



HAL
open science

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

Loïck Kléparski, Grégory Beaugrand, Martin Edwards, Clare Ostle

► **To cite this version:**

Loïck Kléparski, Grégory Beaugrand, Martin Edwards, Clare Ostle. Phytoplankton life strategies, phenological shifts and climate change in the North Atlantic Ocean from 1850 to 2100. *Global Change Biology*, 2023, 29 (13), pp.3833-3849. 10.1111/gcb.16709 . hal-04407524

HAL Id: hal-04407524

<https://hal.science/hal-04407524>

Submitted on 20 Jan 2024

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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

Loïck Kléparski^{1,2}, Grégory Beaugrand¹, Martin Edwards^{3,4}, Clare Ostle²

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

² Marine Biological Association, Citadel Hill, Plymouth PL1 2PB, United Kingdom.

³ Plymouth Marine Laboratory, Prospect Place, Plymouth PL13DH, United Kingdom.

⁴ University of Plymouth, School of Biological and Marine Sciences, Drake Circus, Plymouth, United Kingdom.

Key-words: diatoms, oblates, prolates, dinoflagellates, phenology, annual phytoplankton succession, climate change

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 m³ 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 90th 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 90th percentile of the monthly
 125 abundance of each taxonomic group (P90_m):

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 90th 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 90th 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 3m³ 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⁻²) and dissolved nitrate
143 concentration (mol m⁻³). 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⁻² and 8.5 W m⁻²)
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⁻² every 40 W m⁻² and for nitrate concentration from 0.001 to
206 0.05 mol m⁻³ every 0.005 mol m⁻³. 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⁻³ every 0.001 mol m⁻³. Amplitude for SDR were
208 defined as followed: 1, 3, 5, 8, 10, 15, 20, 50 and 100 W m⁻². 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 90th 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 3m³ 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

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

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 α).

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 90th 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 ± 494.7 cells per CPR sample in 1850-1859 to 1176.9 ± 573.2 or 785.1 ± 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 ± 53.3 cells per CPR sample in 1850-
364 1859 to 360.5 ± 77.5 or 392.6 ± 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 ± 92.8 cells per CPR
370 sample in 1850-1859 to 283.8 ± 97.4 or 192 ± 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 ± 32.7 cells per CPR sample in 1850-1859 to 134.5 ± 18.6 or 148.8 ± 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 ± 336.3 cells per CPR sample in 1850-1859 to 2599.3 ± 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 ± 16 days in 1850-1859 to 107 ± 6 days in 2000-2009 and to 127 ± 13 or
381 143 ± 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 ± 14 or 64 ± 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 ± 6 days in 2000-2009 to 110 ± 11 or 119 ± 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 ± 16 or 197 ± 19 in 2090-2099
399 for scenarios SSP2-4.5 and SSP5-8.5, respectively, in comparison to day 215 ± 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 ± 4
407 in 1850-1859 and 204 ± 16 or 197 ± 19 for SSP2-4.5 and 5-8.5, respectively) and a later termination
408 (around day number 254 ± 9 in 1850-1859 and 262 ± 5 or 268 ± 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 ± 769.1 cells per CPR sample in 2000-2009 *versus* 4055.5 ± 545.4 cells per CPR sample in 2090-
418 2099; Supplementary Table S14) although the duration of their SRP slightly diminished from 87 ± 11
419 days in 2000-2009 to 84 ± 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 ± 31 days in 2000-2009 to 107 ± 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 ± 428.4 cells per CPR sample in
425 2000-2009 to 1914.4 ± 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 ± 769.1 cells per CPR sample in 2000-2009 to 3184.4 ± 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 ± 10.5
434 days in 2000-2009 to 72.8 ± 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 ± 178.6 cells per CPR sample in 2000-
437 2009 to 777.9 ± 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 ± 31
439 days in 2000-2009 to 115 ± 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 ± 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 α). 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 (Klęparski 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 (Séférian 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 (Séférian 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

638 **Acknowledgments:**

639 We acknowledge the World Climate Research Programme, which, through its Working Group on
640 Coupled Modelling, coordinated and promoted CMIP6. We thank the climate modelling groups for
641 producing and making available their model output, the Earth System Grid Federation (ESGF) for
642 archiving the data and providing access, and the multiple funding agencies who support CMIP6 and
643 ESGF. We also thank the owners and crews that have towed the CPRs on a voluntary basis for over 80
644 years contributing to one of the world's largest and longest ongoing ecological experiments. Without
645 these early pioneers of citizen science and broad-scale volunteer monitoring projects this unique
646 ecological dataset would never have been financially or logistically viable.

647

648 **Funding:**

649 Funding that supports data collection has come from a number of contracts since inception of the
650 Continuous Plankton Recorder survey, the current funded projects include: the UK Natural
651 Environment Research Council, Grant/Award Number: NE/R002738/1 and NE/M007855/1; EMFF;
652 Climate Linked Atlantic Sector Science, Grant/Award Number: NE/ R015953/1, DEFRA UK ME-5308,
653 NSF USA OCE-1657887, DFO CA F5955- 150026/001/HAL, NERC UK NC-R8/H12/100, Horizon 2020:
654 862428 Atlantic Mission and AtlantECO 862923, IMR Norway, DTU Aqua Denmark and the French
655 Ministry of Environment, Energy, and the Sea (MEEM). This work was also financially supported by the
656 European Union, European Regional Development Fund (ERDF), the French State, the French Region
657 Hauts-de-France and Ifremer, in the framework of the project CPER IDEAL 2021–2027. LK also received
658 funds as part of a PhD grant co-financed by the French Region Hauts de France region and the Marine
659 Biological Association.

660

661 **Data accessibility:**

662 All the data used in this article are already freely available (see the Materials and Methods section and
663 Supplementary Text S1).

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.

669

670

671

672

673

674

675

676

677

678

679

680 **References**

681 Ackerly, D. D. (2003). Community Assembly, Niche Conservatism, and Adaptive Evolution in Changing
682 Environments. *International Journal of Plant Sciences*, 164(S3), S165–S184.

