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1 **Annual phytoplankton succession results from niche-environment**
2 **interaction**

3 Mariarita Caracciolo¹, Grégory Beaugrand^{2,3,4}, Pierre Helaouët⁴, François Gevaert³, Martin
4 Edwards^{4,5}, Fabrice Lizon³, Loïck Kléparski^{2,3,4}, Eric Goberville⁶.

5 ¹*Sorbonne Université, CNRS, Station Biologique de Roscoff, UMR 7144, ECOMAP, Place*
6 *Georges Teissier, 29680 Roscoff, France.*

7
8 ²*Centre National de la Recherche Scientifique (CNRS), Université de Lille, Université Littoral*
9 *Côte d'Opale, UMR 8187, LOG, Laboratoire d'Océanologie et de Géosciences, F 62930*
10 *Wimereux, France.*

11
12 ³*Université de Lille, CNRS, Univ. Littoral Côte d'Opale, UMR 8187, LOG, Laboratoire*
13 *d'Océanologie et de Géosciences, F 62930 Wimereux, France.*

14
15 ⁴*Marine Biological Association, Citadel Hill, Plymouth PL1 2PB, UK.*

16
17 ⁵*University of Plymouth, School of Biological and Marine Sciences, Drake Circus, Plymouth,*
18 *UK.*

19
20 ⁶*Unité Biologie des organismes et écosystèmes aquatiques (BOREA), Muséum National*
21 *d'Histoire Naturelle, Sorbonne Université, Université de Caen Normandie, Université des*
22 *Antilles, CNRS, IRD, CP53, 61, Rue Buffon 75005 Paris, France.*

23
24 **Corresponding authors:** Mariarita Caracciolo (mariarita.caracciolo@sb-roscoff.fr) and Gregory
25 **Beaugrand** (Gregory.Beaugrand@univ-lille.fr)

26

27

28 **Abstract**

29 Annual plankton succession has been investigated for many decades and hypotheses ranging from
30 abiotic to biotic mechanisms have been proposed to explain this recurrent pattern. Here, using data
31 collected by the Continuous Plankton Recorder (CPR) survey and models originating from the
32 MacroEcological Theory on the Arrangement of Life (METAL), we investigate annual
33 phytoplankton succession in the North Sea at a species level. Our results show that this
34 phenomenon can be well predicted by models combining photosynthetically active radiation,
35 temperature and macro-nutrients. Our findings suggest that annual phytoplankton succession, at
36 community level, originates from the interaction between species ecological niche and annual
37 environmental fluctuations. We discuss our results in the context of traditional hypotheses
38 formulated to explain this recurrent pattern in the marine field, including those on the initiation,
39 the development and the termination of a typical extratropical spring bloom.

40
41 **Keywords**

42 Annual plankton succession, phenology, ecological niche, environment, plankton, Continuous
43 Plankton Recorder (CPR), METAL theory.

44

45 1. INTRODUCTION

46

47 Annual Plankton Succession (APS) is defined as the recurrent pattern of species abundance
48 observed during the annual cycle (Cushing 1959, Winder and Cloern 2010, Sommer et al. 2012,
49 Romagnan et al. 2015). In temperate and polar biomes, phytoplankton abundance varies from
50 periods of proliferation in spring and autumn to periods of decline in summer and winter. In
51 subtropical and tropical waters, where seasonal changes in solar radiation and temperature are less
52 prominent, plankton abundance is more stable at an annual scale (Dakos et al. 2009). In the
53 Mediterranean Sea, eukaryotic primary producers appear from early spring with the following
54 sequence: pico-eukaryotes, silicoflagellates, diatoms and dinoflagellates (Romagnan et al. 2015).

55 APS has been widely described in marine ecosystems, leading to a variety of potential
56 explanations often based on mechanisms such as bottom-up to top-down controls (Sverdrup 1953,
57 Margalef 1978, Sommer et al. 1986, Behrenfeld 2010, Sommer et al. 2012, Smyth et al. 2014,
58 Romagnan et al. 2015, Atkinson et al. 2018). Gilbert et al. (2012), Romagnan et al. (2015) and
59 Barton et al. (2015) have provided evidence for a strong influence of the physical environment on
60 phytoplankton dynamics, suggesting a bottom-up control of annual succession. A substantial
61 impact of species interaction (i.e. grazing) imposing a top-down control (e.g. mesozooplankton
62 species on protists) has also been suggested in the western part of the English Channel, however
63 (Kenitz et al. 2017, Fileman et al. 2010).

64 The seasonal cycles of irradiance, temperature and stratification and the associated changes
65 in pycnocline, thermocline and halocline are known to be closely associated with the onset of
66 phytoplankton growth (Longhurst 1998), and nutrients influence the extent of the phytoplankton
67 bloom (Sommer et al. 2012). Although APS starts typically by the onset of the spring bloom in
68 most extra-tropical regions, winter is a key period preparing the ingredients needed to trigger the
69 start of phytoplankton proliferation (Sommer et al. 2012). During winter, oceans and seas lose heat
70 from their surface waters, which become denser and consequently start to sink (Mann and Lazier
71 1996). Wind intensifies oceanic turbulence, which in turn brings nutrients (nitrate, phosphate and
72 silicic acid) in the euphotic zone (Falkowski and Oliver 2007) while diluting phytoplankton in the
73 water column (Behrenfeld 2010).

74 According to the Sverdrup's model (Sverdrup 1953), the spring phytoplankton bloom can
75 develop when the Mixed Layer Depth (MLD), which can reach several hundred meters in the
76 North Atlantic Ocean during winter (Reygondeau and Beaugrand 2010), is shallower than a critical
77 depth at which the integral of net growth rate becomes zero over the water column. Sverdrup's
78 theory has greatly stimulated research and this hypothesis is applicable to both deep waters and
79 off-shore environments but not in shallow coastal systems (Behrenfeld 2010, Sathyendranah et al.
80 2015, Lévy 2015). The intensity of the phytoplankton bloom is strengthened when solar heating
81 and reduced winds increase vertical stratification, leading to a strong thermocline. Irradiance is an
82 important factor due to its influence on critical depth and vernal stratification, allowing species to
83 remain in the euphotic zone. It has also been observed that the phytoplankton bloom sometimes
84 starts before water stratification, which has led some authors to challenge Sverdrup's concept
85 (Behrenfeld 2010). For instance, the dilution-recoupling hypothesis from Behrenfeld (2010)
86 explains how the spring phytoplankton bloom is the result of an increase in growth at a time of
87 strong dilution of grazers in the water column due to the absence of stratification. Progressive
88 stratification during the bloom reinforces the coupling between phytoplankton and grazers, and

89 the reduction in nutrients availability - combined to a high grazing pressure - induces bloom
90 termination. When the mixed layer deepens and increases macro-nutrients concentration in the
91 euphotic zone, an autumn phytoplankton bloom can occur (Longhurst 1998); it ends rapidly,
92 however, because of light limitation (Sverdrup 1953, Geider et al. 2014).

93 The main objective of this study is to reconstruct APS using models of increasing complexity
94 generated from the Macro-Ecological Theory on the Arrangement of Life (METAL; Beaugrand
95 2015) that consider a set of environmental parameters known to influence marine phytoplankton
96 dynamics such as temperature, photosynthetically active radiation and macro-nutrients. METAL
97 unifies together behavioural, physiological, phenological, biogeographic and long-term
98 community shifts and consequently allows one to predict how communities form and how they are
99 altered by environmental fluctuations, including climatic variability and global climate change
100 (Beaugrand et al. 2010, 2013a, 2014, 2018). The strength of this approach is to consider that, even
101 though ecosystems are complex adaptive systems, basic organisation and sensitivity of
102 communities can be predicted from simple founding principles. A significant proportion of the
103 spatial and temporal adjustments of marine communities are deterministic, being thereby
104 intelligible, which opens the way to testable predictions. In this study, our objectives are to test
105 whether APS is related to the interaction between the ecological niche (*sensu* Hutchinson 1957)
106 of species and seasonal fluctuations in their environment, and to identify the key ecological
107 dimensions of the niche that control the annual phytoplankton dynamics.

108 Here, using data from the Continuous Plankton Recorder (CPR) survey (Reid et al. 2003),
109 we first characterise APS in the North Sea. We model this phenomenon using METAL and
110 compare observed and predicted patterns. We then investigate how natural environmental
111 fluctuations drive phytoplankton seasonality from initiation to termination. Finally, we discuss our
112 results in the context of APS (Widdicombe et al. 2010, Sommer et al. 2012, Romagnan et al. 2015),
113 including hypotheses that have been proposed to explain the spring bloom such as the critical depth
114 and turbulence hypotheses (Sverdrup 1953, Huisman et al. 1999), dilution-recoupling hypothesis
115 (Behrenfeld 2010), and net heat flux hypothesis (Smyth et al. 2014).

116

117 **2. MATERIALS AND METHODS**

118 **2.1. Biological data**

119 Biological data originated from the Continuous Plankton Recorder (CPR,
120 <https://www.cprsurvey.org/data/our-data/>) survey. This marine biological monitoring programme,
121 currently operated by the Marine Biological Association (MBA), has sampled the North Atlantic
122 Ocean and its adjacent seas on a routine monthly basis since 1946 at a depth of approximately 7-
123 10 meters (Reid et al. 2003). Data from this programme have been extensively used to (i)
124 investigate APS (e.g., Colebrook 1979, 1982c, Zhai et al. 2013, Barton et al. 2015), (ii) characterise
125 pelagic biodiversity (e.g., Beaugrand et al. 2002, Barnard et al. 2004), (iii) document distributional,
126 phenological and physiological responses of marine species to climate change (e.g., Helaouët and
127 Beaugrand 2009, Beaugrand et al. 2009, Thackeray et al. 2016, Beaugrand and Kirby, 2018) and
128 (iv) anticipate the consequences of global warming in the pelagic realm (e.g., Reid et al. 1998,
129 Beaugrand et al. 2015).

130 In this study, we restricted our analyses to phytoplankton communities in the North Sea (1°E
131 - 4°E and 54°N - 56°N; Fig. S1) and considered 90 species or taxa commonly monitored by the
132 CPR survey over the period 1946-2016 (Table S1). The area was chosen because it was regularly
133 sampled over the last decades and is located relatively far from the coastline. In the selected area
134 and for all selected taxa, we calculated a climatology for each Julian day (i.e. 365) by averaging
135 the selected taxa abundances over the period 1958-2016.

136 **2.2. Environmental data**

137 Nutrients data originated from the World Ocean Atlas 2013 V2, provided by NOAA
138 National Centers for Environmental Information (NCEI), Silver Spring, Maryland, USA
139 (<https://www.nodc.noaa.gov/OC5/woa13/woa13data.html>) (Locarnini et al. 2013). It is a
140 scientifically quality-controlled database of selected historical *in situ* surface and subsurface
141 oceanographic measurements for phosphate ($\mu\text{mol. L}^{-1}$), silicate ($\mu\text{mol.L}^{-1}$) and nitrate ($\mu\text{mol. L}^{-1}$).
142 Monthly means are provided for these three parameters, on a 3D grid of 1° latitudes by 1°
143 longitude by 37 depth levels. Here, we calculated the average nutrients concentration in the North
144 Sea (1°E - 4°E and 54°N - 56°N; Fig. S1) for the first 20m. From this dataset, we calculated the
145 N/P ratio (Redfield 1958), which is known to modulate APS (Falkowski et al. 2000).

146 We used the Photosynthetically Active Radiation (PAR; Einstein . m^{-2} . day^{-1}), solar radiation
147 spectrum in the wavelength range of 400-700 nm, as a proxy of the level of energy that can be
148 assimilated by photosynthetic organisms (Asrar, Myneni & Kanemasu, 1989). PAR regulates both
149 the composition and evolution of marine ecosystems, influencing the growth of phytoplankton and
150 in turn the development of zooplankton and fish. Data were provided by the Giovanni online data
151 system, developed and maintained by the NASA GES DISC ([http://gdata1.sci.gsfc.nasa.gov/daac-](http://gdata1.sci.gsfc.nasa.gov/daac-bin/G3/gui.cgi?instance_id=ocean_month)
152 [bin/G3/gui.cgi?instance_id=ocean_month](http://gdata1.sci.gsfc.nasa.gov/daac-bin/G3/gui.cgi?instance_id=ocean_month)). A monthly climatology of PAR at a spatial resolution
153 of 9 km was carried out by compiling data of the Sea-viewing Wide Field-of-view Sensor
154 (SeaWiFS) from 2009 to 2012.

