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# Phytoplankton life strategies, phenological shifts and climate change in the North Atlantic Ocean from 1850-2100

Loïck Kléparski<sup>1,2</sup>, Grégory Beaugrand<sup>1</sup>, Martin Edwards<sup>3,4</sup>, Clare Ostle<sup>2</sup>

<sup>1</sup> Univ. Littoral Côte d'Opale, CNRS, Univ. Lille, UMR 8187 - LOG - Laboratoire d'Océanologie et de Géosciences, F-62930 Wimereux, France

<sup>2</sup> Marine Biological Association, Citadel Hill, Plymouth PL1 2PB, United Kingdom.

<sup>3</sup> Plymouth Marine Laboratory, Prospect Place, Plymouth PL13DH, United Kingdom.

<sup>4</sup> University of Plymouth, School of Biological and Marine Sciences, Drake Circus, Plymouth, United Kingdom.

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**Running title:** Phytoplankton life strategies and climate

## Abstract

Significant phenological shifts induced by climate change are projected within the phytoplankton community. However, projections from current Earth System Models (ESMs) understandably rely on simplified community responses that do not consider evolutionary strategies manifested as various phenotypes and trait groups. Here, we use a species-based modelling approach, combined with large-scale plankton observations, to investigate past, contemporary and future phenological shifts in diatoms (grouped by their morphological traits) and dinoflagellates in three key areas of the North Atlantic Ocean (North Sea, North-East Atlantic and Labrador Sea) from 1850 to 2100. Our study reveals that the three phytoplanktonic groups exhibit coherent and different shifts in phenology and abundance throughout the North Atlantic Ocean. The seasonal duration of large flattened (i.e., oblate) diatoms is predicted to shrink and their abundance to decline, whereas the phenology of slow-sinking elongated (i.e., prolate) diatoms and of dinoflagellates is expected to expand and their abundance to rise, which may alter carbon export in this important sink region. The increase in prolates and dinoflagellates, two groups currently not considered in ESMs, may alleviate the negative influence of global climate change on oblates, which are responsible of massive peaks of biomass and carbon export in spring. We suggest that including prolates and dinoflagellates in models may improve our understanding of the influence of global climate change on the biological carbon cycle in the oceans.

## 1. Introduction

41 Current Earth System Models (ESMs) are projecting a decline in phytoplankton abundance (Bopp et  
42 al., 2013; Dutkiewicz et al., 2013; IPCC, 2019; Kwiatkowski et al., 2020) and anticipate significant  
43 phenological shifts (Asch et al., 2019; Henson et al., 2013, 2018; Yamaguchi et al., 2022) that may lead  
44 to trophic desynchronization and community reorganisation (Edwards & Richardson, 2004; IPCC, 2019;  
45 Winder & Schindler, 2004; Yamaguchi et al., 2022). Phenological shifts in phytoplankton are expected  
46 because of ocean warming (and also freshening in the poles) and its strengthening influence on water  
47 column stability, which is expected to diminish nutrients supply in the euphotic zone, favouring small  
48 phytoplankton (e.g., nanoplankton and picoplankton) at the expense of diatoms (Bopp et al., 2005;  
49 Marinov et al., 2010), a major group thought to be responsible for 40% of total marine primary  
50 production (Field et al., 1998; Tréguer et al., 2018).

51

52 Although shifts in phytoplankton phenology are now widely observed among marine and freshwater  
53 ecosystems (Friedland et al., 2018; Poloczanska et al., 2013; Thackeray et al., 2016), the examination  
54 of diatom seasonality in some regions of the North Atlantic suggests a relative stability (Chivers et al.,  
55 2020; Edwards & Richardson, 2004). These unexpected results may originate from the range of  
56 strategies that have been developed by diatoms and enable them to occur in diverse environments  
57 (Kemp & Villareal, 2013, 2018). Among those strategies, diatom morphological traits might have an  
58 important influence on species phenology (Kléparski et al., 2022). Indeed, it has recently been shown  
59 that diatom cell shape has evolved as a key adaptation that confers to a species a specific phenology,  
60 oblate (i.e., flattened) diatoms being dominant in well-mixed, nutrients-rich, low-stratified waters  
61 whereas prolate (i.e., elongated) diatoms dominate in the stratified low-nutrient waters (Kléparski et  
62 al., 2022). Cell elongation of prolate diatoms enhances their buoyancy without altering their capacity  
63 to absorb nutrients, conferring them a selective advantage in stratified low-nutrient waters (Kléparski  
64 et al., 2022).

65

66 Most projected phenological shifts (Asch et al., 2019; Henson et al., 2013, 2018; Yamaguchi et al.,  
67 2022), which rely on the analyses of variables such as chlorophyll concentration or net primary  
68 production, originate from ESMs that only consider a few phytoplankton types (only one for diatoms  
69 and none for dinoflagellates). Therefore, those models cannot anticipate subtle changes in  
70 phytoplankton community (Kemp & Villareal, 2018; Séférian et al., 2020; Tréguer et al., 2018) and  
71 some discrepancies have been reported between satellite observations and model projections (Cabré  
72 et al., 2016). Here we applied a species-based modelling approach, combined with large-scale plankton  
73 observations, to investigate past, contemporary and future long-term changes (1850-2100) in the  
74 phenology of oblates, prolates and dinoflagellates by using six ESMs and two climate warming  
75 scenarios (a medium and a high emission scenario, i.e., SSP2-4.5 and SSP5-8.5).

76

## 77 **2. Materials and Methods**

78

### 79 **2.1. Biological data**

80

81 Phytoplankton data came from the Continuous Plankton Recorder (CPR) survey. The CPR is a long-term  
82 plankton monitoring programme that has collected plankton on a monthly basis in the North Atlantic  
83 Ocean and its adjacent seas since 1946. The sampling instrument is a high-speed plankton recorder  
84 towed behind voluntary merchant ships (called “ships of opportunity”) at a depth of approximately 7m  
85 (Beaugrand et al., 2003; Reid et al., 2003). As phytoplankton sampling remained unchanged since 1958

86 (Warner & Hays, 1994) and historical climatic simulations ended in 2014 (see section 2.2 below), we  
 87 used the abundance data collected for the diatoms and the dinoflagellates between 1958 and 2014.  
 88 Each value of abundance corresponds to a number of cells per CPR sample, which corresponds to ~3  
 89 m<sup>3</sup> of seawater filtered (Jonas et al., 2004). Species that were first identified after 1958 were discarded  
 90 from the analyses. In order to account for the climatic variability that was observed in the North  
 91 Atlantic sector during the period (Beaugrand et al., 2019; Edwards et al., 2002) and minimize the noise  
 92 associated with the CPR sampling (e.g., exceptional high abundance caused by local hydro-  
 93 meteorological events, patchiness or abundance misestimation), we calculated a daily mean  
 94 abundance climatology (based on 365 days) for each species for three 18-year periods: 1958-1976,  
 95 1977-1995 and 1996-2014 (a total of 365 days x 3 = 1095 days). The three periods were chosen to be  
 96 of even length. Therefore, we were able to consider the seasonal signal and the long-term trend, which  
 97 would have been impossible by using a single climatology based on the entire available time period  
 98 (Mannocci et al., 2017). Climatologies were estimated in three distinct oceanic regions of the North  
 99 Atlantic: (i) the North Sea (51°N to 60°N, -3°E to 9°E), (ii) the North-East Atlantic (61°N to 63.5°N, -21°E  
 100 to -8°E) and (iii) the Labrador Sea (48°N to 60°N, -55°E to -40°E). Climatologies were calculated in a  
 101 given region for the species/taxa that were present in more than 100 CPR samples. A total of 44  
 102 species/taxa were therefore selected (Supplementary Table S1). Climatologies (for the three periods)  
 103 were smoothed in each region by means of a double 6-order simple moving average (i.e., thirteen-day  
 104 window) and subsequently standardised between 0 and 1, applying the approach of Caracciolo and  
 105 colleagues (Caracciolo et al., 2021). Standardisation was performed as follows:

106

$$107 \quad A_{(i,j)}^* = \frac{A_{ij}}{\max(A_j)} \quad (1)$$

108

109 With  $A_{(i,j)}^*$  the standardised abundance of species  $j$  on day  $i$ ,  $A_{ij}$  the abundance of species  $j$  on day  $i$   
 110 and  $\max(A_j)$  the maximal abundance of species  $j$  in the three regions (i.e., North Sea, North-East  
 111 Atlantic and Labrador Sea) between 1958 and 2014. By doing so, the variations in  $A_{(i,j)}^*$  reflect both  
 112 the differences within and between the three regions. We then estimated the 90<sup>th</sup> percentile of the  
 113 abundance (P90) of each species using the non-standardised daily climatologies in the three oceanic  
 114 regions (Supplementary Table S1).

115

116 Species were divided into three groups: oblate and prolate diatoms and dinoflagellates, which are  
 117 known to have distinct environmental requirements (Irwin et al., 2012; Kléparski et al., 2022) (see  
 118 Supplementary Table S1). The oblate group gathered diatoms (species or taxa) that have a mean cell  
 119 diameter greater than their mean cell height and the prolate group the diatoms (species or taxa) that  
 120 have a mean cell diameter smaller than their mean cell height. Information on diatom cell shapes were  
 121 retrieved from Kléparski *et. al* 2022 (Kléparski et al., 2022) (their Figure 3). Mean monthly abundances  
 122 between 1958 and 2014 were estimated for each group and in each oceanic region (Figure 1a-i). Data  
 123 were subsequently smoothed by means of a first-order simple moving average (i.e., three-month  
 124 smoothing window) and then standardised between 0 and 1 by using the 90<sup>th</sup> percentile of the monthly  
 125 abundance of each taxonomic group (P90<sub>m</sub>):

126

$$127 \quad N_m^* = \frac{N_m}{P90_m} \quad (2)$$

128

129 With  $N_m^*$  the standardised monthly abundance of a taxonomic group for month  $m$ ,  $N_m$  the monthly  
130 abundance for month  $m$  and  $P90_m$  the 90<sup>th</sup> percentile of the monthly abundance of the taxonomic  
131 group. In rare cases, standardised monthly abundance above 1 were fixed to 1. We chose to use the  
132 90<sup>th</sup> percentile here instead of the maximum abundance value (as in equation (1)) because the latter  
133 would have been too sensitive to outliers that may originate from multiple causes (e.g., exceptional  
134 abundance, patchiness or abundance misestimated from only 3m<sup>3</sup> of seawater filtered; see  
135 Supplementary Figure S1).

