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1 **On the conditions promoting *Pseudo-nitzschia* spp. blooms in the eastern English**
2 **Channel and southern North Sea**

3

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11 **Abstract:**

12

13 This study investigated the drivers of the blooms of *Pseudo-nitzschia seriata* and *Pseudo-*
14 *nitzschia delicatissima* complexes in the eastern English Channel and southern North Sea.
15 Phytoplankton data series acquired from 1992 to 2020 were analyzed with a multivariate
16 statistical approach based on Hutchinson's niche concept. *P. seriata* and *P. delicatissima*
17 complexes were found to be typically present year round, but they bloomed at different
18 periods because they occupied different realized ecological niches. *P. delicatissima* complex
19 occupied a more marginal niche and was less tolerant than *P. seriata* complex. *P.*
20 *delicatissima* complex typically bloomed in April-May at the same time as *Phaeocystis*
21 *globosa* while *P. seriata* complex blooms were more frequently observed in June during the
22 decline of low intensity *P. globosa* blooms. *P. delicatissima* and *P. seriata* complexes were
23 both favored by low-silicate environments and relatively low turbulence but they responded
24 differently to water temperature, light, ammonium, phosphate and nitrite + nitrate conditions.
25 Niche shifts and biotic interactions played important roles in the control of the blooms of *P.*
26 *delicatissima* and *P. seriata* complexes. The two complexes occupied different sub-niches
27 during their respective low abundance and bloom periods. The phytoplankton community
28 structure and the number of other taxa presenting a niche overlapping the niches of *P.*
29 *delicatissima* and *P. seriata* complexes also differed between these periods. *P. globosa* was
30 the taxa contributing the most to the dissimilarity in community structure. *P. globosa*
31 interacted positively with *P. delicatissima* complex and negatively with *P. seriata* complex.

32 1 Introduction:

33

34 Blooms of the diatom *Pseudo-nitzschia* are recognized worldwide as a public health
35 threat because several species in this genus are known to produce the neurotoxin domoic acid
36 (DA) causing amnesic shellfish poisoning (ASP) (Bates et al., 2018; Grattan et al., 2016;
37 Lelong et al., 2012; Petroff et al., 2021; Trainer et al., 2008). Since the report of the first ASP
38 event in 1987 (Perl et al., 1990), *Pseudo-nitzschia* has become the focus of considerable
39 international scientific attention. Temperature, salinity, nutrients, irradiance, photoperiod and
40 upwelling events have been identified as factors influencing its growth and toxicity (Bates et
41 al., 1998; Bates et al., 2018; Clark et al., 2019; Downes-Tettmar et al., 2013; Fehling et al.,
42 2006; Klein et al., 2010; Lelong et al., 2012; Marchetti et al., 2004; McCabe et al., 2016;
43 Thorel et al., 2017; Trainer et al., 2012; Trainer et al., 2008). However, in spite of intense
44 research, the current understanding of the conditions controlling *Pseudo-nitzschia* spp.
45 blooms remains elusive since the aforementioned abiotic factors are generally insufficient to
46 explain the occurrence, intensity and demise (often abrupt) of *Pseudo-nitzschia* spp. blooms
47 (Azanza et al., 2018). A part of our lack of understanding is because environmental cues
48 triggering *Pseudo-nitzschia* spp. blooms are complex and can be unique to the bay, coastal or
49 open ocean region where they occur making any generalization of the findings almost
50 impossible (Trainer et al., 2012). Another reason might be the methodology employed.
51 Harmful algae (including *Pseudo-nitzschia* spp.) are usually studied in monospecific cultures
52 in the laboratory and field studies often neglect to characterize surrounding phytoplankton
53 community (Wells and Karlson, 2018). As such, competitive interactions are not taken into
54 account.

55 Biotic interactions between *Pseudo-nitzschia* spp. and the other members of the
56 phytoplankton community are of interest because competition for resources is well known to

57 impact the dominance of certain phytoplankton species (Litchman, 2007; Sommer, 1989;
58 Tilman, 1977). Besides, positive interactions such as facilitations (Bruno et al., 2003) have
59 also recently been shown to play a role in some microalgae species successions (Krichen et
60 al., 2019). Therefore, as it has already been demonstrated in terrestrial plants community
61 successions (Brooker et al., 2008), some pioneer microalgae species could modify their
62 surrounding environment, making it more favorable for the subsequent colonization by other
63 microalgae species. Some examples of *Pseudo-nitzschia* species attached on colonies of other
64 phytoplankton species have also been observed in the field, such as *Pseudo-nitzschia*
65 *pseudodelicatissima* on *Chaetoceros socialis*, *Pseudo-nitzschia americana* and *Pseudo-*
66 *nitzschia linea* on *Chaetoceros* spp. and *Odontella* spp., *Pseudo-nitzschia delicatissima* on
67 *Phaeocystis globosa* or *Pseudo-nitzschia cf. granii var. curvata* on *Phaeocystis pouchettii*,
68 suggesting that some kind of relationships may exist between these species (Lelong et al.,
69 2012 and references therein). However, to our knowledge, the potential role of biotic
70 interactions influencing *Pseudo-nitzschia* spp. blooms has never been explored. Turbulence is
71 another factor that has not been considered and would deserve more attention since it affects
72 plankton dynamics (Estrada and Berdalet, 1997; Gibson, 2000; Mann and Lazier, 2013;
73 Schmitt, 2020). There is evidence that turbulence affects most of the parameters influencing
74 diatoms survival. It influences settling velocity and cell re-suspension (Estrada and Berdalet,
75 1997; Ruiz et al., 2004), nutrients acquisition and availability (Dell'Aquila et al., 2017;
76 Estrada and Berdalet, 1997; Pahlow et al., 1997), genes expression (Amato et al., 2017), chain
77 morphology (Amato et al., 2017; Clarson et al., 2009; Dell'Aquila et al., 2017) and encounter-
78 based processes such as interactions with grazers and diatom-diatom encounter rate for
79 reproduction and chain formation (Rothschild and Osborn, 1988).