155 Because of the well-known influence of temperature (Beaugrand et al. 2018), we assessed
156 the thermal environment of the 90 phytoplankton species over our region of interest using Sea
157 Surface Temperature (SST) from the Optimum Interpolation (OI), which is based on both *in situ*
158 and satellite observations (see Reynolds et al. 2002 for a full description of the OI analysis). In
159 contrast to other environmental data which were only available at a monthly resolution, we used
160 daily SST for a finer estimation of the thermal preferendum of species. We first calculated daily
161 SSTs on a 1° by 1° grid from January 1982 to December 2017 and data were then averaged in the
162 area ranging from 1°E to 4°E and from 54°N to 56°N (Fig. S1). Annual changes in the
163 environmental parameters are shown in Fig. 1.

164 **2.3. Examination of APS from the CPR survey**

165 First, we removed species that had average annual abundance < 0.5 in the target area (Table
166 S1, Fig. S1). This procedure led to the selection of 81 phytoplankton species (Table S1) for which
167 we estimated average daily abundances over the region of interest for the period 1946-2015. To
168 minimise short-term fluctuations and reduce the noise inherent to these data, we applied an order-
169 6 symmetrical moving average on each daily time series (Legendre and Legendre 1998).

170 A standardised Principal Component Analysis (PCA; Jolliffe 1986) was applied on the
171 correlation matrix 81 phytoplankton species x 365 days and the first three principal components

172 (PCs) were examined to identify changes in annual succession. Species were then sorted according
 173 to their phenology by using normalised eigenvectors, i.e. linear correlation values with the
 174 corresponding PCs higher than |0.5| (Table S1). Only significant axes (PCs) were represented
 175 (Fig. 2).

176 Finally, we clustered phytoplankton species into five groups: Bacillariophyceae,
 177 Dinophyceae, Primmnesiophyceae, Dictyochophyceae and Cyanophyceae.

178 2.4. Generation of pseudo-species using models from the METAL theory

179 We modeled patterns of APS using METAL (Beaugrand et al. 2014, 2018). First, we
 180 generated a pool of uni-dimensional niches (i.e., niches with only one ecological dimension) by
 181 using a Gaussian model (Ter Braak 1996):

$$182 \quad A = c e^{-\left(\frac{(x-x_{opt})^2}{2t^2}\right)} \quad (1)$$

183 where A is the abundance of a species as a function of the value of a given environmental
 184 parameter x; c is the maximum abundance of a pseudo-species with c being fixed to 1 (Beaugrand,
 185 2015); x_{opt} is the environmental optimum (e.g. the best environmental condition for a given species
 186 that can reach the highest level of abundance) and t is the ecological amplitude of a pseudo-species
 187 (i.e. the environmental range where a species can occur) for a given environmental factor (Table
 188 S3). Species abundance along environmental gradients is generally modelled using a Gaussian
 189 model (Gauch et al. 1974).

190 Multi-dimensional niches (i.e., niches with 2 or more ecological dimensions) were modelled
 191 as follows:

$$192 \quad A = C e^{-\frac{1}{2} \left[\left(\frac{x_1 - x_{opt1}}{t_1} \right)^2 + \dots + \left(\frac{x_n - x_{optn}}{t_n} \right)^2 \right]} \quad (2)$$

193 with $2 \leq n \leq 5$ ecological dimensions, x_1 to x_n the values of the environmental parameters,
 194 x_{opt1} to x_{optn} , the optimum values of x_1 to x_n , and t_1 to t_n , the ecological amplitudes of x_1 to x_n .

195 Our simulations were based upon six environmental parameters: (i) SST, (ii) PAR, (iii)
 196 nitrate, (iv) phosphate, (v) silicate, and (vi) N/P ratio. When the N/P ratio was considered, neither
 197 nitrate nor phosphate concentrations were included in the models to avoid possible bias related to
 198 multicollinearity. We performed simulations using all possible environmental combinations from
 199 one to five ecological dimensions (Table S2), leading to a total of 84 runs (i.e. simulations): 16
 200 uni-dimensional runs, 23 two-dimensional runs, 29 three-dimensional runs, 13 four-dimensional
 201 runs and 3 five-dimensional runs (Table S2). The characteristics (optimum and ecological
 202 amplitude) of all niches are presented in Table S3. For example, for temperature, we defined 7
 203 optimum values (i.e. values corresponding to the highest abundance for a given pseudo-species)
 204 ranging from 0 to 36°C by increment of 6°C and 4 ecological amplitudes from 1 to 10°C by
 205 increment of 3°C, leading to the creation of 28 (4 x 7) virtual (or pseudo-) niches.

206 For each run, a large number of niches (from 21 to 15,431,472) was created (Table S3). To
 207 determine the total number of niches per run, we multiplied the number of niches generated for a

208 given dimension by the number generated for all other ecological dimensions. For example, for a
209 run based on temperature, PAR and nitrate (i.e. a three-dimensional run), the total number of niches
210 was $28 \times 21 \times 27 = 15,876$ ecological niches (with 28 niches for SST, 21 for PARc and 27 for
211 nitrate; Table S3).

212 To test whether the resolution of niches (i.e. the number of points along the niches) affected
213 our analyses, we compared two extreme cases of uni-dimensional models (i.e. low and high
214 resolutions) using each ecological variable. We added the term “bis” after the name of the variable
215 to identify high-resolution niche (Tables S3-S4). When the word ‘bis’ was absent, the uni-
216 dimensional niche had a low resolution. Because of the high number of categories generated in
217 the high-resolution case (e.g. 144,648,000 categories for a run based on temperature bis, PARa bis
218 and phosphate bis), we did not perform high-resolution analyses based on more than one
219 dimension because of calculation time estimated to be ~4 months on a high-performance computer
220 of 88 cores.

221 To examine the sensitivity of our analyses to low PAR values, we considered three minimum
222 values: 1 (termed “PARa”, Table S3), 10 (“PARb”) and 20 (“PARc”) $E.m^{-2}.day^{-1}$.

223 Finally, annual estimations of pseudo-species abundances were assessed by performing a
224 cubic interpolation of the 1-5D niches with the corresponding environmental variables. Four runs
225 on APS are closely examined as examples: (i-iii) three uni-dimensional runs based on either (i)
226 SST, (ii) PAR or (iii) nitrate (Fig. 3) and (iv) one three-dimensional run based on SST, PAR and
227 nitrate (Fig. 4).

228 **2.5. Comparisons of predicted and observed seasonal patterns**

229 Comparisons between predicted and observed annual patterns in phytoplankton abundance
230 were performed in two ways. First, we calculated the coefficient of linear correlation (Pearson’s
231 correlation coefficient; Fig. 5 and Fig. S3). Second, we used the Mean Absolute Error (MAE; Fig.
232 S3) that measures the average magnitude of the errors in a set of predictions, without considering
233 their direction.

$$234 \quad MAE = \sum_{i=1}^n \frac{|X_i - Y_i|}{n} \quad (3)$$

235 with n the number of differences to be tested, X_i is prediction i and Y_i is observation i .
236 Equation (3) represents the absolute differences between predictions and observations, divided by
237 the number of differences to be tested (with all individual differences having equal weight). It is a
238 negatively-oriented score, which means that the lower values are related to the strongest
239 correlations.

240 Pearson’s correlation coefficients and MAEs were calculated for each run between all
241 observed and predicted daily patterns in (pseudo-) species abundance, leading to a correlation or
242 MAE matrix $u \times v$ (species \times pseudo-species). We then identified the highest positive correlations
243 and the lowest MAE values. For each run, we therefore obtained two vectors using the average
244 correlation and MAE values calculated for each species (Fig. S4). The daily normalised (between
245 0 and 1) pseudo-species abundances that showed the highest correlation with observed species
246 were plotted against daily observed species abundances to graphically depict the relationships (Fig.
247 5).

248 We then tested both correlations and MAEs using null models that considered (or not)
249 temporal autocorrelation. First, we randomly generated a number of daily time series

250 corresponding to the total number of pseudo-species generated for each run. Although the number
251 of time series was small for 1D runs, it became important when the number of dimensions
252 increased as we multiplied the number of niches per parameter. The procedure was repeated 1000
253 times and, for each simulation, the average correlation and MAE values were calculated. To
254 consider temporal autocorrelation, we generated two million of time series and kept the first 1000
255 with a 30-order (i.e., 30 days/~one-month autocorrelation for daily time series) autocorrelation
256 higher than average 30-order autocorrelation found in observed daily time series. We represented
257 the results in a diagram that exhibited the observed average correlation for each run and the 1000
258 correlations found using the null model with (red) and without (blue) autocorrelation (Fig. S3).
259 For each combination of environmental variables (i.e. 84 runs), we calculated the probability of
260 significance of each correlation (Table S4). Finally, we used contour diagrams to identify (i) the
261 most important environmental parameters and (ii) the number of dimensions to accurately
262 reconstruct APS. This graphical examination allowed us to highlight the number of species that
263 exhibits the highest correlations in each run (Fig. 6).
264

265 **3. RESULTS**

266 **3.1. Seasonal changes in environmental parameters in the North Sea**

267 Temperature exhibited a minimum at the beginning of March and a maximum at the end of
268 July-August (Fig. 1). PAR showed minimum and maximum values in December-January and June,
269 respectively. The highest concentrations in nitrate, phosphate and silicate were observed in winter
270 and reached their lowest concentrations from the end of spring to the end of summer. Except for
271 SST, no variation was captured within a given month because monthly means were used for all
272 other parameters.

273 **3.2. Observed annual phytoplankton succession**

274 We examined APS based on CPR plankton data by means of a PCA (Fig. 2). The use of the
275 first three principal components allowed us to differentiate five periods, each being characterised
276 by a species assemblage: (i) an early-spring stage (Fig. 2b left part of the panel, 8 species
277 negatively correlated to PC1), (ii) a spring stage (Fig. 2c, 22 species positively correlated to PC2),
278 (iii) a widespread summer stage (Fig. 2a, 28 species positively related to PC1), (iv) a late
279 summer/beginning of autumn stage (Fig. 2d, 13 species negatively correlated to PC3) and (v) an
280 autumn stage (Fig. 2b right part of the panel, 8 species negatively correlated to PC1). The summer
281 stage (Fig. 2a) was characterised by the highest species richness, but showed a low proportion of
282 diatoms in comparison to both spring or autumn stages; silicoflagellates were also present (Table
283 S1). Other principal components were not represented because they did not bring additional
284 information.

285 **3.3. Modelled annual phytoplankton succession**

286 We reconstructed APS by using models of growing complexity (i.e., by considering a
287 growing number of niche dimensions) including all combinations of SST, PAR, nitrate, phosphate,
288 silicate and N/P ratio (a total of 84 runs). Here, we focused on four examples of modelled APS
289 reconstructed by using different ecological dimensions (Fig. 3 and 4). The first run, based on SST
290 only, showed two main phases of high phytoplankton abundance (also representative of a high
291 species richness) in summer (Fig. 3a) and winter (Fig. 3b) and two minor phases in spring (Fig.

292 3c) and autumn (Fig. 3c). The winter phase of high abundance did not correspond to any observed
293 patterns (Fig. 2 *versus* Fig. 3). The second run, based on PAR only, showed several peaks of high
294 phytoplankton abundance in spring, summer and autumn (Fig. 3d-f). These patterns were close to
295 observed patterns of annual succession (Fig. 2), suggesting an important role of PAR in the
296 modulation of APS. The third model, based on nitrate only (Fig. 3g-i), showed an important winter
297 peak in phytoplankton abundance, not detected in the observations (Fig. 2 *versus* 3). This result
298 suggests that considering nitrate only was not sufficient to reconstruct APS. The fourth model, that
299 combined SST, PAR and nitrate (Fig. 4a-e), was more efficient to reproduce APS observed in the
300 CPR data, especially the late-summer phase (Fig. 4 *versus* Fig. 2). A closer examination of the
301 relationships between predicted and observed APS is performed below.