136

## 137 2.2. CMIP6 climate simulations 1850-2100

138

139 Species responses to environmental variability was modelled by using three environmental variables  
140 known to influence phytoplankton phenology at high latitudes (Beaugrand & Kirby, 2018; Boyce et al.,  
141 2017; Caracciolo et al., 2021; Lewandowska & Sommer, 2010; Miller, 2004): i.e., Sea Surface  
142 Temperature (SST; °C), Surface Downwelling Shortwave Radiation (SDSR; W m<sup>-2</sup>) and dissolved nitrate  
143 concentration (mol m<sup>-3</sup>). Climate projections for the three variables originated from the Coupled Model  
144 Intercomparison Project Phase 6 (CMIP6)(Eyring et al., 2016) and were obtained from the Earth System  
145 Grid Federation (ESGF). We used the Shared Socioeconomic Pathways (SSP) 2-4.5 and 5-8.5  
146 corresponding respectively to a medium and a high radiative forcing by 2100 (4.5 W m<sup>-2</sup> and 8.5 W m<sup>-2</sup>)  
147 (O'Neill et al., 2016, 2017). The simulations of six different ESMs (i.e., CNRM-ESM2-1, GFDL-ESM4,  
148 IPSL-CM6A-LR, MPI-ESM1-2-LR, NorESM2-LM and UKESM1-0-LL) covering the time period 1850-2014  
149 (historical simulation) and 2015-2100 (future projections for the two SSP scenarios) were used. An  
150 historical perspective is important to better understand the magnitude of the present and future shifts  
151 (Beaugrand et al., 2015). The six ESMs were chosen on the basis of data availability for 1850-2100 and  
152 the two warming scenarios. All the data were interpolated into daily on a 0.5° by 0.5° regular grid. Key  
153 references (i.e., DOI and dataset version) are provided in Supplementary Text S1. Long-term projected  
154 changes of the three variables, for the six models, the two scenarios and the three regions are  
155 displayed in Supplementary Figures S2-4.

156

## 157 2.3. The MacroEcological Theory on the Arrangement of Life (METAL)

158

159 A framework from the METAL theory was used to investigate past, contemporary and future  
160 phenological changes of the three taxonomic groups. METAL is a theory that attempts to explain how  
161 biodiversity, from the individual to the community level, is organised in space and time and how it  
162 responds to environmental changes (Beaugrand, 2015). Based on the concept of the ecological niche  
163 *sensu* Hutchinson (i.e., the set of conditions enabling a species to growth and reproduce)(Hutchinson,  
164 1957), one fundamental assumption of METAL is that the niche-environment interaction is a  
165 fundamental interaction that enables one to unify and predict a large number of ecological and  
166 biogeographical phenomena, as well as the effect of climate-induced environmental changes on  
167 individuals, species and communities (Beaugrand, 2015; Beaugrand & Kirby, 2016, 2018). Recently, it  
168 has been shown that a framework originating from METAL and using the data collected by the CPR  
169 survey, could also explain phytoplankton phenology and the resulting annual plankton succession in  
170 the North Sea, based on SST, SDSR and nitrate concentration (Caracciolo et al., 2021). By creating a  
171 local pseudo-community, composed of fictive species (i.e., pseudo-species), it was possible to  
172 reconstruct at a species level phytoplankton phenology and at a community level the annual plankton  
173 succession (Caracciolo et al., 2021). We therefore applied the same framework here to explore how

174 diatom (oblate and prolate) and dinoflagellate phenology might be modified in the coming decades  
175 with global climate change.

176

#### 177 2.4. Niches characterisation

178

179 We first estimated daily climatologies (based on 365 days) of the three environmental variables  
180 described above (i.e., SST, SDR and nitrate concentration) for three time periods (1958-1976, 1977-  
181 1995 and 1996-2014 i.e., 365 days x 3 = 1095 days), three oceanic regions (North Sea, North-East  
182 Atlantic and Labrador Sea) and based on six ESMs (i.e., CNRM-ESM2-1, GFDL-ESM4, IPSL-CM6A-LR,  
183 MPI-ESM1-2-LR, NorESM2-LM and UKESM1-0-LL). The daily climatologies were then visually compared  
184 against the observations originating from the ERA5 dataset (for SST and SDR;  
185 <https://cds.climate.copernicus.eu/cdsapp#!/dataset/reanalysis-era5-pressure-levels?tab=overview>)  
186 and the World Ocean Atlas (for nitrate concentration; [https://www.ncei.noaa.gov/products/world-](https://www.ncei.noaa.gov/products/world-ocean-atlas)  
187 [ocean-atlas](https://www.ncei.noaa.gov/products/world-ocean-atlas)). For SST and SDR, because of data availability, daily means were estimated in the three  
188 regions between 1959 and 2014 and then converted into daily climatologies for the three time periods  
189 (1959-1976, 1977-1995 and 1996-2014). For nitrate concentration, a monthly climatology for the time  
190 period 1955-2017 was downloaded from the World Ocean Atlas and a mean was then calculated over  
191 the three oceanic regions. Comparisons between observed and reconstructed climatologies from the  
192 six ESMs in the North Sea, the North-East Atlantic and the Labrador Sea are displayed in Supplementary  
193 Figures S5, S6 and S7 respectively.

194

195 Then, we generated a set of 1,755,000 pseudo-species (i.e., fictive species) and we calculated their  
196 abundance along the daily climatologies by using a three-dimensional Gaussian niche (Caracciolo et  
197 al., 2021):

198

$$199 \quad B = ce^{-\frac{1}{2}\left[\left(\frac{x_1-x_{opt1}}{t_1}\right)^2 + \dots + \left(\frac{x_n-x_{optn}}{t_n}\right)^2\right]} \quad (3)$$

200

201 With  $B$  the abundance of a pseudo-species along a given environmental gradient  $x$ ,  $c$  the maximum  
202 abundance of a pseudo-species (here  $c$  was fixed to 1),  $x_1$  to  $x_n$  the environmental gradients, with  $n=3$   
203 (SST, SDR and nitrate concentration).  $x_{opt1}$  to  $x_{optn}$  are the ecological niche optima along  $x_1$  to  $x_n$   
204 and  $t_1$  to  $t_n$  the niche amplitude along  $x_1$  to  $x_n$ . Niche optima were defined for SST from 0 to 25°C  
205 every 1°C, for SDR from 0 to 400 W m<sup>-2</sup> every 40 W m<sup>-2</sup> and for nitrate concentration from 0.001 to  
206 0.05 mol m<sup>-3</sup> every 0.005 mol m<sup>-3</sup>. Niche amplitudes were defined for SST from 1 to 10°C every 2°C and  
207 for nitrate concentration from 0.001 to 0.015 mol m<sup>-3</sup> every 0.001 mol m<sup>-3</sup>. Amplitude for SDR were  
208 defined as followed: 1, 3, 5, 8, 10, 15, 20, 50 and 100 W m<sup>-2</sup>. Each pseudo-species was therefore defined  
209 by a unique combination of optima and amplitudes along the three environmental gradient, i.e., by a  
210 unique niche, according to the principle of competitive exclusion (Gause, 1934; Hutchinson, 1978).  
211 Therefore, the total number of pseudo-species (1,755,000) corresponds to the total number of unique  
212 combinations. Niche intervals were chosen to optimise computational cost while covering the largest  
213 set of combinations.

214

215 We compared the modelled and observed (CPR) abundance at a species and a group (oblates, prolates  
216 and dinoflagellates) level. At a species level, we calculated the Mean Absolute Error (MAE) between  
217 the daily abundance climatology (based on 365 days x 3 temporal periods = 1095 days) of each species

218 and each of the 1,755,000 pseudo-species we created, for each oceanic region and ESM. Some species  
 219 exhibited erratic short peaks that were difficult to explain in some regions. To prevent our model to  
 220 be influenced by these events that might be related to misidentification, CPR silk contamination or  
 221 species expatriation (i.e. species occurring in unsuitable environmental conditions because of their  
 222 passive drift induced by oceanic currents) (Pulliam, 2000; van der Spoel, 1994), we only summed MAEs  
 223 from the regions where a given species had a standardised abundance greater than 0.1 during more  
 224 than 90 days. The use of different thresholds did not alter our conclusions substantially. Finally, for  
 225 each ESM, we chose a pseudo-species to represent an observed species when it has the lowest MAE  
 226 in the three regions (Figure 2a-c and Supplementary Table S2). Therefore, the 44 species may be  
 227 characterised by different pseudo-species from one ESM to another. This allowed us to examine inter-  
 228 ESM variability (Supplementary Figures S2-7) and the uncertainty associated with the characterisation  
 229 of a species niche but also to create a unique bias correction for each ESM. Relationships between  
 230 modelled and observed daily abundance species climatologies in each region were examined by means  
 231 of a Spearman rank correlation (Figure 2d-f and Supplementary Tables S3-S5).