80 *Pseudo-nitzschia* spp. are regularly present along all the French coasts (Belin et al.,
81 2021) but in some regions, the blooms of *Pseudo-nitzschia* spp. have received few attention.

82 This is the case of the eastern English Channel and southern North Sea. Phytoplankton
83 research in this area has mainly focused on the understanding of the massive *P. globosa*
84 blooms that occur every spring (Breton et al., 2000; Breton et al., 2022; Genitsaris et al.,
85 2015; Grattepanche et al., 2011; Hernández-Fariñas et al., 2014; Peperzak, 2002).
86 Consequently, the number of studies dealing with *Pseudo-nitzschia* spp. ecology in this region
87 is very limited. Delegrange et al. (2018) described the diversity and toxicity of *Pseudo-*
88 *nitzschia* spp. during one year (2012) at a single station in the southern Bight of the North
89 Sea. Lefebvre and Dezécache (2020) studied the possibility to use *P. globosa* and diatoms
90 (including *Pseudo-nitzschia* spp.) as indicators of eutrophication. Karasiewicz and Lefebvre
91 (2022) found that *Pseudo-nitzschia* spp. could bloom several times during the same year or
92 bloom over a large period of time; however, these blooms patterns could be driven by
93 different species of *Pseudo-nitzschia*. Three *Pseudo-nitzschia* species (*P. delicatissima*, *P.*
94 *fraudulenta* and *P. pungens*) belonging to two different complexes (*Pseudo-nitzschia*
95 *delicatissima* complex and *Pseudo-nitzschia seriata* complex) have been detected in this
96 region by Delegrange et al. (2018). In the present study, it was thus hypothesized that the two
97 *Pseudo-nitzschia* complexes might occupy different ecological niches and present contrasted
98 bloom periods controlled by different environmental factors. Understanding these potential
99 differences in the ecology of the two *Pseudo-nitzschia* complexes is important because the
100 species belonging to these complexes can present different levels of toxicity (e.g. Trainer et
101 al., 2012). It was also thought that biotic interactions with the other members of the
102 phytoplankton community and turbulence might influence *Pseudo-nitzschia* spp. blooms.

103 By using a methodology based on the concept of realized ecological niche (i.e. the set
104 of favorable conditions under which a species survives, grows, reproduces and can be
105 observed (Hutchinson, 1957)), the present study aimed: 1) to determine the bloom periods of
106 *Pseudo-nitzschia delicatissima* complex and *Pseudo-nitzschia seriata* complex, 2) to

107 investigate the main factors favoring these blooms and, 3) to define the role of the
108 surrounding phytoplankton community by identifying potential biotic interactions between
109 *Pseudo-nitzschia* spp. and the other phytoplankton species.

110

111 **2 Materials and Methods:**

112 2.1 Study area

113

114 The eastern English Channel and southern North Sea are temperate eutrophic shallow
115 shelf seas with a macrotidal range (3-9 m). The water column is constantly well mixed. Tides
116 are characterized by a residual water circulation parallel to the coast with coastal waters
117 drifting from the English Channel to the North Sea. This so-called "coastal flow" separates the
118 coastal waters from offshore waters by a transient tidally controlled frontal area (Brylinski et
119 al., 1991). Coastal waters are influenced by freshwater runoffs from the Seine, Somme,
120 Authie and Canche estuaries and from the Liane river. [The eastern English Channel and](#)
121 [southern North Sea present an unusual phytoplankton succession occurring every spring. Each](#)
122 [year, the Haptophyte *P. globosa* forms massive blooms between March and May and these](#)
123 [blooms are preceded and followed by two diatom blooms with distinct species composition](#)
124 [\(Breton et al., 2000; Breton et al., 2022; Genitsaris et al., 2015; Grattepanche et al., 2011;](#)
125 [Hernández-Fariñas et al., 2014\).](#)

126

127 2.2 Data sets and sampling strategy

128

129 [Data come from three monitoring programs with similar methodology: 1\) SNO-](#)
130 [SOMLIT \(National coastal observation service, \[www.somlit.fr\]\(http://www.somlit.fr\)\), 2\) IFREMER French](#)
131 [Observation and Monitoring program for Phytoplankton and Hydrology in coastal waters](#)

132 (REPHY, 2021) and 3) Regional Observation and Monitoring Program for Phytoplankton and
133 Hydrology in the eastern English Channel (SRN, 2017). The complete dataset comprised a
134 total of 1213 samples collected over 28 years of phytoplankton observations (SNO-SOMLIT:
135 1996-2020 and REPHY/SRN: 1992-2019).