683 <https://doi.org/10.1086/368401>

684 Asch, R. G., Stock, C. A., & Sarmiento, J. L. (2019). Climate change impacts on mismatches between
685 phytoplankton blooms and fish spawning phenology. *Global Change Biology*, 25(8), 2544–

686 2559. <https://doi.org/10.1111/gcb.14650>

687 Beaugrand, G. (2015). *Marine biodiversity, climatic variability and Global Change*. Routledge.

688 Beaugrand, G., Brander, K. M., Lindley, J. A., Souissi, S., & Reid, P. C. (2003). Plankton effect on cod
689 recruitment in the North Sea. *Nature*, 426(6967), 661–664.

690 <https://doi.org/10.1038/nature02164>

691 Beaugrand, G., Conversi, A., Atkinson, A., Cloern, J., Chiba, S., Fonda-Umani, S., Kirby, R. R., Greene,
692 C., Goberville, E., Otto, S. A., Reid, P. C., Stemmann, L., & Edwards, M. (2019). Prediction of
693 unprecedented biological shifts in the global ocean. *Nature Climate Change*, 9, 10.

694 Beaugrand, G., Edwards, M., Raybaud, V., Goberville, E., & Kirby, R. R. (2015). Future vulnerability of
695 marine biodiversity compared with contemporary and past changes. *Nature Climate Change*,

696 5(7), 695–701. <https://doi.org/10.1038/nclimate2650>

697 Beaugrand, G., & Kirby, R. R. (2016). Quasi-deterministic responses of marine species to climate
698 change. *Climate Research*, 69(2), 117–128. <https://doi.org/10.3354/cr01398>

699 Beaugrand, G., & Kirby, R. R. (2018). How Do Marine Pelagic Species Respond to Climate Change?
700 Theories and Observations. *Annual Review of Marine Science*, 10(1), 169–197.
701 <https://doi.org/10.1146/annurev-marine-121916-063304>

702 Bopp, L., Aumont, O., Cadule, P., Alvain, S., & Gehlen, M. (2005). Response of diatoms distribution to
703 global warming and potential implications: A global model study. *Geophysical Research*
704 *Letters*, 32(19), L19606. <https://doi.org/10.1029/2005GL023653>

705 Bopp, L., Resplandy, L., Orr, J. C., Doney, S. C., Dunne, J. P., Gehlen, M., Halloran, P., Heinze, C., Ilyina,
706 T., Séférian, R., Tjiputra, J., & Vichi, M. (2013). Multiple stressors of ocean ecosystems in the
707 21st century: Projections with CMIP5 models. *Biogeosciences*, 10(10), 6225–6245.
708 <https://doi.org/10.5194/bg-10-6225-2013>

709 Boyce, D. G., Petrie, B., Frank, K. T., Worm, B., & Leggett, W. C. (2017). Environmental structuring of
710 marine plankton phenology. *Nature Ecology & Evolution*, 1(10), 1484–1494.
711 <https://doi.org/10.1038/s41559-017-0287-3>

712 Brun, P., Kiørboe, T., Licandro, P., & Payne, M. R. (2016). The predictive skill of species distribution
713 models for plankton in a changing climate. *Global Change Biology*, 22(9), 3170–3181.
714 <https://doi.org/10.1111/gcb.13274>

715 Cabré, A., Shields, D., Marinov, I., & Kostadinov, T. S. (2016). Phenology of Size-Partitioned
716 Phytoplankton Carbon-Biomass from Ocean Color Remote Sensing and CMIP5 Models.
717 *Frontiers in Marine Science*, 3. <https://doi.org/10.3389/fmars.2016.00039>

718 Caracciolo, M., Beaugrand, G., Hélaouët, P., Gevaert, F., Edwards, M., Lizon, F., Kléparski, L., &
719 Goberville, E. (2021). Annual phytoplankton succession results from niche-environment
720 interaction. *Journal of Plankton Research*, 43(1), 85–102.
721 <https://doi.org/10.1093/plankt/fbaa060>

722 Chivers, W. J., Edwards, M., & Hays, G. C. (2020). Phenological shuffling of major marine
723 phytoplankton groups over the last six decades. *Diversity and Distributions*, 26(5), 536–548.
724 <https://doi.org/10.1111/ddi.13028>

725 Cushing, D. H. (1990). Plankton Production and Year-class Strength in Fish Populations: An Update of
726 the Match/Mismatch Hypothesis. *Advances in Marine Biology*, 26, 249–293.
727 [https://doi.org/10.1016/S0065-2881\(08\)60202-3](https://doi.org/10.1016/S0065-2881(08)60202-3)

728 Dutkiewicz, S., Cermeno, P., Jahn, O., Follows, M. J., Hickman, A. E., Taniguchi, D. A. A., & Ward, B. A.
729 (2020). Dimensions of marine phytoplankton diversity. *Biogeosciences*, 17(3), 609–634.
730 <https://doi.org/10.5194/bg-17-609-2020>

731 Dutkiewicz, S., Scott, J. R., & Follows, M. J. (2013). Winners and losers: Ecological and biogeochemical
732 changes in a warming ocean. *Global Biogeochemical Cycles*, 27(2), 463–477.
733 <https://doi.org/10.1002/gbc.20042>

734 Dybwad, C., Assmy, P., Olsen, L. M., Peeken, I., Nikolopoulos, A., Krumpen, T., Randelhoff, A., Tatarek,
735 A., Wiktor, J. M., & Reigstad, M. (2021). Carbon Export in the Seasonal Sea Ice Zone North of
736 Svalbard from Winter to Late Summer. *Frontiers in Marine Science*, 7, 525800.
737 <https://doi.org/10.3389/fmars.2020.525800>

738 Edwards, M., Beaugrand, G., Kléparski, L., Helaouët, P., & Reid, P. C. (2022). Climate variability and
739 multi-decadal diatom abundance in the Northeast Atlantic. *Communications Earth &*
740 *Environment*, 3, 162. <https://doi.org/10.1038/s43247-022-00492-9>