232  
 233 In order to assess whether the use of climatologies based on three temporal periods (1958-1976, 1977-  
 234 1995 and 1996-2014) might influence model skill and performance, we also estimated the MAEs  
 235 between the observed and modelled daily abundance climatologies based on a single (1958-2014) and  
 236 two temporal periods (1958-1985 and 1986-2014) (Supplementary Figures S8-S9).

## 237 238 2.5. Long-term changes in the abundance of the three taxonomic groups

239  
 240 Daily abundances of the 44 species were estimated from Equation 3 between 1850 and 2100, using  
 241 environmental variables assessed from the six models and for the two scenarios (Section 2.4 above).  
 242 To assess the mean abundance of each group, we weighted species abundance by using their P90  
 243 (Section 2.1 and Supplementary Table S1) to account for species contemporary difference in  
 244 abundance within the three groups (oblates, prolates, and dinoflagellates). We used the 90<sup>th</sup> percentile  
 245 instead of the maximum abundance value because the latter would have been too sensitive to outliers  
 246 that may originate from multiple causes (e.g., exceptional abundance, patchiness or abundance  
 247 misestimated from only 3m<sup>3</sup> of seawater filtered). Predicted abundances were finally standardised  
 248 between 0 (the lowest abundance) and 1 (the highest) for each taxonomic group, all ESMs and  
 249 scenarios as follows (Figures 4b-g, 5b-g and 6b-g-):

$$250$$

$$251 D_m^* = \frac{D_{(m)} - \min(D)}{\max(D) - \min(D)} \quad (4)$$

252  
 253 With  $D_m^*$  the standardised predicted abundance of a group for a given ESM, scenario and month  $m$ ,  
 254  $D_m$  the predicted abundance for month  $m$  and  $\min(D)$  and  $\max(D)$  the minimal and maximal  
 255 predicted abundance between 1850 and 2100 in a given oceanic region, respectively. Finally, the  
 256 relationships between modelled and observed standardised monthly abundances were quantified for  
 257 1958-2014 (i.e., overlapping period of observed and modelled data) by using the Spearman correlation  
 258 coefficient (Figure 1a-r and Table 1). Differences between observed and modelled standardised  
 259 monthly abundances were also calculated to compare the seasonal and long-term trends (Figure 1s-  
 260  $\alpha$ ).

261

262 To test whether the long-term changes in phenology and abundance of the three groups were well  
263 modelled by our approach, we also estimated the annual (long-term changes) and monthly (seasonal  
264 variations) average of the modelled and observed abundances of the three groups in the three regions,  
265 between 1958 and 2014 (Supplementary Figures S10-11). Annual and monthly patterns were  
266 subsequently compared by means of a Spearman rank correlation coefficient (Supplementary Tables  
267 S6-7).

268

## 269 2.6. Long-term phenological changes of the three taxonomic groups.

270

271 We examined phenological shifts of the three taxonomic groups between 1850 and 2100, for the two  
272 scenarios and the six ESMs in the three regions. Average daily abundances of each group were  
273 smoothed by means of a 15-order moving average (i.e., time scale covering a month) and then, for  
274 each year between 1850 and 2100, we estimated six phenological indices: i.e., (1) Maximum Annual  
275 Abundance (MAA), (2) the day where MAA is reached, (3) initiation and (4) termination of the Seasonal  
276 Reproductive Period (SRP), i.e., the first and the last days where the abundance is  $\geq 50\%$  of MAA, (5)  
277 seasonal duration, i.e., the number of consecutive days where abundance is  $\geq 50\%$  of MAA, and (6)  
278 Integrated Mean Annual Abundance (IMAA) (Figure 3). The six indices were calculated for each  
279 taxonomic group, all models, scenarios and North Atlantic regions. Bimodality (i.e., two population  
280 peaks within a single year) was sometimes observed for the diatoms in the three regions, but as this  
281 pattern fluctuated in time (i.e. short erratic peaks) and was not well reproduced by all ESMs, when a  
282 bimodality was observed we only considered the peak with the highest abundance. An average of the  
283 results of the six ESMs was then calculated for 1850-2100 for each scenario and North Atlantic region  
284 (Figures 4-6). In addition, we focussed on three decades: 1850-1859, 2000-2009 and 2090-2099. For  
285 these decades, we assessed the inter-model average and the associated standard deviation of each  
286 index (mean  $\pm$  uncertainty; Supplementary Tables S8-16)(Kwiatkowski et al., 2020).

287

## 288 3. Results

289

290 Visual comparisons between observed and reconstructed SST, SDSR and nitrate concentration showed  
291 that the seasonal cycle and the long-term trend of each variable was in general well reconstructed by  
292 the ESMs in the three oceanic regions and for the three time periods (except for nitrate long-term  
293 trend, see Materials and Method and Supplementary Figures S5, S6 and S7).

294

### 295 3.1. Model performances

296

297 Model performance was first assessed by visually comparing the observed and modelled daily  
298 abundance of each species for the three periods and North Atlantic regions (Supplementary Animation  
299 S1-3). The phenology of most species was well modelled by our approach and the Mean Absolute Error  
300 (MAE) between the observed and modelled abundance was generally low (below 0.1 for diatoms and  
301 below 0.2 for dinoflagellates; Figure 2a-c and Supplementary Table S2; see Materials and Methods).  
302 MAEs calculated between observed and modelled abundance based on a single (1958-2014) or two  
303 temporal periods (1958-1985 and 1986-2014) climatologies were higher, indicating that our model  
304 performed better when based on the three temporal periods climatologies (Supplementary Figures S8  
305 and S9). We then estimated the Spearman rank correlation coefficient between daily observed and  
306 modelled patterns, which revealed that for most species, correlations were highly positive (Figure 2d-



307 f and Supplementary Tables S3-S5). A few low correlations were observed, however, indicating that  
308 for some species our approach did not work well in some North Atlantic regions and for some ESMs.  
309 Low correlations between observations and model reconstructions may be caused by some regional  
310 hydro-meteorological events that are not well reproduced by an ESM or by some methodological  
311 limitations of our approach (see Discussion). However, their weight in the subsequent analyses was  
312 low, as shown by the value of their P90 (i.e., the 90<sup>th</sup> percentile of their abundance, Materials and  
313 Methods, Figure 2d-f and Supplementary Table S1); the higher the P90, the higher the abundance of a  
314 species in a North Atlantic region and therefore the greater its weight in subsequent analyses at the  
315 group level (Figure 4-6).

316

317 Modelled species abundances were finally aggregated at a monthly scale for each group (oblates,  
318 prolates and dinoflagellates) by weighting the abundance of each species according to the value of  
319 their P90 (Supplementary Table S1). A monthly scale was first chosen for comparison of the modelling  
320 approach with the *in situ* monthly observations collected by the CPR survey, whom sampling is carried  
321 out at a monthly interval (Richardson et al., 2006). Differences between observed and modelled long-  
322 term changes in monthly abundance showed that model performance varied greatly among regions  
323 and species groups, mostly because of the nature of the CPR data (i.e., large variability in observed  
324 abundance; see Figure 1a-i versus 1j-r and Discussion) and because the reconstructed climatic  
325 variability was not supposed to exactly match the variability that was observed between 1958 and  
326 2014 (Stock et al., 2011). On the contrary, Spearman rank correlations calculated between observed  
327 and modelled mean monthly abundances were all positively correlated significantly, although the  
328 correlations were statistically more significant in the North Sea and the North-East Atlantic than in the  
329 Labrador Sea (Spearman rank correlations coefficient between 0.7 and 0.83 in the North Sea, 0.64 and  
330 0.73 in the North-East Atlantic and 0.5 and 0.58 in the Labrador Sea; Figure 1 and Table 1). The  
331 comparison between long-term changes in the annual abundance of prolates in the three regions, of  
332 oblates in the North-East Atlantic and of oblates and dinoflagellates in the Labrador Sea were globally  
333 well reconstructed (Supplementary Figure S10), but the correlations were not always significant,  
334 suggesting that some periods and years did not match well (Supplementary Table S6). On the contrary,  
335 our model did not fully reconstruct the long-term trends in oblates and dinoflagellates in the North  
336 Sea and of dinoflagellates in the North-East Atlantic (Supplementary Figure S10), which was confirmed  
337 by Spearman rank correlations (Supplementary Table S6). Such difficulties to explain observed long-  
338 term changes in abundance were expected since ESMs are known to have some difficulties to  
339 reconstruct high frequency natural variability in climate well (Stock et al., 2011). Finally, the  
340 comparison between observed and modelled monthly changes in abundance revealed that the  
341 seasonal cycles of the three groups in the three regions were correctly reconstructed (significant  
342 Spearman rank correlations above 0.85; Supplementary Figure S11 and Supplementary Table S7).

343

344

### 345 3.2. Phenological shifts in the North Atlantic

346

347 In the North Atlantic Ocean, phenological shifts projected by our models were relatively moderate for  
348 1850-1950 (Figures 4-6). Major changes were expected to occur from the end of 1970s onwards when  
349 the rate of ocean warming increased and led to an increase in water column stratification (IPCC, 2019)  
350 (see also Supplementary Figures S2-S4). A decline in oblate abundance was generally observed under  
351 both scenarios in the three regions, associated with a reduction of their SRP, whereas an increase in

352 prolate and dinoflagellate abundance was projected, associated with an expansion of their SRP (Figures  
353 4-6). Expectedly, the magnitude of the projected changes in phenology and abundance appeared to  
354 be more important under the high warming scenario (Figures 4-6).

