Boerlage, & Dixon, 2017; Glibert, Berdalet, Burford, Pitcher, & Zhou, 2018; Gobler et al., 2017; Heil, Glibert, & Fan, 2005), and our results suggest that the timing of the seasonal peaks of HAB taxa are moving both earlier and later in the year: the seasonal peaks of most taxa known to cause harmful blooms and examined here have moved earlier in the year, but some of the diatom HAB taxa have moved later in the year.

Our results suggest a linear, rather than nonlinear, shift in the timing of peak abundance by dinoflagellates across 59 years and hence the pace of phenological change has remained constant. This pattern contrasts with that reported in terrestrial systems, where there are instances of the rate of phenological change itself changing over time, such as a decline in the rate of change of spring leaf unfolding which may be due to adaptation (Fu et al., 2015). For marine dinoflagellates in the North Sea, it may be that there are currently no selective pressures driving adaptation and hence the continuous phenological shift in seasonal timing that we observed across six decades. Our work also underscores the rate at which marine plankton respond to changing conditions in comparison with terrestrial systems—the scale of the change observed in dinoflagellate blooming is far greater than advances reported for terrestrial taxa (Keenan et al., 2014; Parmesan, 2006; Root et al., 2003; Thackeray et al., 2016; Wolkovich et al., 2012).

Our results help shed light on previously reported major changes that have occurred in plankton phenology. Using integrated measures of phytoplankton biomass from both in situ sampling as well as satellite observations, there is evidence of a shift in the North Sea from a pattern of two distinct phytoplankton seasonal peaks (spring vs. late summer) in the 1950s to a more continuous spring-summer bloom since the mid-1980s (Raitso et al., 2014). Our results show the earlier blooming of dinoflagellates is likely a key driver of this shift to a continuous bloom.

It is well known that phenological shifts in plankton prey availability can dominate levels of recruitment to commercial fisheries (Asch, 2015; Beaugrand, Brander, Lindley, Souissi, & Reid, 2003; Chevillot et al., 2017; Plagányi, 2017; Thackeray et al., 2016). Hence, while the reasons for the very different phenological shifts that we identified between diatoms and dinoflagellates remain equivocal, the wider ecosystem impacts are likely to be profound.

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## CONFLICT OF INTERESTS

The authors declare no competing financial interests.

## DATA AVAILABILITY STATEMENT

All code was written in the R statistical language (R Core Team, 2015), which is open source and freely available. Enquiries about the code used here can be directed to the corresponding author.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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