741 Edwards, M., Beaugrand, G., Reid, P. C., Rowden, A. A., & Jones, M. B. (2002). Ocean climate
742 anomalies and the ecology of the North Sea. *Marine Ecology Progress Series*, 239, 1–10.
743 <https://doi.org/10.3354/meps239001>

744 Edwards, M., & Richardson, A. J. (2004). Impact of climate change on marine pelagic phenology and
745 trophic mismatch. *Nature*, 430(7002), 881–884. <https://doi.org/10.1038/nature02808>

746 Eyring, V., Bony, S., Meehl, G. A., Senior, C. A., Stevens, B., Stouffer, R. J., & Taylor, K. E. (2016).
747 Overview of the Coupled Model Intercomparison Project Phase 6 (CMIP6) experimental

748 design and organization. *Geoscientific Model Development*, 9(5), 1937–1958.
749 <https://doi.org/10.5194/gmd-9-1937-2016>

750 Field, C. B., Behrenfeld, M. J., Randerson, J. T., & Falkowski, P. G. (1998). Primary Production of the
751 Biosphere: Integrating Terrestrial and Oceanic Components. *Science*, 281, 237–240.

752 Friedland, K. D., Mouw, C. B., Asch, R. G., Ferreira, A. S. A., Henson, S. A., Hyde, K. J. W., Morse, R. E.,
753 Thomas, A. C., & Brady, D. C. (2018). Phenology and time series trends of the dominant
754 seasonal phytoplankton bloom across global scales. *Global Ecology and Biogeography*, 27(5),
755 551–569. <https://doi.org/10.1111/geb.12717>

756 Fu, W., Randerson, J. T., & Moore, J. K. (2016). Climate change impacts on net primary production
757 (NPP) and export production (EP) regulated by increasing stratification and phytoplankton
758 community structure in the CMIP5 models. *Biogeosciences*, 13(18), 5151–5170.
759 <https://doi.org/10.5194/bg-13-5151-2016>

760 Gause, G. F. (1934). *The struggle for existence* (Williams and Wilkins.).

761 Helaouët, P., & Beaugrand, G. (2007). Macroecology of *Calanus finmarchicus* and *C. helgolandicus* in
762 the North Atlantic Ocean and adjacent seas. *Marine Ecology Progress Series*, 345, 147–165.
763 <https://doi.org/10.3354/meps06775>

764 Henson, S. A., Cole, H., Beaulieu, C., & Yool, A. (2013). The impact of global warming on seasonality of
765 ocean primary production. *Biogeosciences*, 10, 4357–4369. [https://doi.org/10.5194/bg-10-](https://doi.org/10.5194/bg-10-4357-2013)
766 [4357-2013](https://doi.org/10.5194/bg-10-4357-2013)

767 Henson, S. A., Cole, H. S., Hopkins, J., Martin, A. P., & Yool, A. (2018). Detection of climate change-
768 driven trends in phytoplankton phenology. *Global Change Biology*, 24, e101–e111.
769 [https://doi.org/DOI: 10.1111/gcb.13886](https://doi.org/DOI:10.1111/gcb.13886)

770 Henson, S. A., Lampitt, R., & Johns, D. (2012). Variability in phytoplankton community structure in
771 response to the North Atlantic Oscillation and implications for organic carbon flux. *Limnology*
772 *and Oceanography*, 57(6), 1591–1601. <https://doi.org/10.4319/lo.2012.57.6.1591>

773 Henson, S. A., Laufkötter, C., Leung, S., Giering, S. L. C., Palevsky, H. I., & Cavan, E. L. (2022).
774 Uncertain response of ocean biological carbon export in a changing world. *Nature*
775 *Geoscience*, 15(4), 248–254. <https://doi.org/10.1038/s41561-022-00927-0>

776 Hutchinson, G. E. (1957). Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology*,
777 22, 415–427.

778 Hutchinson, G. E. (1978). *An introduction to population ecology* (Yale University Press).

779 IPCC. (2019). Technical Summary. In D. C. Roberts, H. O. Pörtner, V. Masson-Delmotte, P. Zhai, E.
780 Poloczanska, K. Mintenbeck, M. Tignor, A. Alegria, M. Nicolai, A. Okem, J. Petzold, B. Rama, &
781 N. M. Weyer (Eds.), *IPCC Special Report on the Ocean and Cryosphere in a Changing Climate*
782 (pp. 39–69). Cambridge University Press.

783 Irwin, A. J., Nelles, A. M., & Finkel, Z. V. (2012). Phytoplankton niches estimated from field data.
784 *Limnology and Oceanography*, 57(3), 787–797. <https://doi.org/10.4319/lo.2012.57.3.0787>

785 Jonas, T. D., Walne, A. W., Beaugrand, G., Gregory, L., & Hays, G. C. (2004). The volume of water
786 filtered by a Continuous Plankton Recorder sample: The effect of ship speed. *Journal of*
787 *Plankton Research*, 26(12), 1499–1506. <https://doi.org/10.1093/plankt/fbh137>

788 Karp-Boss, L., & Boss, E. (2016). The Elongated, the Squat and the Spherical: Selective Pressures for
789 Phytoplankton Shape. In P. M. Glibert & T. M. Kana (Eds.), *Aquatic Microbial Ecology and*
790 *Biogeochemistry: A Dual Perspective* (pp. 25–34). Springer International Publishing.
791 https://doi.org/10.1007/978-3-319-30259-1_3

792 Kemp, A. E. S., & Villareal, T. A. (2013). High diatom production and export in stratified waters – A
793 potential negative feedback to global warming. *Progress in Oceanography*, 119, 4–23.
794 <https://doi.org/10.1016/j.pocean.2013.06.004>

795 Kemp, A. E. S., & Villareal, T. A. (2018). The case of the diatoms and the muddled mandalas: Time to
796 recognize diatom adaptations to stratified waters. *Progress in Oceanography*, 167, 138–149.
797 <https://doi.org/10.1016/j.pocean.2018.08.002>