355

### 356 3.3. Phenological shifts in the North Sea

357

358 In the North Sea (Figure 4a), modelled long-term daily phenological changes exhibited similar patterns  
359 for both SSP scenarios, with a shift in the diatom community composition, although changes were  
360 highest under SSP5-8.5 (Figure 4b-q). Oblate diatoms are expected to decline, the MAA decreasing  
361 from  $1671.1 \pm 494.7$  cells per CPR sample in 1850-1859 to  $1176.9 \pm 573.2$  or  $785.1 \pm 347.7$  cells per  
362 CPR sample in 2090-2099 for scenarios SSP2-4.5 and SSP5-8.5, respectively (Figure 4b and e and  
363 Supplementary Table S8). In contrast, prolate MAA rose from  $302 \pm 53.3$  cells per CPR sample in 1850-  
364 1859 to  $360.5 \pm 77.5$  or  $392.6 \pm 115.5$  cells per CPR sample in 2090-2099 for SSP2-4.5 and SSP5-8.5,  
365 respectively (Figure 4c and f and Supplementary Table S9). No significant changes in the duration of  
366 the SRP was found for both groups (Figure 4h-i and Supplementary Tables S8-9), although they exhibit  
367 an earlier and a later (both initiation and termination) phenology, respectively (Figure 4j-k and m-n  
368 and Supplementary Tables S8-9). These phenological shifts were accompanied by a shift in their IMAA,  
369 our results suggesting that oblates may experience a strong decrease from  $390 \pm 92.8$  cells per CPR  
370 sample in 1850-1859 to  $283.8 \pm 97.4$  or  $192 \pm 59$  cells per CPR sample in 2090-2099 for scenarios SSP2-  
371 4.5 and SSP5-8.5, respectively. An opposite pattern is predicted for prolates, although it may be less  
372 important (from  $122.8 \pm 32.7$  cells per CPR sample in 1850-1859 to  $134.5 \pm 18.6$  or  $148.8 \pm 30.1$  cells  
373 per CPR sample in 2090-2099 for SSP2-4.5 and SSP5-8.5, respectively; Figure 4p-q and Supplementary  
374 Tables S8-9).

375

376 Modelled changes in dinoflagellates exhibited a phenological expansion. Their MAA remained constant  
377 throughout the period, although they decreased at the very end of the century under SSP5-8.5 from  
378  $2853.9 \pm 336.3$  cells per CPR sample in 1850-1859 to  $2599.3 \pm 553.2$  in 2090-2099 (Figure 4d and g and  
379 Supplementary Table S10). The duration of their SRP is expected to rise throughout the twenty first  
380 century (from a mean of  $103 \pm 16$  days in 1850-1859 to  $107 \pm 6$  days in 2000-2009 and to  $127 \pm 13$  or  
381  $143 \pm 25$  days in 2090-2099 under SSP2-4.5 and SSP5-8.5 respectively; Figure 4h-i and Supplementary  
382 Table S10) with both an earlier initiation and a later termination of their SRP (Figure 4l and o and  
383 Supplementary Table S10), associated with an increase in their IMAA (Figure 4p-q and Supplementary  
384 Table S10).

385

### 386 3.4. Phenological shifts in the North-East Atlantic

387

388 In the North-East Atlantic region (Figure 5a), phenological shifts were also predicted by our approach,  
389 the magnitude of which depending upon warming intensity (Figure 5b-q). Oblate MAA decreased after  
390 the end of the twenties century whereas prolate MAA rose *circa* 2050 under both scenarios (Figure  
391 5b-c and e-f, Supplementary Tables S11-12). Oblates underwent a phenological contraction from  $76 \pm$   
392  $22$  days in 2000-2009 to  $69 \pm 14$  or  $64 \pm 15$  days in 2090-2099 for SSP2-4.5 and SSP5-8.5, respectively  
393 (Figure 5h-i and Supplementary Table S11), accompanied by an earlier initiation in their SRP (Figure 5j  
394 and m and Supplementary Table S11). In contrast, prolates exhibited a strong phenological dilatation  
395 from  $91 \pm 6$  days in 2000-2009 to  $110 \pm 11$  or  $119 \pm 22$  days in 2090-2099 for scenarios SSP2-4.5 and  
396 SSP5-8.5, respectively (Figure 5h-i and Supplementary Table S12), with an earlier initiation and a later

397 termination of their SRP (Figure 5k and n and Supplementary Table S12). At the end of the century,  
398 they reached earlier their MAA in the year, i.e., around day number  $204 \pm 16$  or  $197 \pm 19$  in 2090-2099  
399 for scenarios SSP2-4.5 and SSP5-8.5, respectively, in comparison to day  $215 \pm 4$  in 1850-1859 (Figure  
400 5k and n and Supplementary Table S12). Oblate IMAA remained constant under scenario SSP2-4.5 but  
401 decreased under SSP5-8.5. Prolate IMAA slightly increased under both scenarios but remained below  
402 the value observed for oblates (Figure 5p-q and Supplementary Tables S11-12).

403  
404 Dinoflagellates also underwent a phenological expansion, associated with an increase of their MAA  
405 throughout the twenty first century (Figure 5d and g and Supplementary Table S13), a longer duration  
406 (Figure 5h-i and Supplementary Table S13) caused by an earlier initiation (around day number  $215 \pm 4$   
407 in 1850-1859 and  $204 \pm 16$  or  $197 \pm 19$  for SSP2-4.5 and 5-8.5, respectively) and a later termination  
408 (around day number  $254 \pm 9$  in 1850-1859 and  $262 \pm 5$  or  $268 \pm 9$  in 2090-2099 for scenarios SSP2-4.5  
409 and SSP5-8.5, respectively, Supplementary Table S13) of their SRP. Their IMAA rose above those of  
410 oblates during the first half of the twenty first century, although there was a high inter-model variance  
411 (Figure 5p-q and Supplementary Table S13).

412

### 413 3.5. Phenological shifts in the Labrador Sea

414

415 In the Labrador Sea (Figure 6a), distinct phenological shifts were found, also depending upon the SSP  
416 scenarios (Figure 6b-q). Under scenario SSP2-4.5, oblates exhibited a slight increase of their MAA (i.e.,  
417  $3770.1 \pm 769.1$  cells per CPR sample in 2000-2009 *versus*  $4055.5 \pm 545.4$  cells per CPR sample in 2090-  
418 2099; Supplementary Table S14) although the duration of their SRP slightly diminished from  $87 \pm 11$   
419 days in 2000-2009 to  $84 \pm 13$  days in 2090-2099 (Figure 6h and j and Supplementary Table S14).  
420 Prolates maintained both their MAA and IMAA throughout the period 1850-2100 (Figure 6c and p and  
421 Supplementary Table S15), the most significant changes occurring in the duration of their SRP (from  
422  $97 \pm 31$  days in 2000-2009 to  $107 \pm 36$  in 2090-2099; Figure 6h and Supplementary Table S15)  
423 accompanied by an earlier phenology (Figure 6k and Supplementary Table S15). Dinoflagellates should  
424 exhibit a large increase of their MAA, especially after 2050, from  $910 \pm 428.4$  cells per CPR sample in  
425 2000-2009 to  $1914.4 \pm 1125.2$  in 2090-2099 (Figure 6d and Supplementary Table S16) without a  
426 significant increase in the duration of their SRP (Figure 6h and Supplementary Table S16) or a change  
427 in initiation or termination (Figure 6l and Supplementary Table S16). Their IMAA slightly increased but  
428 remained above that of oblates (Figure 6p and Supplementary Tables S14 and 16).

429

430 Under SSP5-8.5, our approach predicted a shift from a system dominated by oblates to a system  
431 dominated by dinoflagellates (Figure 6b-q). The oblates exhibited a decrease of their MAA from  $3770.1$   
432  $\pm 769.1$  cells per CPR sample in 2000-2009 to  $3184.4 \pm 727.2$  in 2090-2099 (Figure 6e and  
433 Supplementary Table S14), accompanied by a decrease in the duration of their SRP from  $86.9 \pm 10.5$   
434 days in 2000-2009 to  $72.8 \pm 8.3$  days in 2090-2099 (Figure 6i and Supplementary Table S14), and an  
435 earlier initiation (Figure 6m and Supplementary Table S14). Their IMAA sharply decreased, especially  
436 during the second half of the twenty first century, from  $1077.1 \pm 178.6$  cells per CPR sample in 2000-  
437 2009 to  $777.9 \pm 245.5$  in 2090-2099 (Figure 6q and Supplementary Table S14). No changes were found  
438 for prolate MAA (Figure 6f and Supplementary Table S15) but their SRP lasted longer, from  $97 \pm 31$   
439 days in 2000-2009 to  $115 \pm 35$  in 2090-2099 (Figure 6i and n and Supplementary Table S15). Their IMAA  
440 was low under this scenario (Figure 6p-q and Supplementary Table S15). Dinoflagellate shifts were  
441 amplified, their MAA increased substantially, from  $910 \pm 428.4$  cells per CPR sample in 2000-2009 to

442 2898.2 ± 1052.0 in 2090-2099 (Figure 6g and Supplementary Table S16). These changes were more  
443 prominent at the end of the twenty first century, from 66 ± 12 days in 2000-2009 to 82 ± 18 in 2090-  
444 2099 (Figure 6i and Supplementary Table S16), resulting in a phenological dilatation (Figure 6o and  
445 Supplementary Table S16). Their IMAA tripled between the beginning and the end of the twenty first  
446 century, from 204.5 ± 66.9 cells per CPR sample in 2000-2009 to 738.8 ± 319.3 in 2090-2099  
447 (Supplementary Table S16), resulting in a shift from oblates to dinoflagellates. As the long-term  
448 phenological changes of the three groups were more difficult to reconstruct in this region (Table 1),  
449 our predictions should be considered with degree of caution.