302 **3.4. Relationships between observed and modelled annual phytoplankton succession**

303 **3.4.1. Reconstruction of species seasonal patterns**

304 We calculated the Pearson's correlation coefficients between observed and simulated
305 (pseudo-) species for all 84 runs; we remind here that our runs were characterised by a growing
306 number of ecological dimensions - ranging from one to five - and that all combinations (C=84) of
307 environmental parameters were tested. We chose the best correlations and examined graphically
308 the relationships between observed and predicted phytoplankton abundances (Fig. 5). Figure 5
309 shows all the relationships between phytoplankton species considered in the analyses and pseudo-
310 species created from METAL. For all phytoplankton groups, simulated pseudo-species reproduced
311 observed seasonal patterns well: most annual phytoplankton patterns in observed and simulated
312 phytoplankton species were closely related (e.g., *Skeletonema costatum* and *Thalassiosira* spp.)
313 with the exception of *Paralia sulcata* and *Dactyliosolen antarcticus* (Fig. 5). Correlation and MAE
314 values are examined in detail in the following sections.

315 **3.4.2. Identification of key ecological dimensions to reconstruct APS**

316 To identify key ecological dimensions, we calculated the average of the best correlations and
317 MAEs between observed and simulated (pseudo-) species for all 84 runs (Table S4, Fig. S3). We
318 tested our correlations and MAEs using a null model with and without consideration for temporal
319 autocorrelation. While some MAE values were significant for some 1D runs (Fig.S3), APS was
320 better reproduced when at least three dimensions were considered (Fig. S3). Not all correlations
321 were significant for models based on three or more ecological dimensions while considering five
322 dimensions did not improve the percentage of explained variance (i.e. model quality). This
323 suggests that the selection of relevant environmental variables is more important than considering
324 a too high number of ecological dimensions.

325 **3.4.3. Identification of key environmental variables to reconstruct APS**

326 We then identified the most relevant environmental parameters and the number of ecological
327 dimensions that best reproduce APS (Fig. 6). We remind here that APS is the result of species
328 phenology (i.e., species seasonal patterns). Uni-dimensional models (1D, Runs 1-16) explained
329 poorly observed seasonal changes in species abundance, with the exception of Run 2 that was
330 exclusively based on SST (Fig. 6a); for Run 2, eight species showed their highest correlations
331 between observed and modelled seasonal patterns. Bi-dimensional models (Runs 17-39) also
332 explained poorly species seasonal patterns and only 3 species exhibited their highest correlations
333 when the model was based on both temperature and PAR (Fig. 6a, Table S2). Better results were

334 achieved when models were based on three or more ecological dimensions. Three-dimensional
335 models (Runs 40-68) had 29 highest correlations between observed and modelled seasonal patterns
336 (Fig. 6a). Run 51 based on SST, N/P and PAR_c (i.e., a minimum value of PAR=20 E.m⁻².day⁻¹)
337 exhibited 10 highest correlations. Four-dimensional (Runs 69-81) and five-dimensional models
338 (Runs 82-84) had 25 and 14 highest correlation values, respectively.

339 We also examined the correlations between each simulated and observed seasonal patterns
340 for all species and runs (Fig. 6b). The figure showed that even if best results were achieved for
341 models based on SST only (Run 2), results were similar when three or more dimensions were
342 included. Low correlations generally appeared when the triplet SST/PAR/macro-nutrient was not
343 used (Fig. 6b and Table S2, e.g., Runs 53-56), revealing that the combination of these variables
344 was important to reproduce most species seasonal patterns.

345

346 4. DISCUSSION

347 4.1. Annual phytoplankton succession

348

349 The METAL theory suggests that large-scale patterns in biodiversity emerged from the
350 niche-environment interactions that propagate from the species to the community level (Beaugrand
351 et al. 2013b, Beaugrand et al. 2015, Beaugrand et al. 2018). Here, our results show that APS -
352 including the spring bloom - may also originate from the niche-environment interaction (Fig. 5).
353 APS has been frequently investigated at the group level (e.g. plankton functional type, plankton
354 ecology groups or categories). However, our study shows that even within a given ecological or
355 taxonomic group, species reacts to environmental fluctuations individually through the niche-
356 environment interaction, conforming themselves to the principle of species individuality
357 (Whittaker 1975) (Fig. 5). Our study therefore suggests that it is important to investigate APS by
358 exploring ecological patterns and processes at a species level.

359 Our results show a prominent control of APS by environmental conditions in the North Sea.
360 Studying APS in the Mediterranean Sea, Romagnan et al. (2015) have also provided evidence for
361 a strong control of the physical environment on APS. Even though our modelling approach
362 reproduced well the seasonal cycle of eight species when based on SST only, better results were
363 achieved when three or more ecological dimensions were considered (Fig. 6). Considering five
364 dimensions did not improve substantially the percentage of explained variance, probably because
365 seasonal changes in nitrate, phosphate and silicate concentrations are highly correlated in the North
366 Sea.

367 Our investigation of APS revealed four main microphytoplanktonic succession in the North
368 Sea (see Table S1 for a list of the species considered in our study). The first assemblage is
369 composed of species that exhibited their highest abundance at the beginning of spring and a second
370 less important peak in autumn (PC1 in Fig. 2b, Fig. 5). This microphytoplanktonic assemblage,
371 generally composed of large diatoms (Table S1 and Fig. 5, e.g. *Thalassionema nitzschioides*,
372 *Ditylum brightwellii*), was primarily controlled by PAR and nutrients availability in our models.
373 PAR is an essential parameter limiting photosynthesis and its influence on growth rate is well
374 known (Eppley & Sloan, 1966). PAR is a strong limiting factor in areas above the polar circle
375 (McMinn & Martin, 2013) but also in lower latitude regions such as the North Sea (Peeters et al.

376 1993). Nutrients positively influenced growth rate and primary production (Goldman 1980,
377 Longhurst 1998). The first assemblage is also psychrophilic, reaching its highest abundance when
378 temperature is lowest and their lowest abundance when temperature is highest (Fig. 1). The
379 assemblage is not detected when PAR is highest and when PAR or nutrients concentration is lowest
380 (Fig. 1). Although not considered in our analyses, turbulence, mixing and high SST variability that
381 characterise early spring and autumn may also positively influence the occurrence of this
382 assemblage, which is more adapted to such an environment than dinoflagellates (Beaugrand et al.
383 2010, Holligan et al. 1980, Margalef 1978). In winter, PAR (or the number of daily light hours)
384 and to a lesser extent temperature limit diatom growth and deep-water column mixing combined
385 to an absence of biological production enable nutrients to increase at the sea surface.

386 The second assemblage (e.g. *Chaetoceros* spp., *Coscinodiscus concinnus*) occurs generally
387 between April and June at a time when silicate and to a lesser extent nitrate and phosphate
388 concentrations diminish and temperature and PAR increase (Fig. 1, 2c and 5). This assemblage is
389 less psychrophile than the first one and occur at a time when both temperature and PAR increase
390 (Fig. 1).

391 The third assemblage is composed of species, mainly dinoflagellates (e.g. *Ceratium fusus*
392 and *C. furca*) and some small diatoms (e.g. *Guinardia striata*, *G. flaccida*), occurring when
393 temperature and PAR are high and conditions are oligotrophic (Fig. 1, 2a and 5). Silicate depletion
394 played an important role in the change of dominance observed between the second and the third
395 assemblage. In a mesocosm experiment, silicate deficiency was assumed to be the cause of the
396 strong reduction in large spring bloom diatoms and the replacement by flagellates (Jacobsen et al.
397 1995). Small diatoms need less silicic acid for the their skeleton and have a higher surface to
398 volume ratio which increases nutrient absorption (Miller, 2004). Dinoflagellates occur in areas and
399 at time when both temperatures are warm, SST variability low and the water column is well
400 stabilised (Beaugrand et al. 2010, Margalef 1978).

401 The fourth assemblage is composed of species (e.g. the diatom *Bellerochea malleus*,
402 *Biddulphia alternans*) having their occurrence from August to October (Fig. 2d and 5). Those
403 species occur when temperature is high and when nutrients concentration tends to increase. Those
404 warm-temperate species have their northern limit of spatial distribution in the North Sea (e.g.
405 *Bellerochea malleus*)(Barnard et al. 2004).

406 Despite the fact that four main microphytoplanktonic successions were identified by the
407 PCA, many intermediate situations occur (Fig. 5). For example, some species (e.g. *Rhizosolenia*
408 *setigera*) exhibit a higher abundance when PAR are above $10 \text{ E.m}^{-2}.\text{day}^{-1}$ but show a diminution
409 when temperature is high and conditions are oligotrophic (Fig. 5). A summer reduction is
410 sometimes not observed for species occurring between spring and autumn (e.g. *Gyrosigma* spp.).
411 Some species have a peak in late spring and another smaller one in autumn (e.g. *Dactyliosolen*
412 *fragilissimus*). Others have a small peak in spring and a high one in autumn (e.g. *Leptocylindrus*
413 *danicus*). Many species have narrow seasonal peaks not identified by the PCA (e.g. *Asteromphalus*
414 spp., *Ceratium buceros*, *C. carriense*). Because most observed patterns in annual abundance were
415 well reconstructed by our approach, it is likely that APS may result from the niche-environment
416 interaction (Fig. 5). Sharp or gradual environmental gradients interact with the niche of each
417 species within a multidimensional space to generate a variety of phenological patterns (Fig. 5).

418

419 The application of the Plankton Ecology Group (PEG) model in lakes and subsequently in
420 the marine realm (Sommer et al. 1986, Sommer et al. 2012) has suggested that (i) physics (light
421 and stratification) controls the start and the end of the phytoplankton growth season, (ii) grazing
422 by metazoan plankton results in a clear water phase, (iii) nutrients define the carrying capacity of
423 phytoplankton, (iv) food limitation determines zooplankton abundances and (v) fish predation
424 determines zooplankton size structure. The PEG model has emphasised the role of physical factors,
425 grazing and nutrient limitation for phytoplankton. Our results have shown the key role of bottom-
426 up processes in shaping APS and recall the importance of considering a combination of several
427 environmental factors, not only light. PAR and to a lesser extent SST, are important for the
428 initiation of the spring bloom, macronutrients for the end of the spring bloom and both SST and
429 macronutrients for the development of APS. Light (e.g. PAR, photoperiod), nutrients and
430 temperature are seen as master parameters controlling photosynthesis in physiological studies
431 (Geider et al. 1997, Longhurst 1998, McMinn & Martin 2013, Ras et al. 2013). While grazing may
432 have a substantial influence (Kivi et al. 1993, Fileman et al. 2010, Kenitz et al. 2017), the absence
433 of grazing consideration in our analyses did not prevent us to accurately reconstruct species
434 phenology (Fig. 5).

435 **4.2. The spring bloom**

436 Our study also provides evidence for a strong environmental control of the initiation,
437 development and termination phases of the spring bloom although processes are distinct from
438 those formulated by Gran and Braarud (Gran and Braarud 1935) and Sverdrup (1953). The Critical
439 Depth Theory (Sverdrup 1953) proposed that spring blooms in regions close to the North Atlantic
440 Drift Provinces develop when the Mixed Layer Depth (MLD) becomes shallower than the critical
441 depth (i.e., blooming can occur when MLD is less than the critical value), which was derived
442 analytically as a function of the amount of incoming radiation, water transparency and the energy
443 level at the compensation depth (i.e., the depth at which gross photosynthesis balances
444 phytoplankton respiration). According to the CDT, bloom initiation is only possible in spring in
445 high latitudes.