798 Kléparski, L., Beaugrand, G., Edwards, M., Schmitt, F. G., Kirby, R. R., Breton, E., Gevaert, F., &
799 Maniez, E. (2022). Morphological traits, niche-environment interaction and temporal
800 changes in diatoms. *Progress in Oceanography*, *201*, 102747.
801 <https://doi.org/10.1016/j.pocean.2022.102747>

802 Kwiatkowski, L., Torres, O., Bopp, L., Aumont, O., Chamberlain, M., Christian, J. R., Dunne, J. P.,
803 Gehlen, M., Ilyina, T., John, J. G., Lenton, A., Li, H., Lovenduski, N. S., Orr, J. C., Palmieri, J.,
804 Santana-Falcón, Y., Schwinger, J., Séférian, R., Stock, C. A., ... Ziehn, T. (2020). Twenty-first
805 century ocean warming, acidification, deoxygenation, and upper-ocean nutrient and primary
806 production decline from CMIP6 model projections. *Biogeosciences*, *17*(13), 3439–3470.
807 <https://doi.org/10.5194/bg-17-3439-2020>

808 Lewandowska, A., & Sommer, U. (2010). Climate change and the spring bloom: A mesocosm study on
809 the influence of light and temperature on phytoplankton and mesozooplankton. *Marine
810 Ecology Progress Series*, *405*, 101–111. <https://doi.org/10.3354/meps08520>

811 Litchman, E., Edwards, K. F., Klausmeier, C. A., & Thomas, M. K. (2012). Phytoplankton niches, traits
812 and eco-evolutionary responses to global environmental change. *Marine Ecology Progress
813 Series*, *470*, 235–248. <https://doi.org/doi:10.3354/meps09912>

814 Litchman, E., & Klausmeier, C. A. (2008). Trait-Based Community Ecology of Phytoplankton. *Annual
815 Review of Ecology, Evolution, and Systematics*, *39*(1), 615–639.

816 Litchman, E., Klausmeier, C. A., Schofield, O. M., & Falkowski, P. G. (2007). The role of functional
817 traits and trade-offs in structuring phytoplankton communities: Scaling from cellular to
818 ecosystem level. *Ecology Letters*, *10*(12), 1170–1181. [https://doi.org/10.1111/j.1461-
819 0248.2007.01117.x](https://doi.org/10.1111/j.1461-0248.2007.01117.x)

820 Lürling, M. (2021). Grazing resistance in phytoplankton. *Hydrobiologia*, *848*(1), 237–249.
821 <https://doi.org/10.1007/s10750-020-04370-3>

822 Mannocci, L., Boustany, A. M., Roberts, J. J., Palacios, D. M., Dunn, D. C., Halpin, P. N., Viehman, S.,
823 Moxley, J., Cleary, J., Bailey, H., Bograd, S. J., Becker, E. A., Gardner, B., Hartog, J. R., Hazen, E.

824 L., Ferguson, M. C., Forney, K. A., Kinlan, B. P., Oliver, M. J., ... Winship, A. J. (2017). Temporal
825 resolutions in species distribution models of highly mobile marine animals:
826 Recommendations for ecologists and managers. *Diversity and Distributions*, 23(10), 1098–
827 1109. <https://doi.org/10.1111/ddi.12609>

828 Margalef, R. (1978). Life-forms of phytoplankton as survival alternatives in an unstable environment.
829 *Oceanologica Acta*, 1(4), 493–509.

830 Marinov, I., Doney, S. C., & Lima, I. D. (2010). Response of ocean phytoplankton community structure
831 to climate change over the 21st century: Partitioning the effects of nutrients, temperature
832 and light. *Biogeosciences*, 7, 3941–3959. <https://doi.org/10.5194/bg-7-3941-2010>

833 Martin, T. L., & Huey, R. B. (2008). Why “Suboptimal” Is Optimal: Jensen’s Inequality and Ectotherm
834 Thermal Preferences. *The American Naturalist*, 171(3), E102–E118.
835 <https://doi.org/10.1086/527502>

836 Miller, C. B. (2004). *Biological Oceanography*. Blackwell Science Ltd.

837 Naselli-Flores, L., Zohary, T., & Padisák, J. (2021). Life in suspension and its impact on phytoplankton
838 morphology: An homage to Colin S. Reynolds. *Hydrobiologia*, 848, 7–30.
839 <https://doi.org/10.1007/s10750-020-04217-x>

840 O’Neill, B. C., Kriegler, E., Ebi, K. L., Kemp-Benedict, E., Riahi, K., Rothman, D. S., van Ruijven, B. J., van
841 Vuuren, D. P., Birkmann, J., Kok, K., Levy, M., & Solecki, W. (2017). The roads ahead:
842 Narratives for shared socioeconomic pathways describing world futures in the 21st century.
843 *Global Environmental Change*, 42, 169–180.
844 <https://doi.org/10.1016/j.gloenvcha.2015.01.004>

845 O’Neill, B. C., Tebaldi, C., van Vuuren, D. P., Eyring, V., Friedlingstein, P., Hurtt, G., Knutti, R., Kriegler,
846 E., Lamarque, J., Lowe, J., Meehl, G. A., Moss, R., Riahi, K., & Sanderson, B. M. (2016). The
847 Scenario Model Intercomparison Project (ScenarioMIP) for CMIP6. *Geoscientific Model
848 Development*, 9(9), 3461–3482. <https://doi.org/10.5194/gmd-9-3461-2016>

849 Padišak, J., Soroczki-Pinter, E., & Rezner, Z. (2003). Sinking properties of some phytoplankton shapes
850 and the relation of form resistance to morphological diversity of plankton – an experimental
851 study. *Hydrobiologia*, 500, 243–257.