450

#### 451 **4. Discussion**

452

453 Some discrepancies between modelled and observed abundance indicate that our model may have  
454 some limitations (Figure 1, Supplementary Figures S10-11 and Supplementary Animations S1-3). For  
455 example, the increase in the abundance of dinoflagellates in the North Sea and the North-East Atlantic,  
456 and of oblates in the North Sea, were not captured well by our approach (Figure 1 and Supplementary  
457 Figure S10). In the same way, the fit between observed and reconstructed daily abundances varied  
458 among the three different temporal periods (Supplementary Animations S1-3). For example, the  
459 abundance of *Leptocylindrus danicus* in the North Sea was correctly reconstructed for the temporal  
460 periods 1977-1995 and 1996-2014 but not for 1958-1977 (Supplementary Animation S1). These  
461 inconsistencies may originate from (i) our framework, (ii) the CPR sampling and (iii) the ESMs.

462

##### 463 4.1. Limitations of our approach

464

465 In this study, we made a series of choices and assumptions that might have affected model  
466 performance. First, we used an approach based on METAL rather than a species distribution model  
467 (SDM). This choice was made because we showed previously that METAL correctly reconstructs  
468 phytoplankton phenology and annual succession when applied to the CPR data (Caracciolo et al., 2021)  
469 while it has been shown that most SDM poorly performed with those data (Brun et al., 2016). In  
470 addition, using METAL enables us to convert the monthly CPR observations at a daily scale, which is  
471 more adapted (i) to reconstruct/project the long-term phenological changes from 1850 to 2100, (ii) to  
472 examine their trends (Henson et al., 2018) and (iii) to demonstrate that the niche-environment  
473 interaction governs long-term phenological phytoplankton shifts (Beaugrand & Kirby, 2018).

474

475 Second, we used a symmetric gaussian function to model the thermal niche of the 44 phytoplanktonic  
476 species. Phytoplankton are ectotherms and may therefore have asymmetric thermal niches (Martin &  
477 Huey, 2008; Thomas et al., 2012); in particular they might be able to tolerate a larger range of cold  
478 temperatures (i.e., below their thermal optimum) and a narrower range of warm temperatures (i.e.,  
479 above their thermal optimum) (Martin & Huey, 2008). However, Caracciolo and colleagues  
480 reconstructed phytoplankton phenology and annual succession well in the North Sea by using  
481 symmetrical niches (Caracciolo et al., 2021). Furthermore, the use of asymmetrical gaussian functions  
482 would have also increased computational cost. Nevertheless, we acknowledge that the consideration  
483 of asymmetrical niches might perhaps improve our results. For example, the existence of an upper  
484 thermal limit above which the abundance rapidly declined substantially (e.g. the events observed with  
485 the dinoflagellates in the North Sea and the North-East Atlantic; Figure 1g-h and Supplementary

486 Figures S10c and f) was not reproduced by our model; indeed the modelled shifts were almost always  
487 gradual (Figure 1p-q and Supplementary Figure S10c and f).  
488

489 Last, we supposed that species niches will be conserved over the time period 1850-2100 (i.e., the  
490 assumption of niche conservatism), an assumption that is generally formulated by modellers that  
491 project species response to climate change (Soberon & Nakamura, 2009). The large population size  
492 and fast generation time of phytoplankton are supposed to allow a rapid alteration of their niches  
493 (Litchman et al., 2012) but some studies (on zooplankton however) have not seen any niche alteration  
494 at a decadal scale (Helaouët & Beaugrand, 2007) and there must exist fundamental constraints that  
495 limit adaptation (for example, phytoplankton morphological traits, which affect nutrient uptake, are  
496 supposed to be highly conserved) (Beaugrand & Kirby, 2018; Kléparski et al., 2022; Litchman et al.,  
497 2007).  
498

#### 499 4.2. Limitations related to the CPR sampling 500

501 Another source of discrepancy between modelled and observed abundance may originate from the  
502 sampling by the CPR. First, sampling is carried out at a monthly scale over large areas (Richardson et  
503 al., 2006) and it is likely that such a sampling frequency is not always appropriate to properly  
504 characterise blooms as phytoplankton exhibits typically a short life cycle. Second, the CPR machine  
505 uses a 270µm mesh silk that mostly collects large armoured dinoflagellates and chain forming diatoms  
506 but undersamples smaller phytoplankton species. These sampling biases might explain the large  
507 variability observed in the abundance of phytoplankton species, affecting subsequently niche  
508 characterisation and modelled reconstructions (Figure 1a-i). However, our results suggest this is not  
509 the case for the vast majority of species (Supplementary Animations S1-3 and Supplementary Tables  
510 S2-S5). For example, some of the smallest species, e.g. *Thalassionema nitzschioides* and *Cylindrotheca*  
511 *closterium*, are well modelled in the North Sea and the North-East Atlantic but not in the Labrador Sea  
512 (Supplementary Tables S3-S5 and Supplementary Animations S1-S3) suggesting that the problem  
513 might not be related with a sampling bias affecting model performance. Third, the CPR sampling is  
514 heterogeneous in space and time and some regions were not continuously sampled between 1958 and  
515 2014 (Richardson et al., 2006). For example, no CPR sample was available in the Labrador Sea at the  
516 end of the 1980s (white bands in Figure 1c, f, i, u, x and  $\alpha$ ). However, it is thought that the CPR collects  
517 an important fraction of the abundance of each taxon and is therefore thought to be robust to examine  
518 seasonal and interannual patterns (Richardson et al., 2006).  
519

#### 520 4.3. Limitations from ESMs 521

522 The reconstructed regional climatic variability between 1958 and 2014 by ESMs is not supposed to  
523 exactly match the variability that was observed during that time (Stock et al., 2011), a bias that might  
524 have also affected niche estimates and that might therefore explain the discrepancies between  
525 observed and modelled mean long-term changes in abundance (Figure 1a-r and Supplementary Figure  
526 S10). For example, the abundance of *Cylindrotheca closterium* is well modelled in the North Sea with  
527 CNRM-ESM2-1, IPSL-CM6A-LR and NorESM2-LM but not with MPI-ESM1-2-LR, GFDL-ESM4 and  
528 UKESM1-0-LL (Supplementary Table S3). Indeed, there exists large variations in SST, SDSR and nitrate  
529 concentration among the six ESMs in some regions (Supplementary Figures S5-7). Nevertheless, it  
530 should be noticed that our approach consistently modelled the seasonal cycle of the three groups in

531 the three regions and the modelled long-term trends were generally in agreement with the  
532 observations, especially for prolates in the three regions, oblates in the North-East Atlantic and oblates  
533 and dinoflagellates in the Labrador Sea (Supplementary Figures S10-11 and Supplementary Tables S6-  
534 7).

535

#### 536 4.4. Long-term changes in the phenology of diatoms and dinoflagellates

537

538 Modelled shifts are in agreement with theoretical projections, i.e., that spring species (i.e., oblates)  
539 experience a phenological contraction and an earlier phenology whereas late summer species (i.e.,  
540 prolates and dinoflagellates) exhibit a phenological expansion with both an earlier initiation and a later  
541 termination (Beaugrand & Kirby, 2018). The phenological contraction of oblates, associated with a  
542 decline in abundance, is indicative of species/taxa that reach the limits of their phenological plasticity  
543 (Beaugrand & Kirby, 2018), probably because an earlier phenology in spring is impossible as winter  
544 photoperiod and light levels limits primary production at high latitudes (Boyce et al., 2017; Caracciolo  
545 et al., 2021) and/or because the decrease in nitrate concentration (Supplementary Figures S2-4), which  
546 are an essential constituent of proteins and nucleic acids that are in turn critical for the synthesis of  
547 organic matter (Miller, 2004), limits the size of the bloom. Therefore, these diatoms might encounter  
548 more favourable environmental conditions at high latitudes, causing a biogeographical shift, a  
549 postulate that would be in agreement with the increased primary production projected by ESMs in the  
550 Arctic region (Kwiatkowski et al., 2020) and the observed increase and decrease of diatom populations  
551 in the North-Sea and the bay of Biscay, respectively (Edwards et al., 2022). On the contrary, the  
552 phenological expansion of prolates and dinoflagellates is indicative of species/taxa that are adapted to  
553 the reinforced stratified and nutrient-depleted conditions in the future North Atlantic Ocean  
554 (Beaugrand & Kirby, 2018; Kwiatkowski et al., 2020). The elongated cell shape of prolates reduces their  
555 sinking speed while not affecting their capacity to uptake nutrients, enabling them to remain in the  
556 well-lit upper part of the water column (Kl eparski et al., 2022; Padisak et al., 2003). Furthermore, it has  
557 been shown that some taxa belonging to this taxonomic group (e.g., *Rhizosolenia*), were able to  
558 passively migrate between the surface layers and the nutricline, enabling them to harvest nutrients  
559 more efficiently (Kemp & Villareal, 2013, 2018). Similarly, the dinoflagellates have flagella which enable  
560 them to move and actively exploit nutrients in the water column. They are also capable of switching  
561 nutritional strategies to mixotrophy when less nutrients are available (Miller, 2004).

562

563 Because of the shifts in phytoplankton phenology, changes in species succession are expected to  
564 desynchronise species interaction and trigger trophic mismatch (Beaugrand et al., 2003; Edwards &  
565 Richardson, 2004). Mismatch may occur between species that have different range of tolerance along  
566 a single environmental variable. Such alterations of the trophodynamics have already been observed  
567 in freshwater lakes (Winder & Schindler, 2004) but remain difficult to anticipate in the marine  
568 environment because each species has a specific response to environmental variability, which is driven  
569 by its life strategy and its niche (Beaugrand & Kirby, 2018). Furthermore, it has also been shown that  
570 only seasonally heterogeneous environmental changes can lead to a desynchronization in species  
571 interaction (e.g., warmer temperature in spring but not in summer)(Straile et al., 2015). Results from  
572 the METAL theory suggest that trophic mismatch might be limited however, because interacting  
573 species have at least a part of their ecological niche in common, providing that no other important  
574 ecological dimensions or habitat requirements differ among them (Beaugrand & Kirby, 2018). Indeed,  
575 species are more expected to track changes along the environmental variables for which they have the

576 narrowest tolerance (Ackerly, 2003). Therefore, in the pelagic environment, one could expect a  
577 mismatch among species that are not linked to the same habitat components (i.e., the stable- and  
578 substrate-biotope components) (van der Spoel, 1994). For example, it has been shown that a shift in  
579 phytoplankton phenology is more likely to affect the fish that spawn in geographically fixed areas  
580 rather than those that have their spawning grounds moving according to the environmental changes  
581 (Asch et al., 2019).