446 The possibility that the onset of the spring phytoplankton bloom occurs as a consequence of
447 decreased zooplankton grazing pressure has recently been proposed by Behrenfeld (2010). Our
448 models suggest that neither the occurrence of a MLD shallower than the critical depth nor a
449 dilution effect resulting from the occurrence of a deep MLD is necessary to reproduce bloom
450 initiation and more generally species phenology in the investigated North Sea region. The
451 integration of PAR - and to a lesser extent SST - in the models simply explained the initiation of
452 the spring bloom in the North Sea. Average light intensity in the mixed layer is well-known to
453 govern the timing of the spring bloom (Riley 1967; Legendre 1990), even if phytoplankton
454 production losses due to mixing may also be important (Behrenfeld 2010). Some studies have also
455 reported that spring bloom may occur in the absence of water stratification (Townsend et al. 1992),
456 confirming that phytoplankton initiation may precede the establishment of a clear thermocline
457 (Colebrook 1979). Revisiting the dilution-recoupling hypothesis (Behrenfeld 2010), Beaugrand
458 (2015) has also suggested PAR as a key driver of bloom initiation (his figure 5.27). Smyth and
459 colleagues (2014) have conveyed that the spring bloom started in the western part of the English
460 Channel (Station L4, Plymouth) when net heat flux becomes positive. Because net heat flux is
461 highly positively related to irradiance and PAR (Beaugrand 2015), a strong control of PAR on the
462 initiation of the spring bloom may be expected.

463 Our models also suggest that the limitation in macro-nutrients is a key factor for bloom
464 termination, which is only in partial agreement with the Sverdrup and the Behrenfeld hypotheses.
465 To model the end of the spring bloom, we did not have to include grazing (Sverdrup 1953) or a
466 coupling between grazers and phytoplankton (Behrenfeld 2010). Instead, the low macro-nutrients
467 concentrations could explain alone bloom termination. As earlier, we do not state that grazing has
468 not an effect, but we suggest that the physical environment is an important driver. Large seasonal
469 changes in atmospheric forcing and ocean surface conditions shape, to a great degree, the seasonal
470 cycles of phytoplankton biomass, but also the relative abundance of phytoplankton species (Barton
471 et al. 2014). Beaugrand (2015) showed that phytoplankton and zooplankton seasonal fluctuations
472 were closely related in the North Atlantic region investigated by Behrenfeld (his figure 5.28),
473 suggesting a “bottom-up” control. More recently, Atkinson and colleagues (2018) demonstrated
474 that both the increase and termination of the spring bloom are encapsulated by zooplankton,
475 providing strong evidence against a top-down control.

476 Although the succession between diatoms and dinoflagellates can be well explained by
477 macro-nutrients and temperature in our models, it is well-known since Margalef (1979) that water
478 column stability is a key factor to explain the succession between these two functional groups.
479 Dinoflagellates are more sensitive than diatoms to turbulence (Karp-Boss et al. 2000). They can
480 realise significant vertical migration to nutrient rich area but cannot reproduce when turbulence is
481 too high (Estrada and Berdalet 1997). In contrast, diatoms can continue cell division and the
482 photosynthetic energy products are used to synthesize fatty acid that are converted to energy when
483 cells are exported below the euphotic zone; fatty acid can be considered as a buoyancy regulator
484 (Amato et al. 2017). It is possible that mixing and turbulence are not required in our models
485 because temperature is a proxy of mixing and turbulence conditions in the North Sea. Confirmation
486 of our results should be searched in other regions experiencing different sequences of
487 environmental conditions.

488 **4.3. Uncertainties related to our approach**

489 The niche-environment interaction is certainly more unpredictable in the field than in our
490 modelling approach for two main reasons. First, while the fundamental niche (*sensu* Hutchinson)
491 was estimated here, the environment - through random meteorological conditions - may influence
492 the realised niche of microalgae species. Second, phytoplankton community before and/or during
493 the growth of a given species may alter species realised niche by competition for resources that
494 lead to competitive exclusion. The trait-based approach of Breton et al. (2017) suggests that
495 competitive exclusion prevails during *Phaeocystis* spp. bloom.

496 It is well-known that the underwater light available for photosynthesis (PAR) is a key
497 environmental variable for primary production (Cole and Cloern 1987, MacIntyre et al. 2000,
498 Foden et al. 2010, Capuzzo et al. 2013, 2015, 2018). Light field in the water column depends in
499 turn on phytoplankton biomass (self-shading), inorganic suspended particulate materials, colored
500 dissolved organic materials and water itself (IOCCG 2000). Recent works on light quality have
501 also revealed the important role of spectral irradiance on phytoplankton succession (Lawrenz and
502 Richardson 2017). In this study, we used surface PAR data that originated from a climatology. All
503 phytoplankton species can perform photo-regulation or photo-acclimation (i.e., the first occurs at
504 time scales of minutes and the second takes place in a few hours or a day) to limit photo-inhibition
505 in high light surface waters or optimise both light harvesting and Calvin cycle activity in the water
506 column (MacIntyre et al. 2000, Lavaud 2007, Dubinsky and Stambler 2009). In addition, photo-

507 acclimation processes can be conducted on different kinetic models and time scales (Cullen and
508 Lewis 1988), according to environmental conditions and functional phytoplankton groups
509 (MacIntyre et al. 2000). Even if photosynthesis performances between different species remain
510 poorly documented (Goss et Lepetit 2015, Suggett et al. 2015), they can induce a competitive
511 effect between species at a given time.

512

513 **5. CONCLUSIONS**

514 Our study suggests that APS may result from the niche-environment interaction. Our model
515 provides evidence that sharp temporal environmental gradients may be responsible for the strong
516 annual shifts in microphytoplanktonic composition in the North Sea; this occurs when an
517 environmental factor becomes rapidly favourable (e.g. increasing PAR at the end of winter) or
518 limiting (e.g. diminution of macro-nutrients at the end of spring). We identify three key parameters
519 that influence directly the succession: (i) temperature, (ii) PAR and (iii) macro-nutrients. There is
520 a clear effect of temperature on APS with a cline from cold-water species in early spring to warm-
521 water species in late summer. By enabling the initiation of the spring bloom and ending the second
522 bloom in autumn, PAR exerts an important role. Macro-nutrients are critical at the end of the spring
523 bloom and their increases in autumn trigger a secondary bloom which then becomes rapidly limited
524 by PAR and temperature. Mixing is an important process by which macro-nutrients increase in the
525 euphotic zone. In the light of our results the shoaling of the pycnocline should not be directly
526 involved in bloom initiation (i.e., Sverdrup's hypothesis), however, and the increase in grazing is
527 not determinant for its termination (Behrenfeld's hypothesis).

528

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535

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767

768 **Figure legends**

769 **Figure 1. Annual changes in the environmental parameters considered in this study.** (a) Sea
770 Surface Temperature (SST), (b) Photosynthetically Active Radiation (PAR), (c) Nitrate, (d)
771 Silicate, (e) and Phosphate concentrations, and (f) Nitrate/Phosphate (N/P) ratio. Note that SST is
772 at a daily resolution whereas other parameters are at a monthly one (see Materials and Methods).

773 **Figure 2. Annual succession of phytoplankton sorted by PCA.** (a) Species positively and (b)
774 negatively correlated with the first principal component (PC1). (c) Species positively correlated
775 with PC2. (d) Species negatively correlated with PC3. Only annual changes in phytoplankton
776 species with normalised eigenvectors negatively (<-0.5) or positively (>0.5) correlated to a
777 corresponding principal component were represented. See Table S1 for information on species and
778 their relations to the PCs. Tot. Sp. Richness: total species richness.

779 **Figure 3. Reconstructed annual plankton succession from a one-dimensional model based on**
780 **SST (Sea Surface Temperature, left panels), PAR (Photosynthetically Active Radiation,**
781 **middle panels) and nitrate (right panels).** A PCA was performed on the relative pseudo-species
782 abundances to identify the most important seasonal phytoplankton abundance patterns. Only
783 predicted plankton seasonal changes, related substantially negatively or positively (i.e., normalised
784 eigenvectors $>|0.5|$) to the Principal Components (PCs) are shown. SST (a-c): species (a)
785 positively and (b) negatively correlated to PC1, (c) species negatively correlated to PC2. SST:
786 Individual pseudo-species abundance is on the left vertical axis. PAR (d-f): species (d) positively
787 and (e) negatively correlated to PC1, (f) species negatively correlated to PC2. Nitrate (g-i): species
788 (g) positively and (h) negatively correlated to PC1, (i) species negatively correlated to PC2.
789 Relative individual pseudo-species abundances generated from METAL are on the left vertical
790 axis.

791 **Figure 4. Reconstructed annual plankton succession from a three-dimensional run based on**
792 **SST, PAR and nitrate.** A PCA was performed on relative individual pseudo-species abundances
793 to identify the most important seasonal patterns in phytoplankton abundance. Only predicted
794 plankton seasonal changes related substantially negatively or positively (i.e., normalised
795 eigenvectors $>|0.5|$) to the Principal Components (PCs) are shown. Species (a) positively and (b)
796 negatively correlated to PC1. (c) Species negatively correlated to PC2. (d) Species negatively
797 correlated to PC3. (e) Species positively correlated to PC4. Individual pseudo-species abundance
798 is on the left vertical axis.

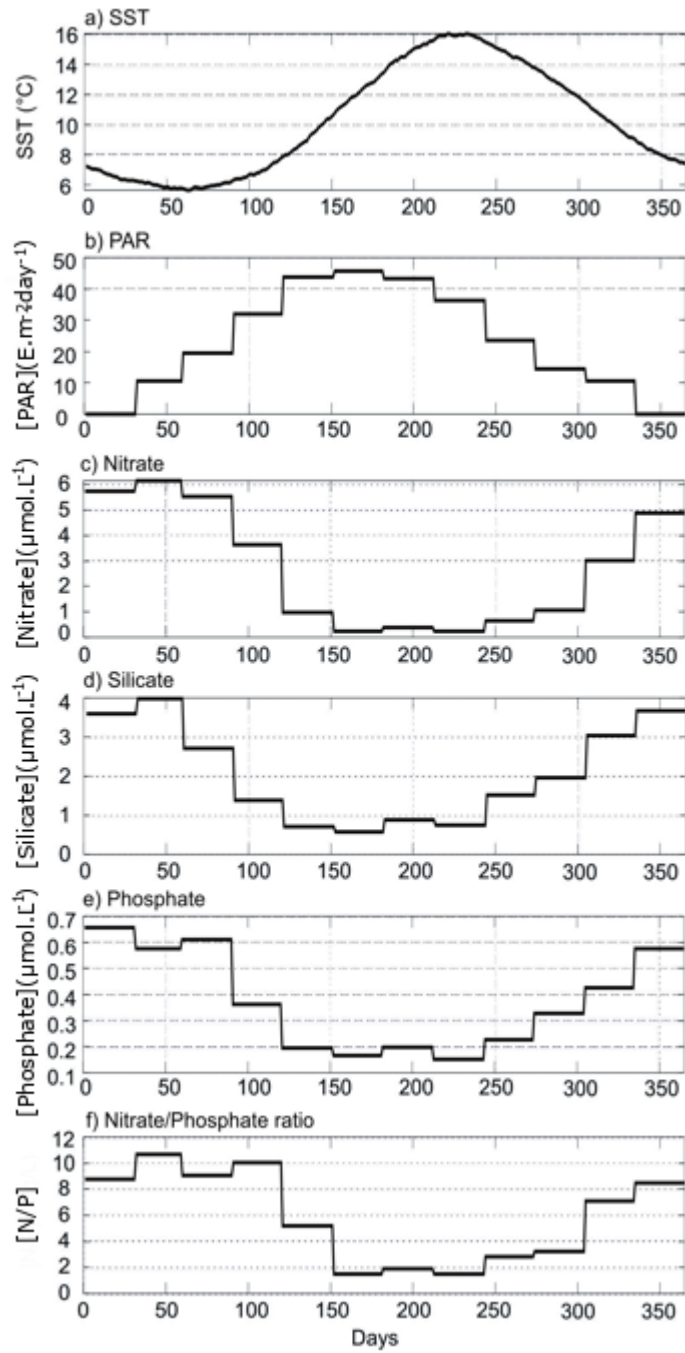
799 **Figure 5. Seasonal patterns in standardised observed and simulated phytoplankton species**
800 **abundances.** Relative abundances of species sampled by the CPR survey (blue) plotted together
801 with relative abundances of pseudo-species reconstructed using METAL (orange). See Table S1
802 for species names.