852 Pančić, M., & Kiørboe, T. (2018). Phytoplankton defence mechanisms: Traits and trade-offs:
853 Defensive traits and trade-offs. *Biological Reviews*, 93(2), 1269–1303.
854 <https://doi.org/10.1111/brv.12395>

855 Passow, U., & Carlson, C. A. (2012). The biological pump in a high CO₂ world. *Marine Ecology*
856 *Progress Series*, 470, 249–271. <https://doi.org/10.3354/meps09985>

857 Poloczanska, E. S., Brown, C. J., Sydeman, W. J., Kiessling, W., Schoeman, D. S., Moore, P. J., Brander,
858 K., Bruno, J. F., Buckley, L. B., Burrows, M. T., Duarte, C. M., Halpern, B. S., Holding, J., Kappel,
859 C. V., O'Connor, M. I., Pandolfi, J. M., Parmesan, C., Schwing, F., Thompson, S. A., &
860 Richardson, A. J. (2013). Global imprint of climate change on marine life. *Nature Climate*
861 *Change*, 3(10), 919–925. <https://doi.org/10.1038/nclimate1958>

862 Pulliam, H. R. (2000). On the relationship between niche and distribution. *Ecology Letters*, 3(4), 349–
863 361. <https://doi.org/10.1046/j.1461-0248.2000.00143.x>

864 Raven, J. A., & Waite, A. M. (2004). The evolution of silicification in diatoms: Inescapable sinking and
865 sinking as escape? *New Phytologist*, 162(1), 45–61. [https://doi.org/10.1111/j.1469-](https://doi.org/10.1111/j.1469-8137.2004.01022.x)
866 [8137.2004.01022.x](https://doi.org/10.1111/j.1469-8137.2004.01022.x)

867 Reid, P. C., Colebrook, J. M., Matthews, J. B. L., Aiken, J., & Continuous Plankton Recorder Team.
868 (2003). The Continuous Plankton Recorder: Concepts and history, from Plankton Indicator to
869 undulating recorders. *Progress in Oceanography*, 58(2–4), 117–173.
870 <https://doi.org/10.1016/j.pocean.2003.08.002>

871 Richardson, A. J., Walne, A. W., John, A. W. G., Jonas, T. D., Lindley, J. A., Sims, D. W., Stevens, D., &
872 Witt, M. (2006). Using continuous plankton recorder data. *Progress in Oceanography*, 68(1),
873 27–74. <https://doi.org/10.1016/j.pocean.2005.09.011>

874 Ryabov, A., Kerimoglu, O., Litchman, E., Olenina, I., Roselli, L., Basset, A., Stanca, E., & Blasius, B.
875 (2020). *Shape matters: The relationship between cell geometry and diversity in phytoplankton*
876 [Preprint]. *Ecology*. <https://doi.org/10.1101/2020.02.06.937219>

877 Séférian, R., Berthet, S., Yool, A., Palmiéri, J., Bopp, L., Tagliabue, A., Kwiatkowski, L., Aumont, O.,
878 Christian, J., Dunne, J., Gehlen, M., Ilyina, T., John, J. G., Li, H., Long, M. C., Luo, J. Y., Nakano,
879 H., Romanou, A., Schwinger, J., ... Yamamoto, A. (2020). Tracking Improvement in Simulated
880 Marine Biogeochemistry Between CMIP5 and CMIP6. *Current Climate Change Reports*, 6(3),
881 95–119. <https://doi.org/10.1007/s40641-020-00160-0>

882 Smayda, T. (1970). The suspension and sinking of phytoplankton in the sea. *Oceanography and*
883 *Marine Biology - An Annual Review*, 8, 353–414.

884 Smetacek, V. (1985). Role of sinking in diatom life-history cycles: Ecological, evolutionary and
885 geological significance. *Marine Biology*, 84, 239–251.

886 Soberon, J., & Nakamura, M. (2009). Niches and distributional areas: Concepts, methods, and
887 assumptions. *Proceedings of the National Academy of Sciences*, 106(Supplement_2), 19644–
888 19650. <https://doi.org/10.1073/pnas.0901637106>

889 Sournia, A. (1982). Form and function in marine phytoplankton. *Biological Reviews*, 57, 347–394.

890 Stock, C. A., Alexander, M. A., Bond, N. A., Brander, K. M., Cheung, W. W. L., Curchitser, E. N.,
891 Delworth, T. L., Dunne, J. P., Griffies, S. M., Haltuch, M. A., Hare, J. A., Hollowed, A. B.,
892 Lehodey, P., Levin, S. A., Link, J. S., Rose, K. A., Rykaczewski, R. R., Sarmiento, J. L., Stouffer,
893 R., ... Werner, F. E. (2011). On the use of IPCC-class models to assess the impact of climate on
894 Living Marine Resources. *Progress in Oceanography*, 88, 1–27.
895 <https://doi.org/10.1016/j.pocean.2010.09.001>

896 Straile, D., Kerimoglu, O., & Peeters, F. (2015). Trophic mismatch requires seasonal heterogeneity of
897 warming. *Ecology*, 96(10), 2794–2805. <https://doi.org/10.1890/14-0839.1>

898 Taucher, J., & Oschlies, A. (2011). Can we predict the direction of marine primary production change
899 under global warming? *Geophysical Research Letters*, *38*, L02603.
900 <https://doi.org/10.1029/2010GL045934>

901 Thackeray, S. J., Henrys, P. A., Hemming, D., Bell, J. R., Botham, M. S., Burthe, S., Helaouet, P., Johns,
902 D. G., Jones, I. D., Leech, D. I., Mackay, E. B., Massimino, D., Atkinson, S., Bacon, P. J.,
903 Brereton, T. M., Carvalho, L., Clutton-Brock, T. H., Duck, C., Edwards, M., ... Wanless, S.
904 (2016). Phenological sensitivity to climate across taxa and trophic levels. *Nature*, *535*(7611),
905 241–245. <https://doi.org/10.1038/nature18608>

906 Thomas, M. K., Kremer, C. T., Klausmeier, C. A., & Litchman, E. (2012). A Global Pattern of Thermal
907 Adaptation in Marine Phytoplankton. *Science*, *338*(6110), 1085–1088.
908 <https://doi.org/10.1126/science.1224836>