582  
583 Diatoms and dinoflagellates have been historically separated into two distinct functional types (Kemp  
584 & Villareal, 2018; Margalef, 1978). According to Margalef's mandala (Margalef, 1978), diatoms thrive  
585 when the water column is poorly stratified and turbulent and when nutrients concentration is  
586 relatively high. In contrast, dinoflagellates dominate in stratified conditions and lower nutrients  
587 concentration. By simplifying Margalef's framework (Margalef, 1978), a decline in primary production  
588 and carbon export (therefore the biological pump (Passow & Carlson, 2012)) is anticipated in the North  
589 Atlantic because ocean warming will enhance water column stratification and reduce nutrients, which  
590 are believed to negatively affect the diatoms as a whole (Bopp et al., 2005; Kemp & Villareal, 2018;  
591 Kléparski et al., 2022; Marinov et al., 2010; Tréguer et al., 2018). Our results nuance these projections.  
592 Although they show that diatom abundance as a whole will decrease, they also suggest that prolates  
593 may indeed persist and increase in a more stratified ocean, albeit probably not to an abundance level  
594 that might compensate the large diminution in the abundance experienced by oblates. Indeed, massive  
595 blooms of those last diatoms in spring generate high carbon export through the generation of marine  
596 snow (Kléparski et al., 2022; Raven & Waite, 2004; Smetacek, 1985) and it is therefore unlikely that the  
597 slight increase in prolates will overcome the decrease in carbon exportation induced by the reduction  
598 in oblate abundance. Furthermore, the transfer efficiency of carbon to the deep ocean is reduced with  
599 smaller sized slow-sinking cells, and therefore the shift from large round oblates to smaller elongated  
600 prolates will also diminish the rate of carbon export (Henson et al., 2022). Whether this shift might  
601 also affect species aggregation remains an open question as the causes of this phenomenon are not  
602 clear (e.g., defence against predation, response to changes in turbulence or buoyancy regulation)  
603 (Lürling, 2021; Pančić & Kiørboe, 2018; Smayda, 1970; Sournia, 1982). Our results also suggest that  
604 dinoflagellate abundance will rise in the three North Atlantic regions. Although the contribution of this  
605 group to the biological pump is poorly understood, a study has shown that dinoflagellate blooms  
606 sometimes coincide with a rise in carbon export at an annual scale in the North-East Atlantic at 3000m  
607 (Henson et al., 2012). It has also been shown that the consideration of mixotrophic organisms (e.g.,  
608 dinoflagellates) within biogeochemical models can increase the flux of carbon export (Ward & Follows,  
609 2016). Therefore, this group might alleviate to some extent the consequences of the reduction in  
610 oblates on the biological pump in the North Atlantic, albeit export from the surface ocean is also  
611 strongly influenced by synergistic effects such as nutrient delivery through remineralisation or direct  
612 inputs, processes that are difficult to predict (Passow & Carlson, 2012).

613  
614 ESMs used as part of CMIP5 included a few functional types to represent the phytoplanktonic  
615 community, often with a single grouping for diatoms (Séférián et al., 2020; Tréguer et al., 2018). The  
616 last generations of ESMs in CMIP6 have improved the representation of phytoplankton ecology by  
617 including more functional types (e.g., diazotrophs for some models), which has enhanced model  
618 performance. However, diatoms still remain represented by a single group (Séférián et al., 2020).  
619 Results from model inter-comparisons highlight the great sensitivity of models to the types of  
620 functional groups they include, as well as the ecological traits they represent (Fu et al., 2016; Taucher

621 & Oschlies, 2011). Dutkiewicz and colleagues have recently used morphological traits (i.e., cell size),  
622 biogeochemical functions and thermal tolerances to define more than 350 phytoplankton types  
623 (Dutkiewicz et al., 2020). Their results showed that species richness projections were altered by the  
624 number as well as the nature of phytoplankton traits, each controlling a distinct aspect of the species'  
625 responses (Dutkiewicz et al., 2020). They concluded that the addition of traits, such as cell shape, might  
626 improve model projections (Dutkiewicz et al., 2020). *In situ* studies have also highlighted the  
627 importance of phytoplankton composition for carbon exportation (Dybwad et al., 2021; Henson et al.,  
628 2012). However, such models with hundreds of phytoplankton types cannot realistically be used to  
629 perform centennial climatic simulations because of computational cost. Hence, although our results  
630 with oblates give some support to the ESMs that only considered a single diatom group, they also  
631 emphasize that prolates and dinoflagellates exhibit distinct alterations of their phenology and  
632 abundance. Therefore, the distinction of oblate and prolate diatoms as well as dinoflagellates in ESM  
633 models may be a simple way to improve model projections because these three groups have different  
634 phenologies and responses to climate change, which may affect our current understanding of the  
635 consequences of phytoplankton shifts on the biological carbon pump (Karp-Boss & Boss, 2016;  
636 Kléparski et al., 2022; Litchman & Klausmeier, 2008; Naselli-Flores et al., 2021; Ryabov et al., 2020).

637

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660

#### 661 **Data accessibility:**

662 All the data used in this article are already freely available (see the Materials and Methods section and  
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664



665 **Author contributions:** L.K and G.B designed the study, performed the analyses and wrote the first  
666 draft. L.K, G.B, M.E and C.O discussed the results and reviewed the manuscript.

667

668 **Conflict of interest:** The authors declare no conflict of interest.

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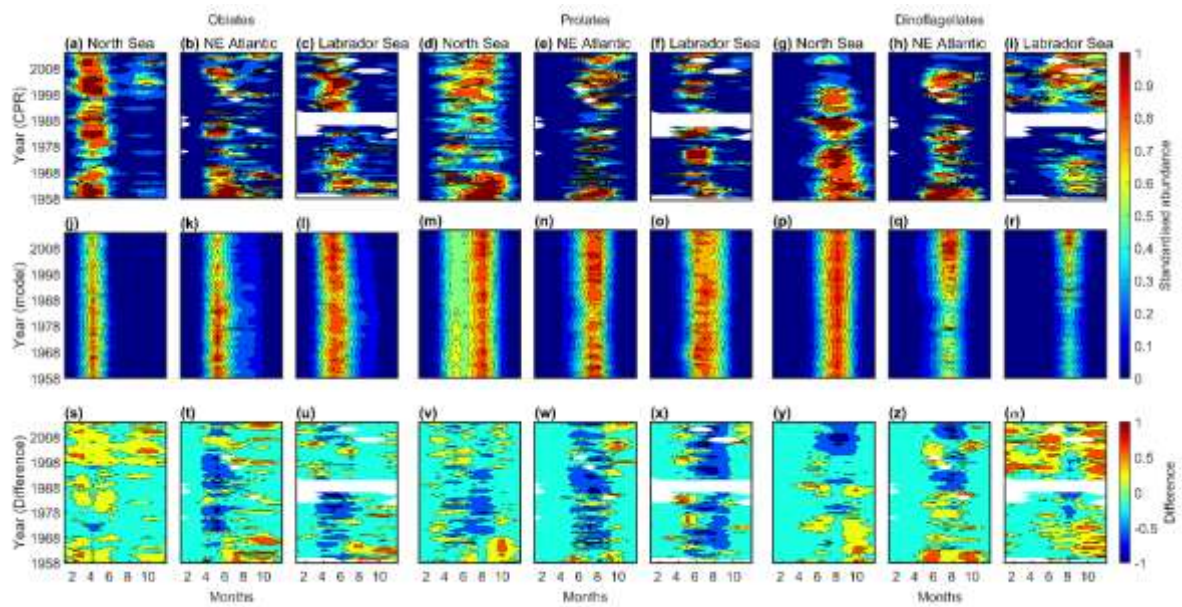
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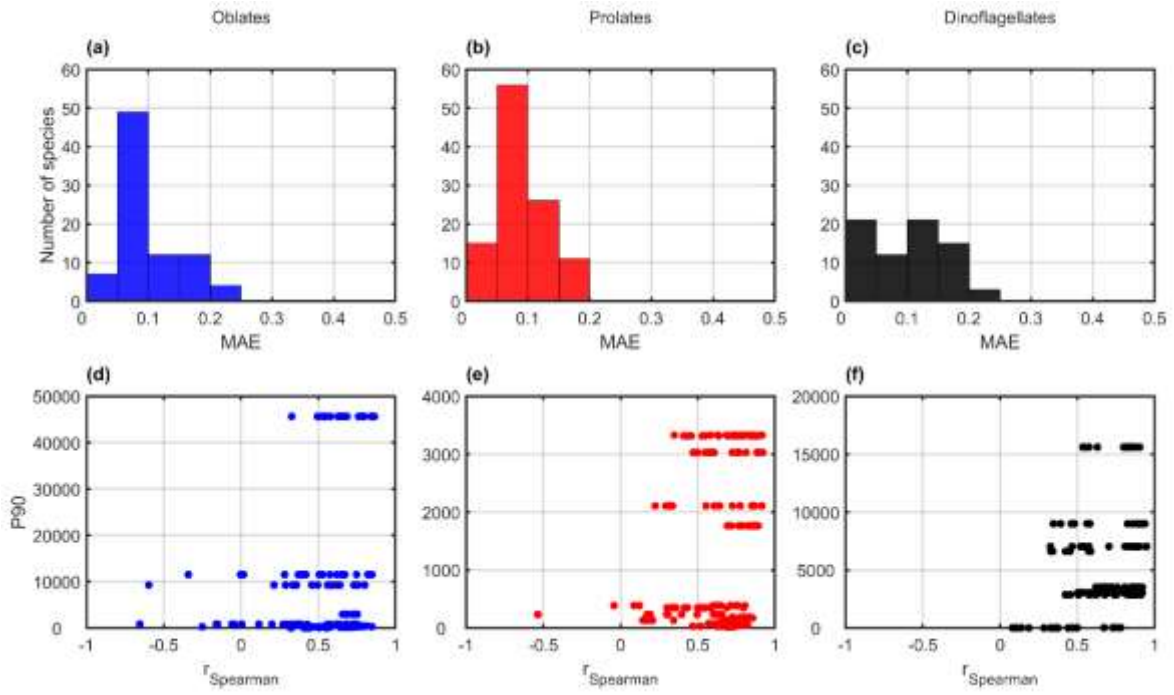
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**Figures**