803 **Figure 6. Identification of the key environmental parameters for reconstructing annual**
804 **phytoplankton succession.** (a) Number of phytoplankton species exhibiting their highest
805 correlation for each model (run). See Table S2 for the correspondence between run numbers and
806 environmental combinations of variables. (b) Highest correlation for a given phytoplankton
807 species and run. The colorbar shows the linear correlation value.

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810 **Figure 1.**

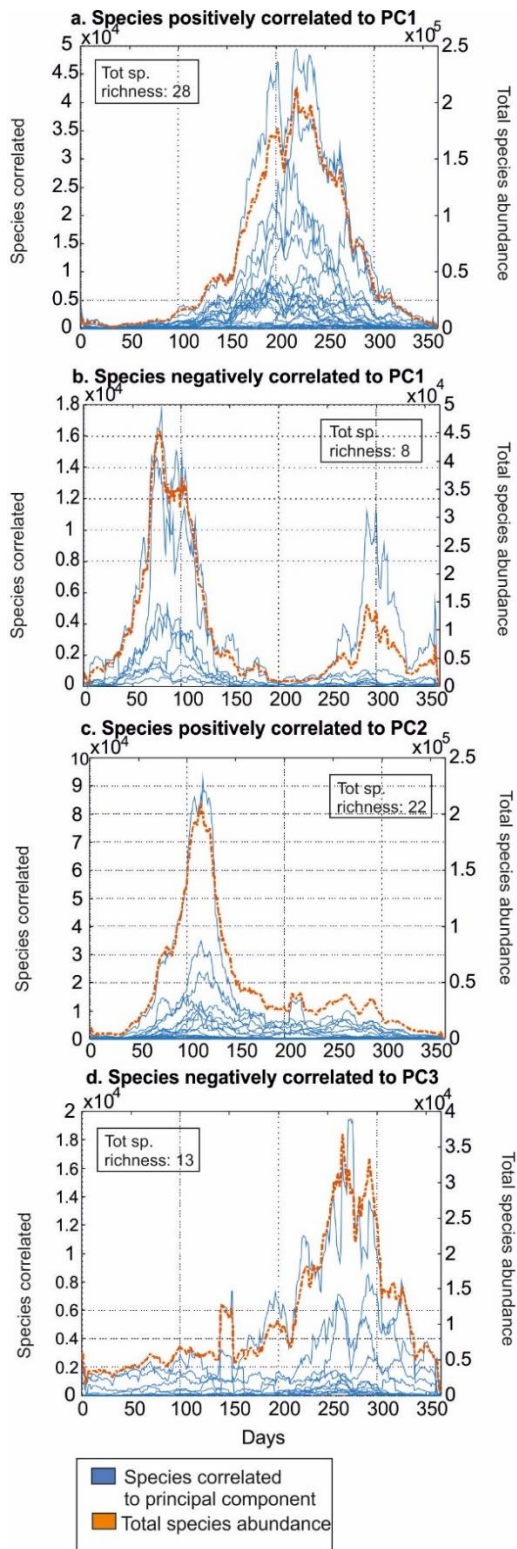


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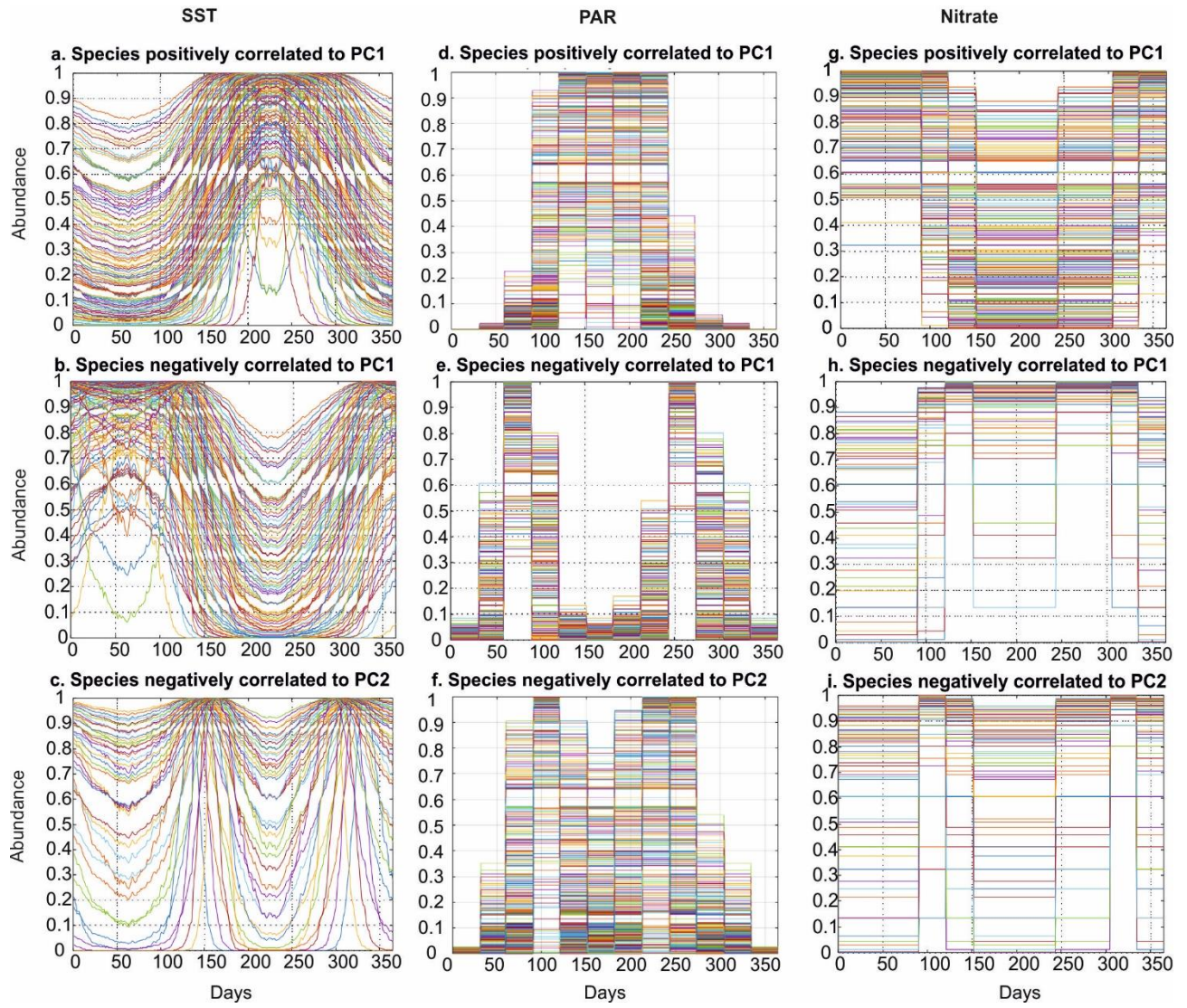
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814 **Figure 2.**