909 Tréguer, P., Bowler, C., Moriceau, B., Dutkiewicz, S., Gehlen, M., Aumont, O., Bittner, L., Dugdale, R.,
910 Finkel, Z., Iudicone, D., Jahn, O., Guidi, L., Lasbleiz, M., Leblanc, K., Levy, M., & Pondaven, P.
911 (2018). Influence of diatom diversity on the ocean biological carbon pump. *Nature*
912 *Geoscience*, *11*(1), 27–37. <https://doi.org/10.1038/s41561-017-0028-x>

913 van der Spoel, S. (1994). The basis for boundaries in pelagic biogeography. *Progress in Oceanography*,
914 *34*(2–3), 121–133. [https://doi.org/10.1016/0079-6611\(94\)90005-1](https://doi.org/10.1016/0079-6611(94)90005-1)

915 Ward, B. A., & Follows, M. J. (2016). Marine mixotrophy increases trophic transfer efficiency, mean
916 organism size, and vertical carbon flux. *Proceedings of the National Academy of Sciences*,
917 *113*(11), 2958–2963. <https://doi.org/10.1073/pnas.1517118113>

918 Warner, A. J., & Hays, G. C. (1994). Sampling by the continuous plankton recorder survey. *Progress in*
919 *Oceanography*, *34*(2–3), 237–256. [https://doi.org/10.1016/0079-6611\(94\)90011-6](https://doi.org/10.1016/0079-6611(94)90011-6)

920 Winder, M., & Schindler, D. E. (2004). Climate change uncouples trophic interactions in an aquatic
921 ecosystem. *Ecology*, *85*(8), 2100–2106. <https://doi.org/10.1890/04-0151>

922 Yamaguchi, R., Rodgers, K. B., Stein, K. J., Timmermann, A., Schlunegger, S., Bianchi, D., Dunne, J. P.,
923 & Slater, R. D. (2022). Trophic level decoupling drives future change in phytoplankton bloom

924 phenology. *Nature Climate Change*, 12, 469–476. <https://doi.org/10.1038/s41558-022->