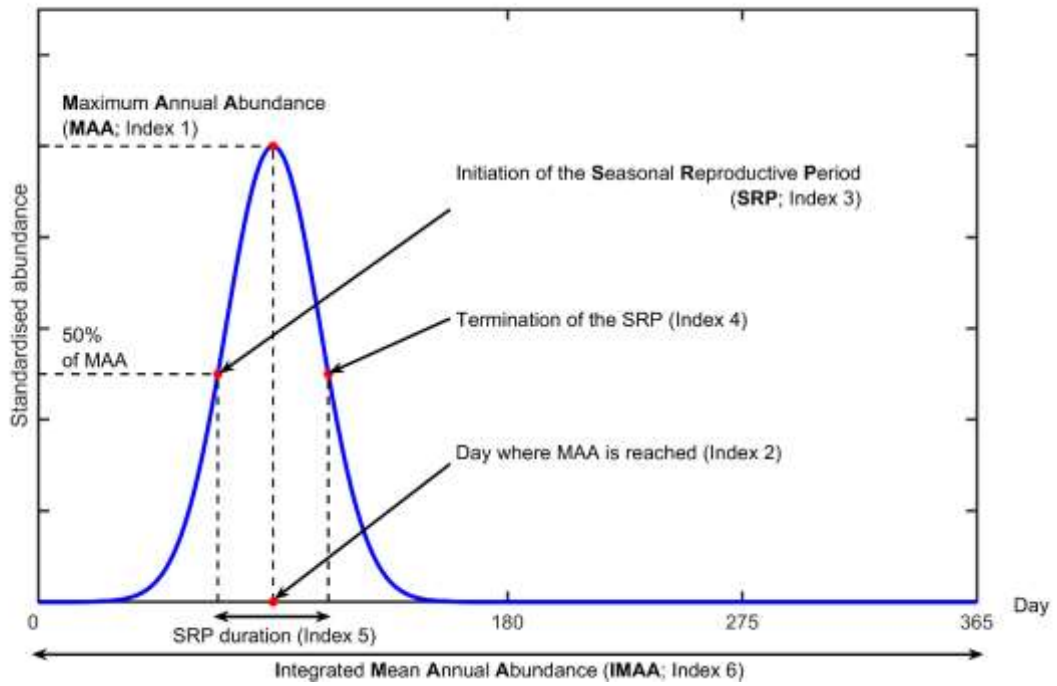


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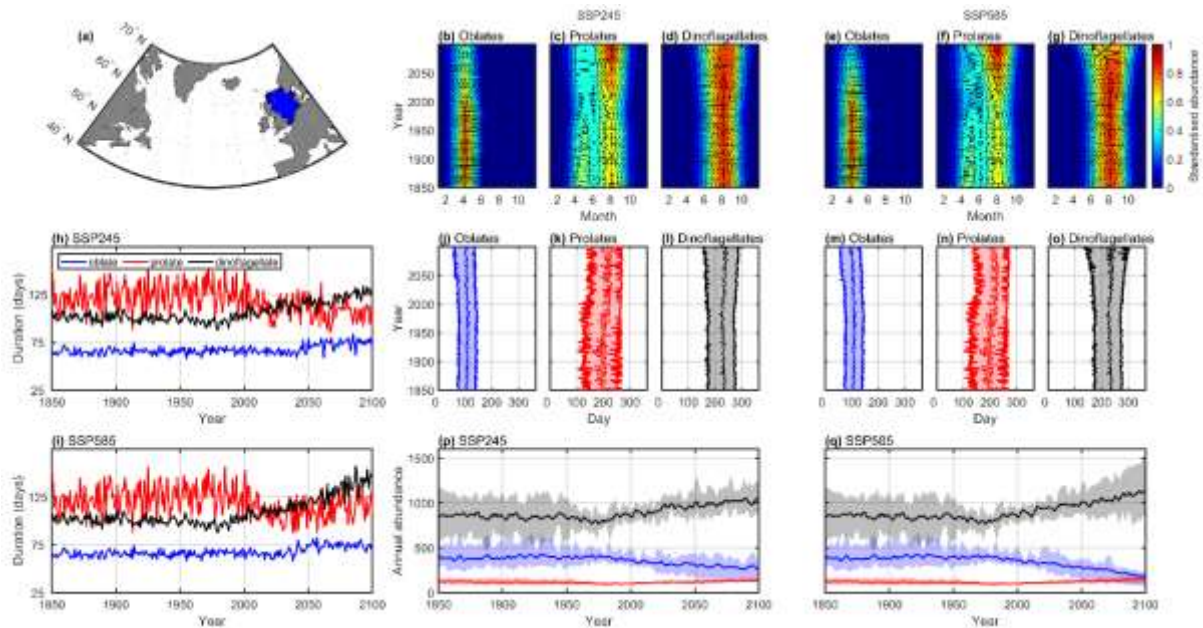
**Figure 1.**



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945 **Figure 2.**  
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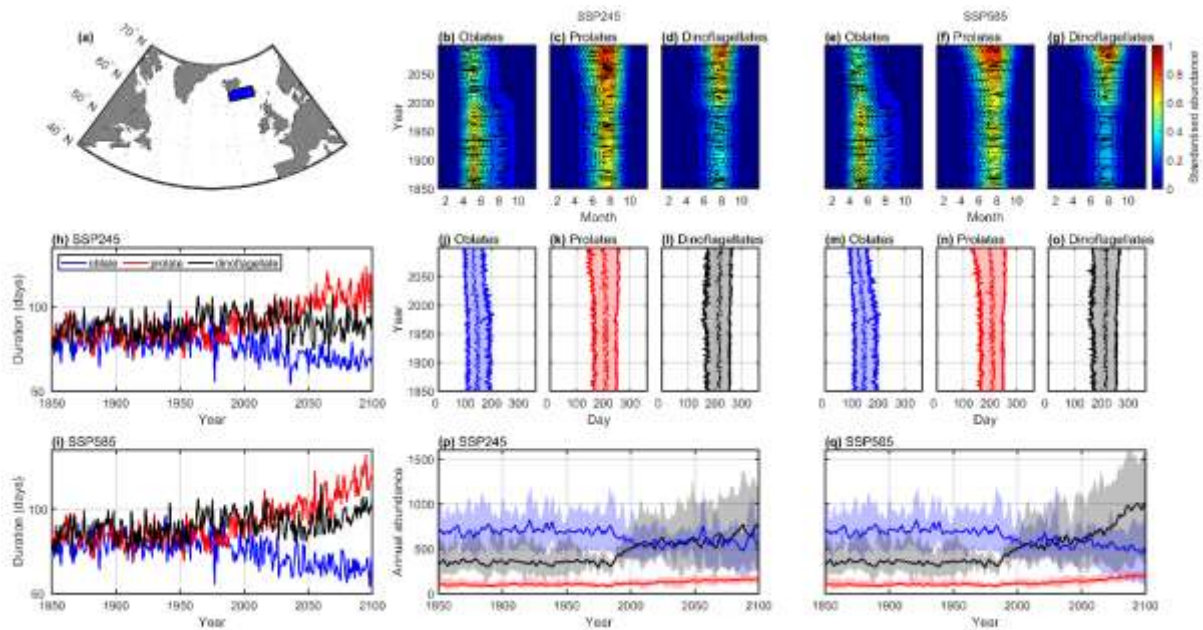


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948 **Figure 3.**  
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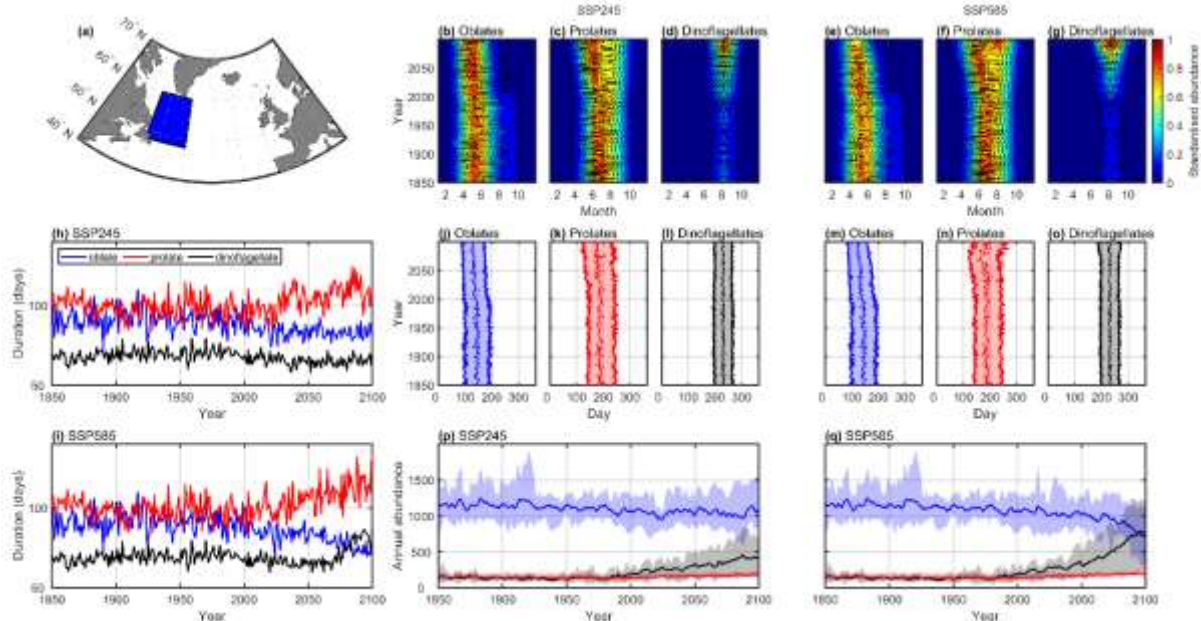
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Figure 4.