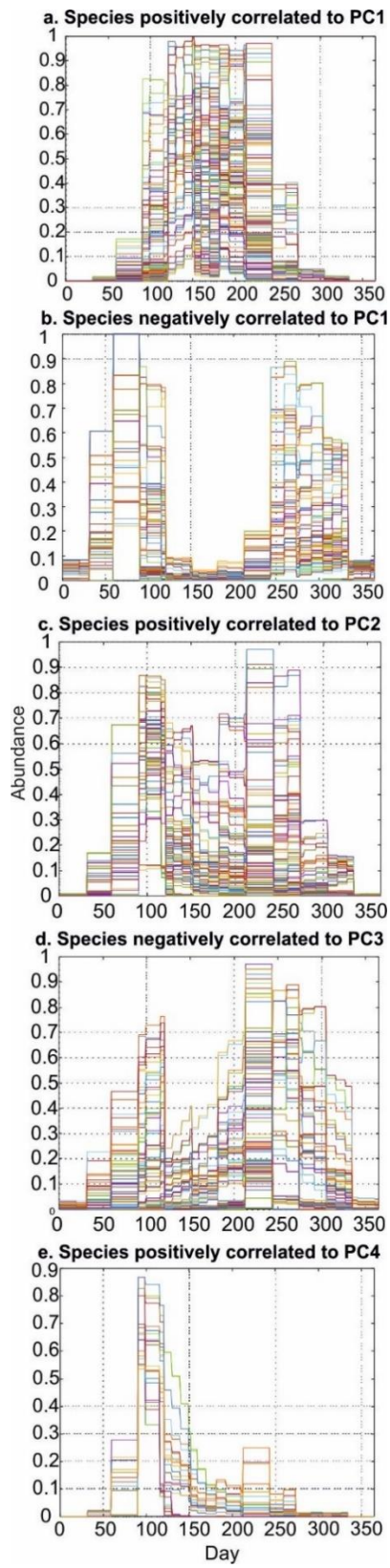


816 **Figure 3.**

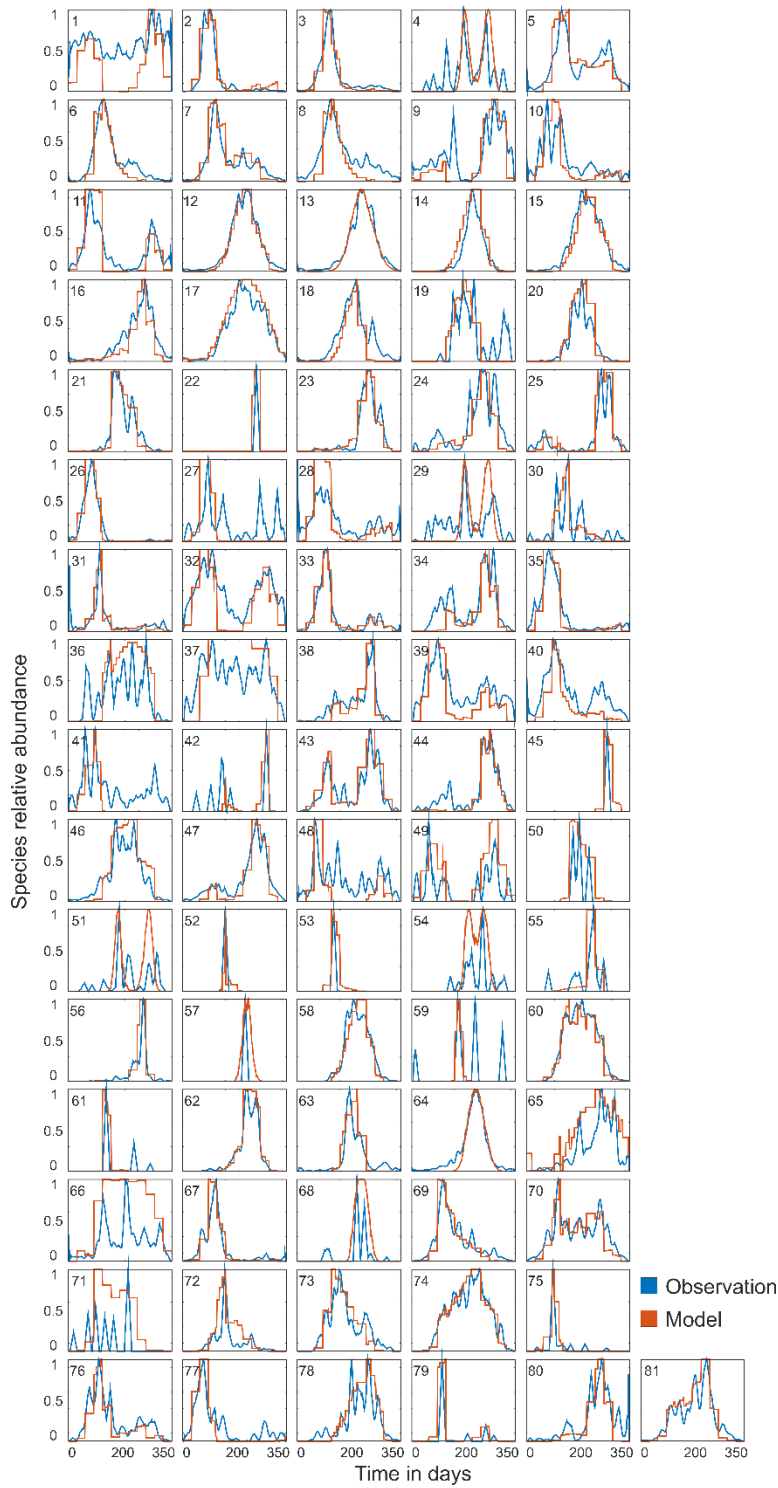


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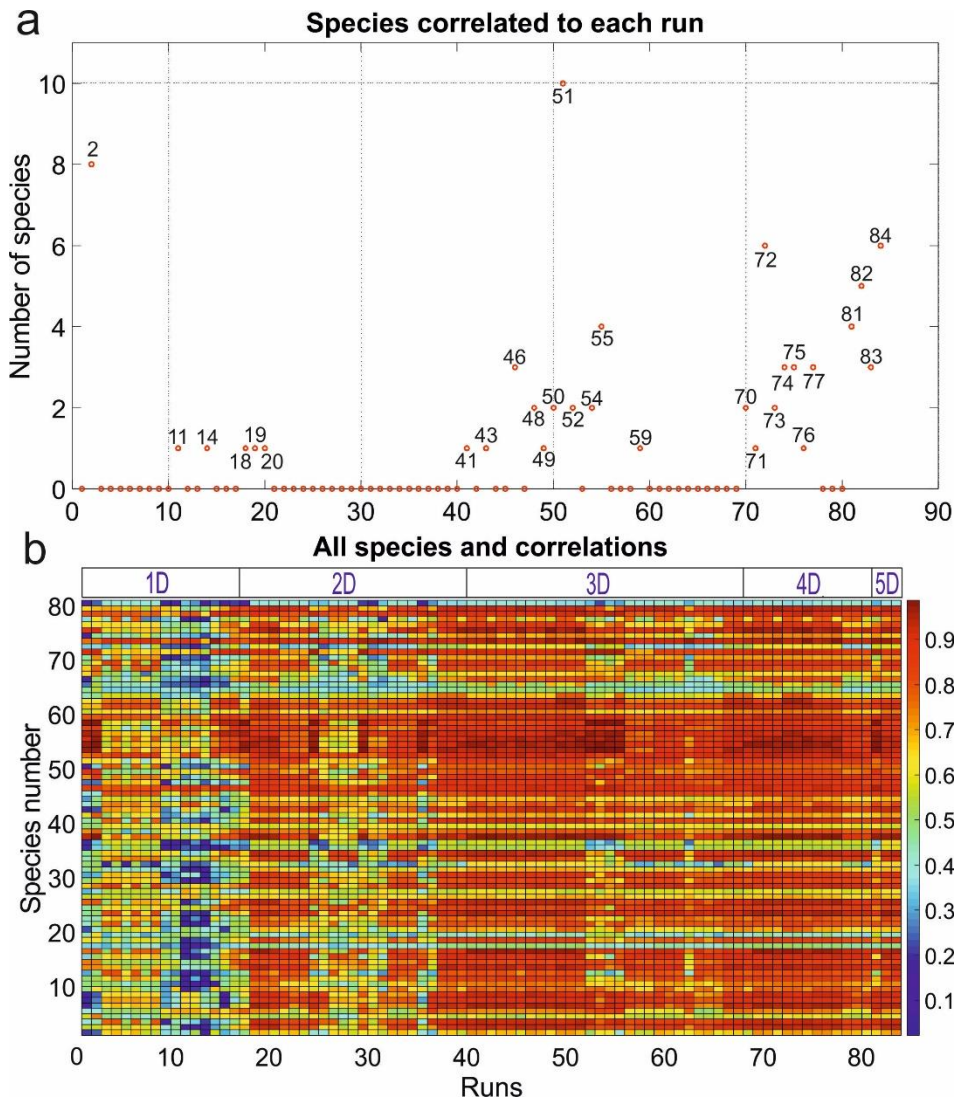
821 **Figure 5.**



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824 **Figure 6.**



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Supporting Information

Annual phytoplankton succession results from niche-environment interaction

Mariarita Caracciolo¹, Grégory Beaugrand^{2,3,4}, Pierre Helaouët⁴, François Gevaert³, Martin Edwards^{4,5}, Fabrice Lizon³, Loïck Kléparski^{2,3,4}, Eric Goberville⁶.

¹*Sorbonne Université, CNRS, Station Biologique de Roscoff, UMR 7144, ECOMAP, Place Georges Teissier, 29680 Roscoff, France.*

²*Centre National de la Recherche Scientifique (CNRS), Université de Lille, Université Littoral Côte d'Opale, UMR 8187 LOG, Laboratoire d'Océanologie et de Géosciences, F 62930 Wimereux, France.*

³*Université de Lille, CNRS, Univ. Littoral Côte d'Opale, UMR 8187, LOG, Laboratoire d'Océanologie et de Géosciences, F 62930 Wimereux, France.*

⁴*Marine Biological Association, Continuous Plankton Recorder (CPR) survey, Citadel Hill, Plymouth PL1 2PB, UK.*

⁵*University of Plymouth, School of Biological and Marine Sciences, Drake Circus, Plymouth, UK.*

⁶*Unité Biologie des organismes et écosystèmes aquatiques (BOREA), Muséum National d'Histoire Naturelle, Sorbonne Université, Université de Caen Normandie, Université des Antilles, CNRS, IRD, CP53, 61, Rue Buffon 75005 Paris, France.*

Corresponding authors: Mariarita Caracciolo (mariarita.caracciolo@sb-roscoff.fr) and Gregory Beaugrand (Gregory.Beaugrand@univ-lille1.fr)

864 **Supplementary Figures and Tables Legends**

865 **Figure S1. Location of the study area.** The geographical boundary of the rectangle (black box)
866 is 54-56°N and 1-4°E.

867
868 **Figure S2. Thermal niche (bottom) and the associated theoretical response (top) of a**
869 **hypothetical species to the fluctuations of an environmental parameter.** The optimal value
870 (x_{opt}) of the ecological niche corresponds to the centre of the species' distributional range and is
871 associated with the highest species' abundance that is located in the optimum zone between the
872 two points X_s . The bimodal distribution of temporal variability exhibits a maximum V_{max}
873 corresponding to greatest slopes (XHV; HV for High Variability) of the niche. X_D is the threshold
874 from where environmental fluctuations are unlikely to be detected because the species' ecological
875 sensitivity becomes too small. X_L are the values where environmental variability becomes lethal.
876 The grey areas indicate the region where the response of the species to environmental changes is
877 expected to be strong. From Beaugrand and Kirby (2016).

878
879 **Figure S3. Average correlation (a) and Mean Absolute Error (MAE) (b) for each run used**
880 **to reconstruct annual phytoplankton succession from uni-dimensional (1D) to 5-dimensional**
881 **(5D) models.** The average value (blue circle) was based on the best correlations (a) or MAEs (b)
882 assessed between observed species and (simulated) pseudo-species. Black and red points show the
883 results of the same calculations based on a null model with (red) and without (black) consideration
884 of temporal autocorrelation.

885
886 **Table S1. List of phytoplankton species and their correlation with the first four principal**
887 **components (PCs).** List of phytoplankton species considered in our study area (see Fig. S1). The
888 81 species were grouped in the following classes: 1: Bacillariophyceae, 2: Dinophyceae, 3:
889 Primmnesiophyceae, 4: Dictyochophyceae and 5: Cyanophyceae. The first four PCs considered in
890 Fig. 2 and their eigenvalues are reported here. A cross indicates a significant correlation ($> |0.5|$)
891 between a species and a principal component. Some species were not correlated. The percentage
892 of explained variance per principal component is indicated into brackets. The seasonal cycles of
893 each phytoplankton species are represented on Fig. S4 (see species numbers, first column of this
894 table, for correspondence).

895 **Table S2. Model simulations.** Information on the 84 runs based on all possible combinations of
896 environmental parameters from one (1D; uni-dimensional) to five (5D; 5-dimensional) variables.
897 T: Sea Surface Temperature, Tbis: Sea Surface Temperature using a higher number of niches,
898 PARa,b,c: Photosynthetically Active Radiation (the letters represent 3 different measures used to
899 calculate the optimum values, $E.m^{-2}.day^{-1}$; see text and Table S3 for details), N: Nitrate ($\mu mol.L^{-1}$),
900 S: Silicate ($\mu mol.L^{-1}$), P: Phosphate ($\mu mol.L^{-1}$), N/P: Nitrate/Phosphate ratio (see Table S3 for
901 a better understanding of the selected SST and PAR values). For each run, computation time
902 required for building pseudo-species and calculating species abundances is reported.

903
904 **Table S3. Environmental variables used for the calculation of pseudo-species abundances**
905 **and respective optimum and tolerance values.** For each environmental parameter the table
906 shows the different range of optimum values and ecological amplitudes defined for niche
907 construction. We used several resolutions (first column) to calculate the environmental niche. For
908 runs ended by "bis", the resolution was improved to examine model sensitivity related to the
909 number of points used to calculate the niche. To examine the sensitivity of our analysis to PAR,

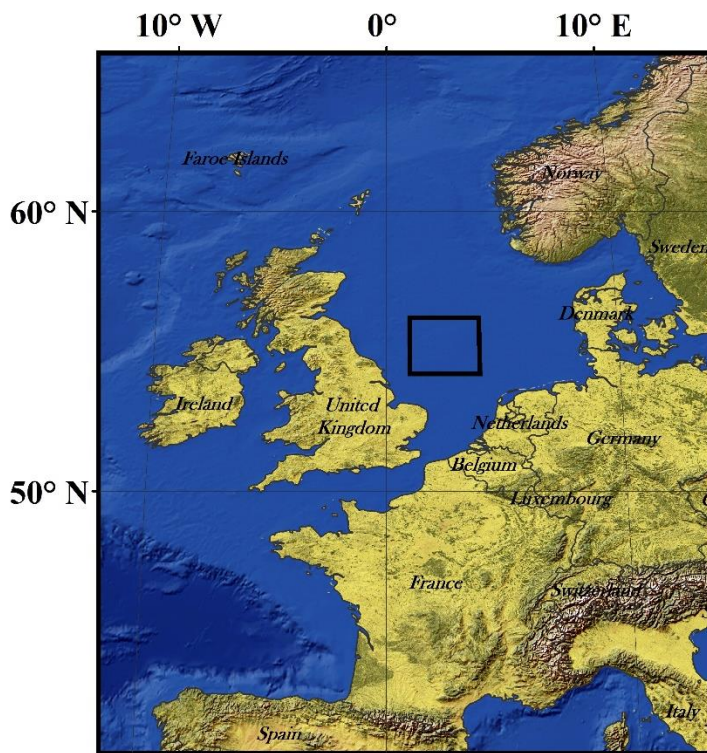
910 three categories (a, b, c) were determined by selecting different minimum values (see text). When
911 more than one factor was considered, the number of niches was multiplied by each ecological
912 dimension to obtain the total number of niches (see text).

913

914 **Table S4. Statistics calculated for the different runs, using several combinations of**
915 **environmental parameters.** For each combination of environmental parameters, the number of
916 species, mean and maximum correlation values and probability values that result from the
917 application of null models for both the Pearson correlation and MAE, with and without
918 consideration of temporal autocorrelation, are reported.