925 01353-1

926

927

928

929

930

931

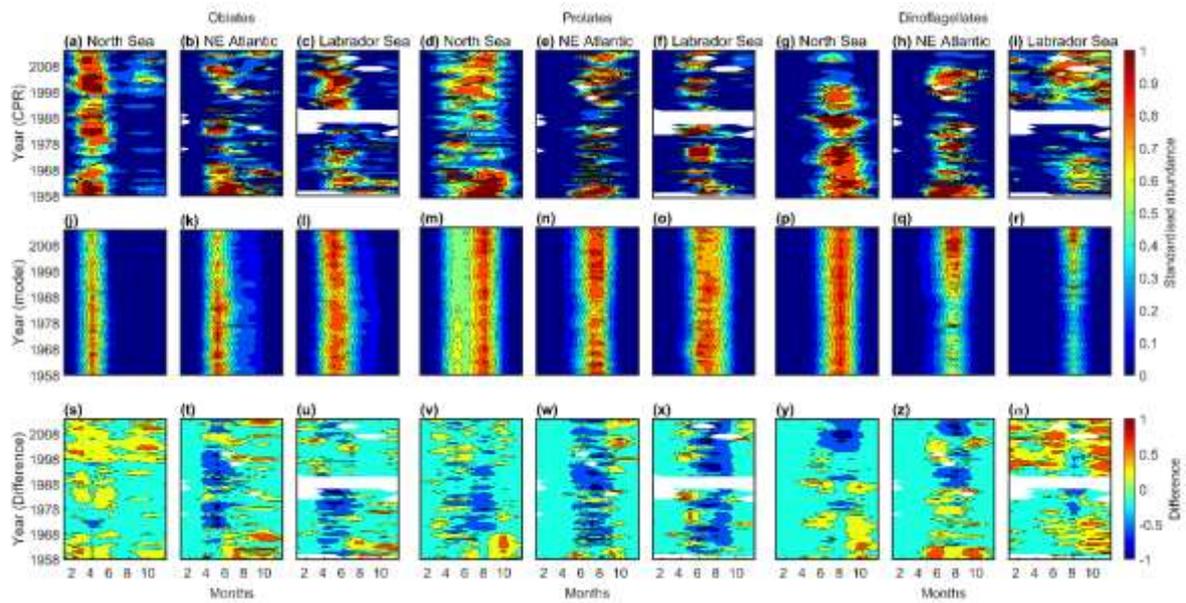
932

933

934

935

936 **Figures**



937

938 **Figure 1.**

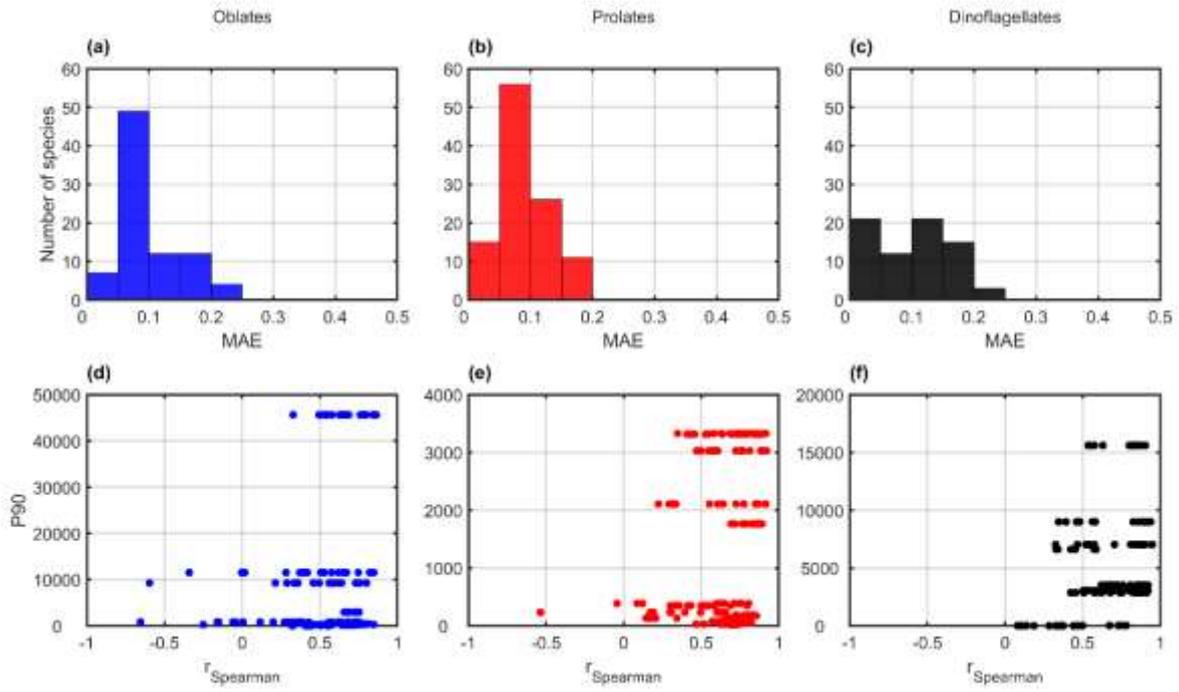
939

940

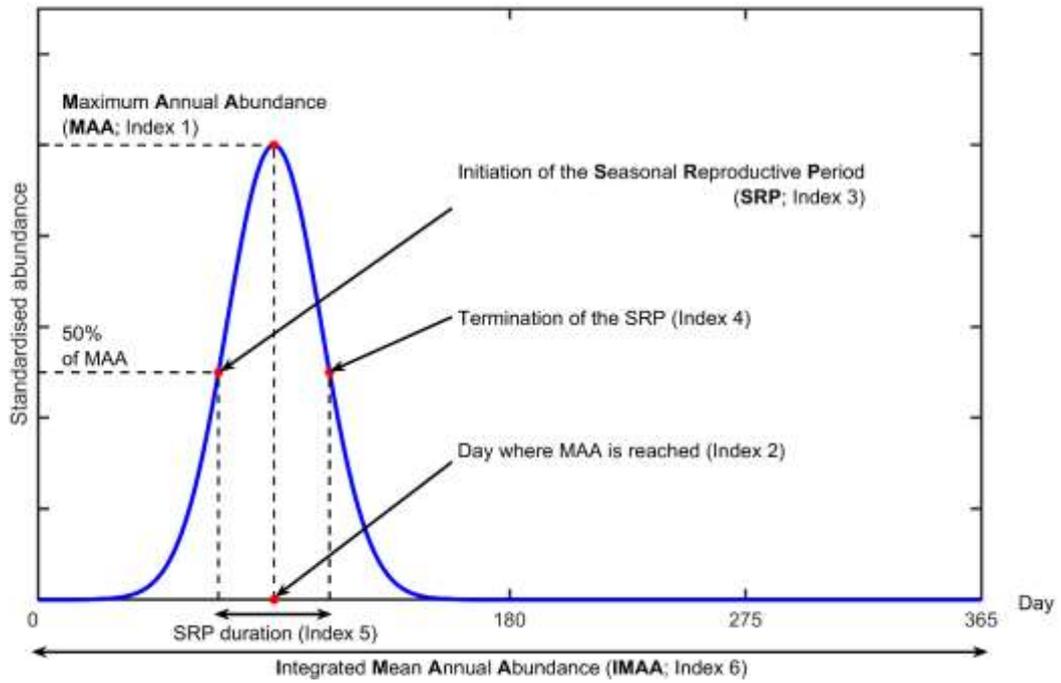
941

942

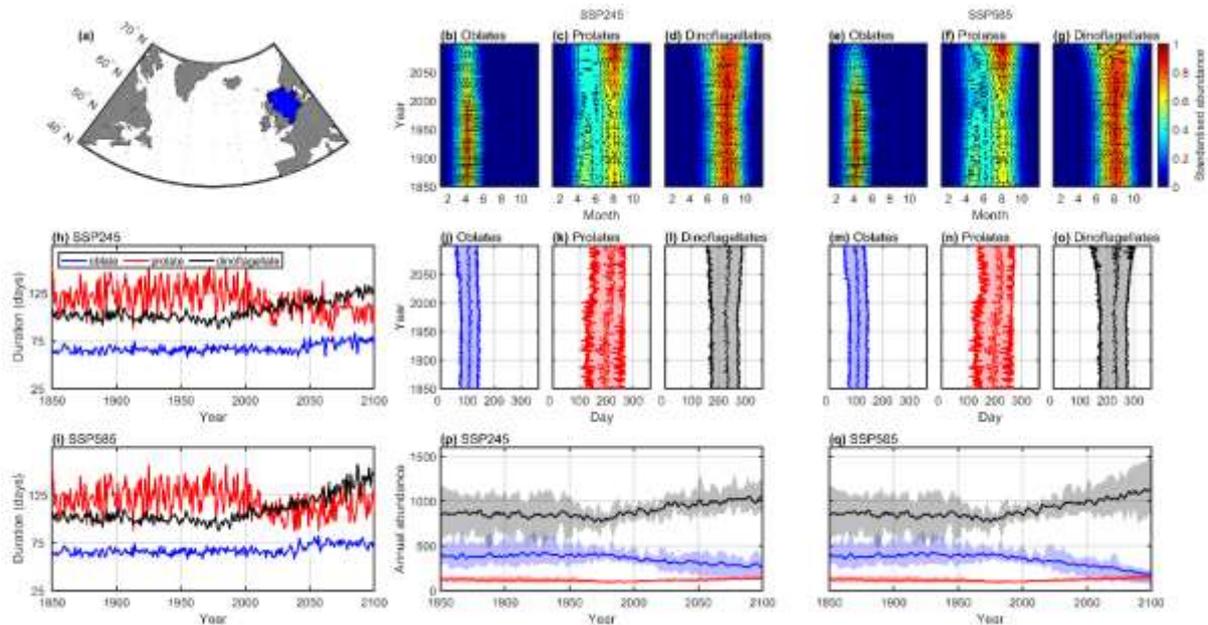
943



944
945 **Figure 2.**
946

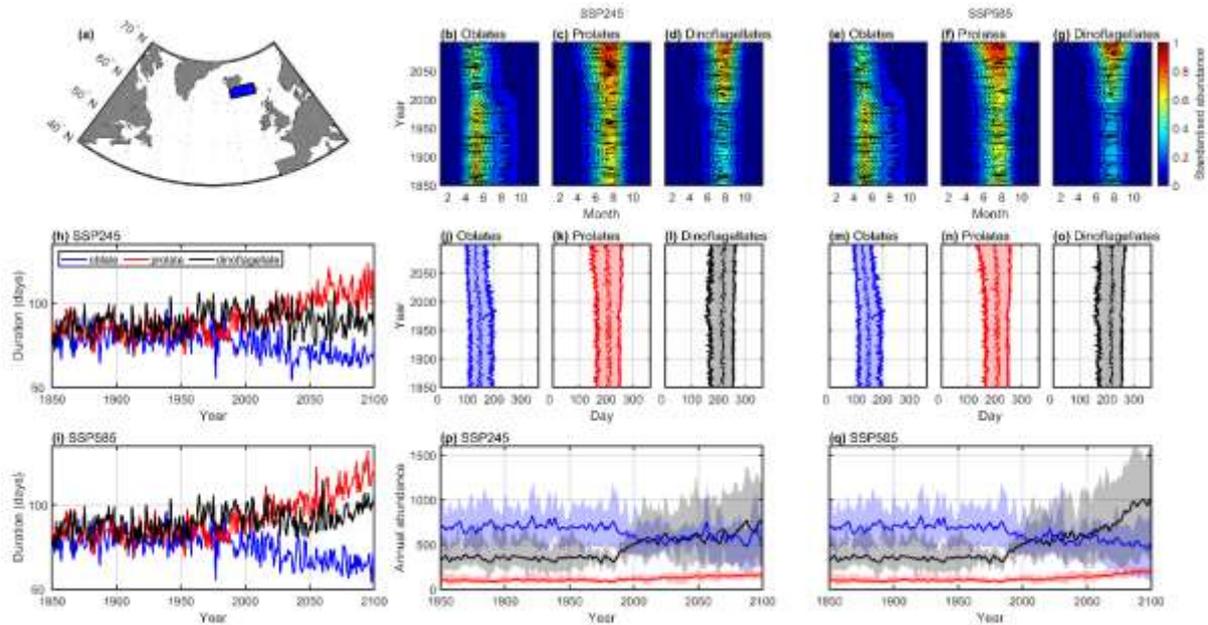


947
948 **Figure 3.**
949
950
951
952
953
954



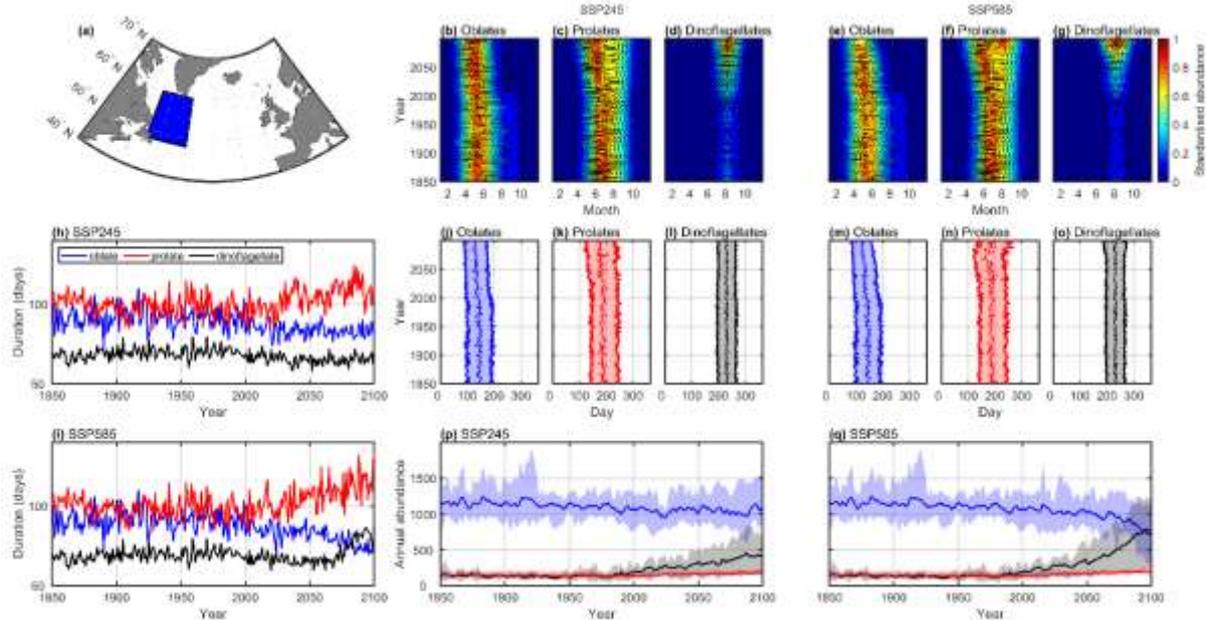
955
956
957
958
959
960

Figure 4.



961
962
963
964
965
966
967
968

Figure 5.



969
970
971
972
973
974
975
976

Figure 6.

977
978
979
980
981
982
983
984
985
986
987
988
989
990
991
992

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).

993
994
995
996
997
998
999

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_{Spearman}) calculated between the observed and the modelled abundances, and the corresponding 90th 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.

1004

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).

1011

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.

1027

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.

1043

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.

1059
1060
1061
1062
1063
1064
1065
1066

1067 **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

1073