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Figure 5.



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Figure 6.

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**Figure 1. Comparisons between observed and modelled long-term monthly abundance of the three taxonomic groups (oblates, prolates and dinoflagellates).** (a-i) Long-term changes in the monthly abundance of (a-c) oblates, (d-f) prolates and (g-i) dinoflagellates in the North Sea (a, d and g), the North-East Atlantic (b, e and h) and the Labrador Sea (c, f and i). (j-r) Modelled long-term changes in the monthly abundance of (j-l) oblates, (m-o) prolates and (p-r) dinoflagellates in the North Sea (j, m and p), the North-East Atlantic (k, n and q) and the Labrador Sea (l, o and r). Differences between observed and modelled mean monthly abundance of (s-u) oblates, (v-x) prolates and (y-α) dinoflagellates in the North Sea (s, v and y), the North-East Atlantic (t, w and z) and the Labrador Sea (u, x and α). In a-r, colours denote the mean monthly observed or modelled abundance of a taxonomic group. The abundance in each panel was standardised between 0 and 1 for comparison purpose (Materials and Methods). Spearman correlation coefficients between observed and modelled abundance are displayed in Table 1. In s-α, colours denote the difference between observed and modelled abundance, red and blue colours indicating an underestimation and an overestimation of the modelled abundance, respectively. Modelled abundances are the average based on the six Earth System Models (ESMs).

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**Figure 2. Model performance.** (a-c) Distribution of the Mean Absolute Errors (MAEs) calculated between observed and modelled abundances of each species/taxa for (a) oblates (blue bars), (b) prolates (red bars) and (c) dinoflagellates (black bars) in the three oceanic regions. (d-f) Relationships between the Spearman rank correlation ( $r_{\text{Spearman}}$ ) calculated between the observed and the modelled abundances, and the corresponding 90<sup>th</sup> percentile of the abundance (P90; see Supplementary Table S1) values for (d) oblates (blue dots), (e) prolates (red dots) and (f) dinoflagellates (black dots) in the three oceanic regions. Displayed MAEs and Spearman rank correlations were calculated for each Earth

1000 System Model (ESM) (see Supplementary Tables S2-5). Comparison between the modelled abundance  
1001 forced by the six ESMs and the observed abundance by the Continuous Plankton Recorder (CPR) survey  
1002 are shown in Supplementary Animations S1-3. Mean monthly observed and predicted standardised  
1003 abundances of the three taxonomic groups in the three oceanic regions are shown in Figure 1.

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1005 **Figure 3. Theoretical diagram explaining graphically the six phenological indices used in this study.**

1006 Six phenological indices were defined: the Maximum Annual Abundance (MAA; Index 1), the day where  
1007 MAA is reached (Index 2), the initiation (Index 3) and the termination (Index 4) of the Seasonal  
1008 Reproductive Period (SRP), i.e., the first and the last days where the abundance is  $\geq 50\%$  of MAA, the  
1009 seasonal duration (Index 5), i.e., the number of consecutive days where abundance is  $\geq 50\%$  of MAA,  
1010 and the Integrated Mean Annual Abundance (IMAA; Index 6).

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1012 **Figure 4. Modelled long-term phenological changes of diatoms and dinoflagellates in the North Sea**

1013 **(1850-2100).** (a) Spatial distribution of Continuous Plankton Recorder (CPR) survey sampling. (b-g)

1014 Long-term monthly changes in the standardised abundance of (b and e) oblates, (c and f) prolates and  
1015 (d and g) dinoflagellates for scenarios (b-d) SSP2-4.5 and (e-g) SSP5-8.5. Each panel was standardised  
1016 between 0 and 1. Colours denote the mean monthly standardised abundance of a taxonomic group.

1017 (h-i) Long-term annual changes in phenology duration for scenarios (h) SSP2-4.5 and (i) SSP5-8.5. (j-o)

1018 Long-term changes in the initiation and termination of the Seasonal Reproductive Period (SRP) for (j  
1019 and m) oblates, (k and n) prolates and (l and o) dinoflagellates. In each panel, the first and last tick line  
1020 denotes the initiation and the termination day of the SRP. Shading denotes the duration of the SRP  
1021 and the dotted line displays the day where Maximum Annual Abundance (MAA) is reached. (p-q) Long-

1022 term changes in Integrated Mean Annual Abundance (IMAA; cell per CPR sample) for scenarios (p)  
1023 SSP2-4.5 and (q) SSP5-8.5. The shade denotes the minimum and maximum mean abundance estimated  
1024 from the environmental variables originating from the six Earth System Models (ESMs). In h-q oblates

1025 are in blue, prolates in red and dinoflagellates in black. In (b-q), each index corresponds to the mean  
1026 of the six ESMs. The meaning of the six phenological indices is summarised in Figure 3.

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1028 **Figure 5. Modelled long-term phenological changes of diatoms and dinoflagellates in the North-East**

1029 **Atlantic (1850-2100).** (a) Spatial distribution of Continuous Plankton Recorder (CPR) sampling. (b-g)

1030 Long-term monthly changes in the standardised abundance of (b and e) oblates, (c and f) prolates and  
1031 (d and g) dinoflagellates for scenarios (b-d) SSP2-4.5 and (e-g) SSP5-8.5. Each panel was standardised  
1032 between 0 and 1. Colours denote the mean monthly standardised abundance of a taxonomic group.

1033 (h-i) Long-term annual changes in phenology duration for scenarios (h) SSP2-4.5 and (i) SSP5-8.5. (j-o)

1034 Long-term changes in the initiation and termination of the Seasonal Reproductive Period (SRP) for (j  
1035 and m) oblates, (k and n) prolates and (l and o) dinoflagellates. In each panel, the first and last tick line  
1036 denotes the initiation and the termination day of the SRP. Shading denotes the duration of the SRP  
1037 and the dotted line displays the day where Maximum Annual Abundance (MAA) is reached. (p-q) Long-

1038 term changes in Integrated Mean Annual Abundance (IMAA; cell per CPR sample) for scenarios (p)  
1039 SSP2-4.5 and (q) SSP5-8.5. The shade denotes the minimum and maximum mean abundance estimated  
1040 from the environmental variables originating from the six Earth System Models (ESMs). In h-q oblates

1041 are in blue, prolates in red and dinoflagellates in black. In (b-q), each index corresponds to the mean  
1042 of the six ESMs. The meaning of the six phenological indices is summarised in Figure 3.

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1044 **Figure 6. Modelled long-term phenological changes of diatoms and dinoflagellates in the Labrador**  
1045 **Sea (1850-2100).** (a) Spatial distribution of Continuous Plankton Recorder (CPR) sampling. (b-g) Long-  
1046 term monthly changes in the standardised abundance of (b and e) oblates, (c and f) prolates and (d  
1047 and g) dinoflagellates for scenarios (b-d) SSP2-4.5 and (e-g) SSP5-8.5. Each panel was standardised  
1048 between 0 and 1. Colours denote the mean monthly standardised abundance of a taxonomic group.  
1049 (h-i) Long-term annual changes in phenology duration for scenarios (h) SSP2-4.5 and (i) SSP5-8.5. (j-o)  
1050 Long-term changes in the initiation and termination of the Seasonal Reproductive Period (SRP) for (j  
1051 and m) oblates, (k and n) prolates and (l and o) dinoflagellates. In each panel, the first and last tick line  
1052 denotes the initiation and the termination day of the SRP. Shading denotes the duration of the SRP  
1053 and the dotted line displays the day where Maximum Annual Abundance (MAA) is reached. (p-q) Long-  
1054 term changes in Integrated Mean Annual Abundance (IMAA; cell per CPR sample) for scenarios (p)  
1055 SSP2-4.5 and (q) SSP5-8.5. The shade denotes the minimum and maximum mean abundance estimated  
1056 from the environmental variables originating from the six Earth System Models (ESMs). In h-q oblates  
1057 are in blue, prolates in red and dinoflagellates in black. In (b-q), each index corresponds to the mean  
1058 of the six ESMs. The meaning of the six phenological indices is summarised in Figure 3.

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**Table**

1068 **Table 1. Spearman rank correlations between long-term changes in observed and modelled monthly**  
1069 **abundance of the three taxonomic groups (oblates, prolates and dinoflagellates) in the three studied**  
1070 **regions.** All correlations were significant ( $p < 0.01$ ). The degree of freedom associated with each oceanic  
1071 region are also indicated. Long-term monthly changes in observed and modelled abundance are  
1072 displayed in Figure 1.

	North Sea	North-East Atlantic	Labrador Sea
Oblates	0.70	0.64	0.55
Prolates	0.79	0.73	0.58
Dinoflagellates	0.83	0.72	0.50
Degree of freedom	684	677	600

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