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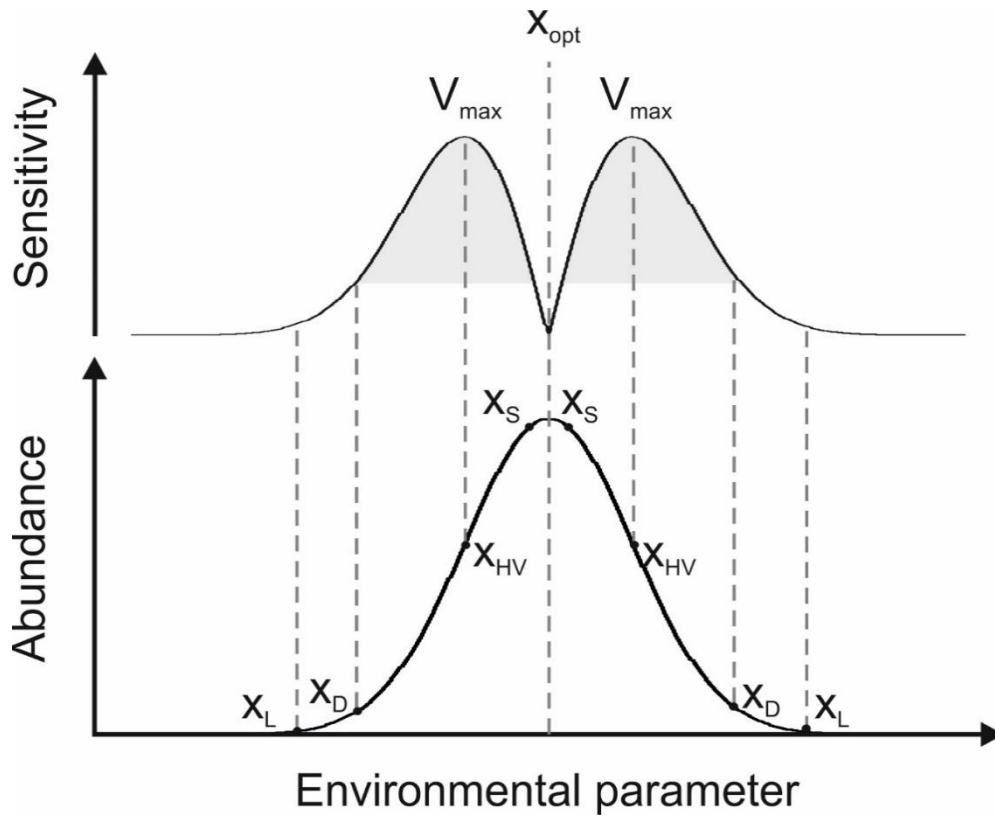
920 **Figure S1.**



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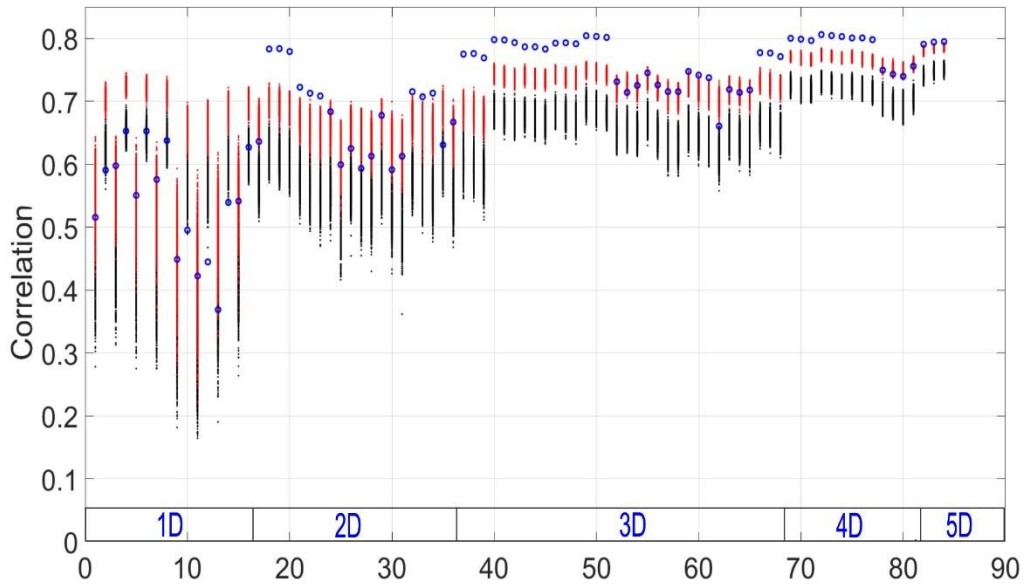
923 **Figure S2.**



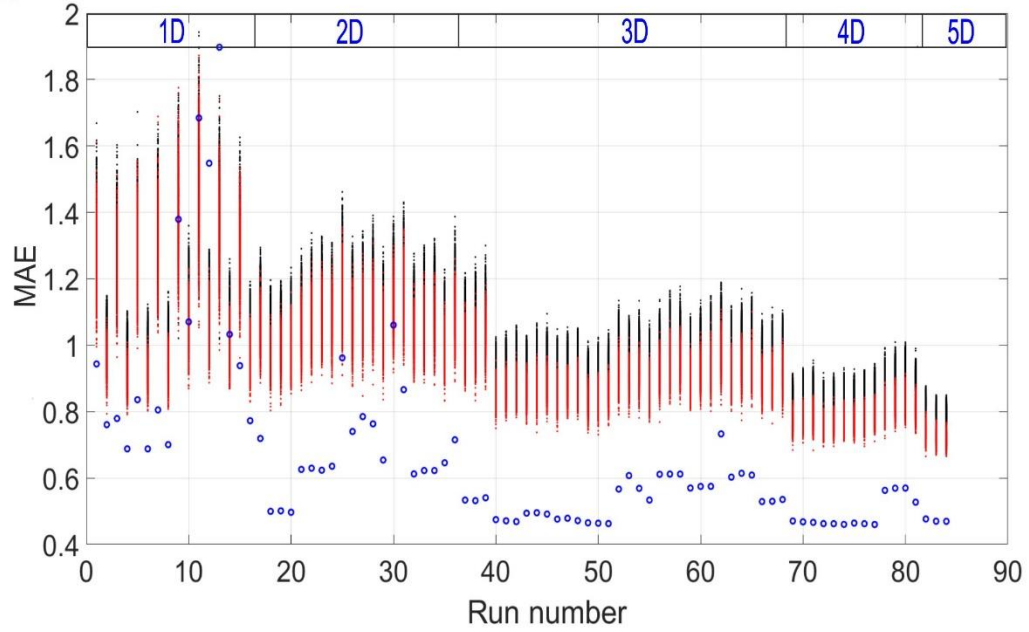
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a.



b.



928 Table S1.

Category	Phytoplankton species	PC1 (26.86 %)	PC2 (18.06 %)	PC3 (12.22 %)	PC4 (5.45 %)
Phylum: Ochrophyta					
Class: Bacillariophyceae					
	1 <i>Paralia sulcata</i>			X	
	2 <i>Skeletonema costatum</i>	X	X		
	3 <i>Thalassiosira</i> spp.		X		
	4 <i>Dactylosolen antarcticus</i>	X			
	5 <i>Rhizosolenia styliformis</i>		X		
	6 <i>Rhizosolenia hebetata semispina</i>		X		
	7 <i>Chaetoceros</i> (<i>Hyalochaete</i>) spp.		X		
	8 <i>Chaetoceros</i> (<i>Phaeoceros</i>) spp.		X		
	9 <i>Odontella sinensis</i>			X	
	10 <i>Thalassiothrix longissima</i>		X		
	11 <i>Thalassionema nitzschioides</i>	X			
	22 <i>Asteromphalus</i> spp.				
	23 <i>Bacteriostrom</i> spp.	X		X	
	24 <i>Bellerochea malleus</i>	X		X	
	25 <i>Biddulphia alternans</i>			X	
	26 <i>Odontella aurita</i>	X			X
	27 <i>Odontella granulata</i>				
	28 <i>Odontella regia</i>	X	X		
	29 <i>Odontella rhombus</i>				
	30 <i>Cerataulina pelagica</i>				X
	31 <i>Coscinodiscus concinnus</i>		X		
	32 <i>Coscinodiscus</i> spp. (Unidentified)	X	X		
	33 <i>Ditylum brightwellii</i>	X	X		
	34 <i>Eucampia zodiacus</i>		X	X	
	35 <i>Fragilaria</i> spp.	X			
	36 <i>Guinardia flaccida</i>				
	37 <i>Gyrosigma</i> spp.		X		
	38 <i>Leptocylindrus danicus</i>	X			
	39 <i>Navicula</i> spp.		X		
	40 <i>Cylindrotheca closterium</i>		X		
	41 <i>Rhaphoneis amphiceras</i>				
	42 <i>Rhizosolenia bergonii</i>				
	43 <i>Rhizosolenia setigera</i>		X		
	44 <i>Stephanopyxis</i> spp.			X	
	48 <i>Nitzschia</i> spp. (Unidentified)			X	
	49 <i>Odontella mobilensis</i>			X	
	64 <i>Proboscia alata</i>	X			
	65 <i>Leptocylindrus mediterraneus</i>	X		X	
	66 <i>Proboscia inermis</i>				
	67 <i>Asterionellopsis glacialis</i>		X		
	68 <i>Ephemera planamembranacea</i>				
	69 <i>Pseudo-nitzschia delicatissima</i> complex		X		
	70 <i>Pseudo-nitzschia seriata</i> complex		X		
	72 <i>Guinardia delicatula</i>				X
	73 <i>Dactylosolen fragilissimus</i>		X		
	74 <i>Guinardia striata</i>	X			
	76 <i>Lauderia annulata</i>		X		
	77 <i>Bacillaria paxillifera</i>	X			
	78 <i>Corethron hystrix</i>	X			
	79 <i>Proboscia curvirostris</i>		X		
	80 <i>Proboscia indica</i>	X		X	
	81 <i>Rhizosolenia imbricata</i>	X			
	75 <i>Helicotheca tamesis</i>				
Class: Dictyochophyceae					
	47 <i>Silicoflagellates</i>	X		X	
Phylum: Dinoflagellata					
Class: Dinophyceae					
	12 <i>Ceratium fusus</i>	X			
	13 <i>Ceratium furca</i>	X			
	14 <i>Ceratium lineatum</i>	X			
	15 <i>Ceratium tripos</i>	X			
	16 <i>Ceratium macroceras</i>	X		X	
	17 <i>Ceratium horridum</i>	X			
	18 <i>Ceratium longipes</i>	X			
	19 <i>Ceratium arcticum</i>	X			
	20 <i>Dinoflagellate</i> cysts (Total)	X		X	
	21 <i>Polykrikos schwartzii</i> cysts	X			
	50 <i>Ceratium arietinum</i>				
	51 <i>Ceratium bucephalum</i>				
	52 <i>Ceratium buceros</i>				X
	53 <i>Ceratium carriense</i>				
	54 <i>Ceratium hexacanthum</i>	X			
	55 <i>Ceratium massiliense</i>	X			
	56 <i>Ceratium minutum</i>			X	
	57 <i>Ceratium teres</i>				
	58 <i>Dinophysis</i> spp. Total	X			
	59 <i>Oxytoxum</i> spp.				
	60 <i>Protoperidinium</i> spp.	X			
	61 <i>Pronoctiluca pelagica</i>				
	62 <i>Prorocentrum</i> spp. Total	X			
	63 <i>Noctiluca scintillans</i>	X			
Phylum: Haptophyta					
Class: Prymnesiophyceae					
	45 <i>Phaeocystis pouchetii</i>				
	46 <i>Coccolithaceae</i> (Total)	X			
Phylum: Cyanobacteria					
Class: Cyanophyceae					
	71 <i>Trichodesmium</i> spp.				

Run n°	Dimension	Variable	Computation time (hh:mm:ss)
Run 1	1D	T	00:00:05
Run 2	1D	T bis	00:00:08
Run 3	1D	PARa	00:00:13
Run 4	1D	PARa bis	00:00:17
Run 5	1D	PARb	00:00:21
Run 6	1D	PARb bis	00:00:25
Run 7	1D	PARc	00:00:05
Run 8	1D	PARc bis	00:00:08
Run 9	1D	N	00:00:05
Run 10	1D	N bis	00:00:08
Run 11	1D	S	00:00:05
Run 12	1D	S bis	00:00:08
Run 13	1D	P	00:00:05
Run 14	1D	P bis	00:00:08
Run 15	1D	N/P	00:00:05
Run 16	1D	N/P bis	00:00:08
Run 17	2D	T and N	00:02:00
Run 18	2D	T and PARa	00:05:00
Run 19	2D	T and PARb	00:03:30
Run 20	2D	T and PARc	00:02:00
Run 21	2D	N and PARa	00:05:00
Run 22	2D	N and PARb	00:03:30
Run 23	2D	N and PARc	00:02:00
Run 24	2D	T and S	00:02:00
Run 25	2D	N and S	00:02:00
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Run 27	2D	S and PARb	00:03:30
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Run 30	2D	N and P	00:02:00
Run 31	2D	S and P	00:02:00
Run 32	2D	P and PARa	00:05:00
Run 33	2D	P and PARb	00:03:30
Run 34	2D	P and PARc	00:02:00
Run 35	2D	T and N/P	00:02:00
Run 36	2D	S and N/P	00:02:00
Run 37	2D	N/P and PARa	00:05:00
Run 38	2D	N/P and PARb	00:18:00
Run 39	2D	N/P and PARc	00:15:00
Run 40	3D	T,N and PARa	00:20:00
Run 41	3D	T,N and PARb	00:18:00
Run 42	3D	T,N and PARc	00:15:00
Run 43	3D	T,S and PARa	00:20:00
Run 44	3D	T,S and PARb	00:18:00
Run 45	3D	T,S and PARc	00:15:00
Run 46	3D	T,P and PARa	00:20:00
Run 47	3D	T,P and PARb	00:18:00
Run 48	3D	T,P and PARc	00:15:00
Run 49	3D	T,N/P and PARa	00:20:00
Run 50	3D	T,N/P and PARb	00:18:00
Run 51	3D	T,N/P and PARc	00:15:00
Run 52	3D	T,N and S	00:15:00
Run 53	3D	T,N and P	00:15:00
Run 54	3D	T,S and P	00:15:00
Run 55	3D	T,S and NP	00:15:00
Run 56	3D	N,S and PARa	00:20:00
Run 57	3D	N,S and PARb	00:18:00
Run 58	3D	N,S and PARc	00:15:00
Run 59	3D	N,P and PARa	00:20:00
Run 60	3D	N,P and PARb	00:18:00
Run 61	3D	N,P and PARc	00:15:00
Run 62	3D	N,S and P	00:15:00
Run 63	3D	S,P and PARa	00:20:00
Run 64	3D	S,P and PARb	00:18:00
Run 65	3D	S,P and PARc	00:15:00
Run 66	3D	S,N/P and PARa	00:20:00
Run 67	3D	S,N/P and PARb	00:18:00
Run 68	3D	S,N/P and PARc	00:15:00
Run 69	4D	T, N, S, PARa	96:00:00
Run 70	4D	T, N, S, PARb	72:00:00
Run 71	4D	T, N, S, PARc	60:00:00
Run 72	4D	T, N/P, PARa,S	120:00:00
Run 73	4D	T, N/P, PARb,S	96:00:00
Run 74	4D	T, N/P, PARc,S	72:00:00
Run 75	4D	T, N, P, PARa	36:00:00
Run 76	4D	T, N, P, PARb	36:00:00
Run 77	4D	T, N, P, PARc	24:00:00
Run 78	4D	S, N,P, PARa	60:00:00
Run 79	4D	S, N,P, PARb	60:00:00
Run 80	4D	S, N,P, PARc	48:00:00
Run 81	4D	T, N, S, P	48:00:00
Run 82	5D	T, N, S, P, PARc	480:00:00
Run 83	5D	T, N, S, P, PARb	984:00:00
Run 84	5D	T, N, S, P, PARa	1176:00:00

933 **Table S3.**

Environmental variable	Optimum	Number of optimum values	Tolerance	Number of ecological amplitudes	Number of niches
Temperature= -2,-1,0,...,44	0,6,12,...,36	7	1,4,7,10	4	28
Temperature bis= -2,1.99,1.98,...,44	0,1,2,...,40	41	1,2,3,...,40	10	410
PARa= 0,1,2,...,70	1,9,17,...,70	9	1,5,9	3	27
PARa bis= 0,0.25,0.50,...,70	1,2,3,...,70	70	1,2,3,...,9	9	630
PARb= 0,1,2,...,70	10,18,26,...,70	8	1,5,9	3	24
PARb bis= 0,0.25,0.50,...,70	10,11,12,...,70	60	1,2,3,...,9	9	540
PARc= 0,1,2,...,70	20,28,36,...,70	7	1,5,9	3	21
PARc bis= 0,0.25,0.50,...,70	20,21,22,...,70	50	1,2,3,...,9	9	450
Nitrate= 0,1,2,...,43	1,6,11,...,41	9	1,4,7	3	27
Nitrate bis= 0,0.01,0.02,...,43	1,2,3,...,41	41	1,2,3,...,7	7	287
Silicate= 0,1,2,...,127	1,20,39,...,126	7	1,6,11,16	4	28
Silicate bis= 0,0.1,0.2,...,127	1,4,7,...,126	42	1,2,3,...,16	16	672
Phosphate= 0,0.1,0.2,...,3.8	0.1,0.4,3.5	3	0.1,0.3,0.5	3	27
Phosphate bis= 0,0.01,0.02,...,3.8	0.1,0.2,0.3,...,3.5	35	0.1,0.13,0.16,...,0.5	16	560
N/P= 0,0.2,0.4,...,25	0,4,8,...,24	7	1,2,3,4	4	28
N/P bis= 0,0.01,0.02,...,25	0,1,2,...,24	25	1,1.25,1.50,...,4	16	400

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Run n°	Parameters	Phytoplankton			Null model	Null model	Null model	Null model
		Mean correlation	Species correlated	Highest correlations	Correlation	Correlation	MAE	MAE
					Without autocorrelation	With autocorrelation	Without autocorrelation	With autocorrelation
Probability	Probability	Probability	Probability					
Run 1	T	0,5156	0	-	2,8	83,8	0	0
Run 2	T.bis	0,5906	8	0,7676	98,3	100	0	0
Run 3	PARa	0,5976	0	-	0	15,7	0	0
Run 4	PARa.bis	0,6527	0	-	59,4	100	0	0
Run 5	PARb	0,5506	0	-	0,1	49,3	0	0
Run 6	PARb.bis	0,6527	0	-	33,9	100	0	0
Run 7	PARc	0,5757	0	-	0	12,3	0	0
Run 8	PARc.bis	0,6376	0	-	42,9	100	0	0
Run 9	N	0,4488	0	-	3,1	66,6	24,5	46,5
Run 10	N.bis	0,4951	0	-	99,7	100	5,4	55,8
Run 11	S	0,4224	1	0,6937	3,9	52	88,4	94,7
Run 12	S.bis	0,4447	0	-	100	100	100	100
Run 13	P	0,3687	0	-	61,3	99	100	100
Run 14	P.bis	0,5392	1	0,6318	99,8	100	7,6	77,5
Run 15	N/P	0,5414	0	-	0,2	62,1	0	0
Run 16	N/P.bis	0,6270	0	-	25,7	100	0	0
Run 17	T and N	0,6362	0	-	0,1	98,8	0	0
Run 18	T and PARa	0,7833	1	0,8790	0	0	0	0
Run 19	T and PARb	0,7838	1	0,8344	0	0	0	0
Run 20	T and PARc	0,7791	1	0,7589	0	0	0	0
Run 21	N and PARa	0,7224	0	-	0	0	0	0
Run 22	N and PARb	0,7128	0	-	0	0	0	0
Run 23	N and PARc	0,7085	0	-	0	0	0	0
Run 24	T and S	0,6835	0	-	0	3,9	0	0
Run 25	N and S	0,5993	0	-	0,1	77,7	0	0,7
Run 26	S and PARa	0,6251	0	-	0,2	98,6	0	0
Run 27	S and PARb	0,5933	0	-	3,2	99,9	0	0
Run 28	S and PARc	0,6129	0	-	0,2	93,1	0	0
Run 29	T and P	0,6776	0	-	0	28,9	0	0
Run 30	N and P	0,5912	0	-	0,9	98,5	1,5	19,1
Run 31	S and P	0,6127	0	-	0,1	66,7	0	0
Run 32	P and PARa	0,7153	0	-	0	0	0	0
Run 33	P and PARb	0,7073	0	-	0	0,1	0	0
Run 34	P and PARc	0,7130	0	-	0	0	0	0
Run 35	T and N/P	0,6308	0	-	8,4	100	0	0
Run 36	S and N/P	0,6670	0	-	0	17,4	0	0
Run 37	N/P and PARa	0,7751	0	-	0	0	0	0
Run 38	N/P and PARb	0,7759	0	-	0	0	0	0
Run 39	N/P and PARc	0,7690	0	-	0	0	0	0
Run 40	T,N and PARa	0,7981	0	-	0	0	0	0
Run 41	T,N and PARb	0,7975	1	0,8276	0	0	0	0
Run 42	T,N and PARc	0,7934	0	-	0	0	0	0
Run 43	T,S and PARa	0,7866	1	0,9613	0	0	0	0
Run 44	T,S and PARb	0,7866	0	-	0	0	0	0
Run 45	T,S and PARc	0,7831	0	-	0	0	0	0
Run 46	T,P and PARa	0,7925	3	0,9384	0	0	0	0
Run 47	T,P and PARb	0,7931	0	-	0	0	0	0
Run 48	T,P and PARc	0,7915	2	0,9162	0	0	0	0
Run 49	T,N/P and PARa	0,8043	1	0,8913	0	0	0	0
Run 50	T,N/P and PARb	0,8031	2	0,7807	0	0	0	0
Run 51	T,N/P and PARc	0,8016	10	0,8644	0	0	0	0
Run 52	T,N and S	0,7313	2	0,8896	0	7,9	0	0
Run 53	T,N and P	0,7142	0	-	0	97,8	0	0
Run 54	T,S and P	0,7253	2	0,9691	0	34,2	0	0
Run 55	T,S and NP	0,7452	4	0,8548	0	4,7	0	0
Run 56	N,S and PARa	0,7261	0	-	0	24,3	0	0
Run 57	N,S and PARb	0,7154	0	-	0	19,6	0	0
Run 58	N,S and PARc	0,7154	0	-	0	21,5	0	0
Run 59	N,P and PARa	0,7475	1	0,4239	0	0,1	0	0
Run 60	N,P and PARb	0,7415	0	-	0	0,1	0	0
Run 61	N,P and PARc	0,7374	0	-	0	0	0	0
Run 62	N,S and P	0,6605	0	-	0,1	100	0	0
Run 63	S,P and PARa	0,7189	0	-	0	53,8	0	0
Run 64	S,P and PARb	0,7141	0	-	0	53,4	0	0
Run 65	S,P and PARc	0,7180	0	-	0	14,8	0	0
Run 66	S,N/P and PARa	0,7774	0	-	0	0	0	0
Run 67	S,N/P and PARb	0,7767	0	-	0	0	0	0
Run 68	S,N/P and PARc	0,7710	0	-	0	0	0	0
Run 69	T, N, S, PARa	0,8002	0	-	0	0	0	0
Run 70	T, N, S, PARb	0,7988	2	0,8240	0	0	0	0
Run 71	T, N, S, PARc	0,7966	1	0,9490	0	0	0	0
Run 72	T, NP, PARa,S	0,8062	6	0,8390	0	0	0	0
Run 73	T, NP, PARb,S	0,8045	2	0,8274	0	0	0	0
Run 74	T, NP, PARc,S	0,8030	3	0,7431	0	0	0	0
Run 75	T, N, P, PARa	0,8008	3	0,8920	0	0	0	0
Run 76	T, N, P, PARb	0,8008	1	0,7896	0	0	0	0
Run 77	T, N, P, PARc	0,7980	3	0,8575	0	0	0	0
Run 78	S, N,P,PARa	0,7497	0	-	0	90,8	0	0
Run 79	S, N,P,PARb	0,7431	0	-	0	96	0	0
Run 80	S, N,P,PARc	0,7397	0	-	0	97,1	0	0
Run 81	T, N, S, P	0,7558	4	0,8849	0	76,5	0	0
Run 82	T, N, S, P,PARc	0,7906	5	0,7922	0	0	0	0
Run 83	T,N,S,P,PARb	0,7941	3	0,8741	0	0	0	0
Run 84	T,N,S,P,PARa	0,7948	6	0,8378	0	0	0	0