136 Samples were collected at 13 stations distributed along four coastal-offshore transects
137 located in three main areas: the coasts of Boulogne-sur-Mer and Dunkerque and the Bay of
138 Somme (Fig. 1). Water samples for laboratory analyses of nutrient concentrations and
139 phytoplankton were collected at high tide in subsurface with a five-liter Niskin bottle. These
140 sampling were done fortnightly during the SNO-SOMLIT monitoring while during the
141 REPHY/SRN monitoring, samples were collected fortnightly from March to June and
142 monthly the rest of the year. Phytoplankton samples (1 L) were fixed with neutral or acid
143 Lugol's Iodine solution (final concentration 2%).

144

145 2.3 Abiotic parameters

146

147 Seawater temperature and salinity profiles were measured in situ with a CTD probe
148 (conductivity, temperature, depth). Silicate (SiOH_4), nitrate + nitrite ($\text{NO}_3^- + \text{NO}_2^-$),
149 ammonium (NH_4^+) and phosphate (PO_4^{3-}) concentrations were analyzed following the Aminot
150 and K  rouel (2004; 2007)'s methodology. Turbulence was characterized by a proxy of the
151 mean dissipation rate (ϵ in m^2/s^3) using MacKenzie and Leggett (1993)'s equation:

$$152 \quad \epsilon = (5.82 \cdot 10^{-6}) W^3 / z$$

153 with z = sampling depth (in m) and W = wind speed (in m s^{-1}). Wind speed was measured at
154 the meteorological stations of Boulogne-sur-Mer, Dunkerque and Cayeux-sur-Mer and was
155 provided by M  teo France. Daily photosynthetically active radiation (PAR in einstein $\text{m}^{-2} \text{day}$
156 ¹) from 1998 to 2020 was downloaded on GlobColour website (<https://hermes.acri.fr>). PAR

157 was estimated from satellite products using Frouin et al. (2003)'s algorithm. Five-day
158 averages of turbulence and PAR values were used in the realized ecological niche analyses
159 (four previous days and day of phytoplankton sampling) (Hernández Fariñas et al., 2015;
160 Houliez et al., 2021).

161

162 2.4 Taxonomic determination of phytoplankton species

163

164 10-100 mL of the fixed phytoplankton samples were settled for at least 24h following
165 the Utermöhl method (Utermöhl, 1958). Phytoplankton species were identified to the lowest
166 possible taxonomic level and enumerated using an inverted optical microscope (x 200 to x
167 400 magnification). To reduce bias in the datasets due to difficulties in differentiating some
168 species or genera using an optical microscope and to guarantee homogeneity over time and
169 among sampling sites, some species and genera were grouped into taxonomic units. A
170 taxonomic unit was thus composed either by a single species (easily identifiable) or a group of
171 several species or genus difficult to distinguish. *Pseudo-nitzschia* spp. were separated into
172 three groups: *Pseudo-nitzschia americana* and two complexes with different cell width and
173 shape: *Pseudo-nitzschia delicatissima* complex (cell width <3µm, linear shape, delicate forms
174 with very fine structure) and *Pseudo-nitzschia seriata* complex (cell width >3µm, lanceolate
175 shape) (Hasle and Syvertsen, 1996). This classification based on the size and shape of the
176 cells has already demonstrated its usefulness in the understanding of *Pseudo-nitzschia* spp.
177 ecology (Ajani et al., 2020; Bowers et al., 2018; Delegrange et al., 2018; Downes-Tettmar et
178 al., 2013; Stern et al., 2018; Thorel et al., 2017).

179

180

181 2.5 Statistical analyses

182 2.5.1 Realized ecological niches and sub-niches

183

184 The Outlying Mean Index (OMI, Dolédec et al., 2000) and Within Outlying Mean
185 Indexes (WitOMI, Karasiewicz et al., 2017) were used to characterize respectively the
186 realized ecological niche and realized ecological sub-niches of the two *Pseudo-nitzschia*
187 complexes and of the other species composing surrounding phytoplankton community. OMI
188 and WitOMI are both based on Hutchinson's (1957) realized ecological niche concept (for
189 more details read the supplementary materials). The OMI analysis was carried out using the
190 "niche" and "rtest" functions available in the R ade4 package (Dray and Dufour, 2007) while
191 the WitOMI analysis was performed with the R subniche package (Karasiewicz et al., 2017).

192 The OMI analysis is a multivariate statistical analysis defining the realized ecological
193 niche of each taxa composing a community along environmental gradients (Dolédec et al.,
194 2000; Karasiewicz et al., 2020). It depends on the response of each taxa to their environment
195 and describes their habitat. Three parameters characterize the realized niche of each taxa:
196 tolerance, marginality, and residual tolerance. Tolerance (also known as niche breadth)
197 corresponds to the niche extent. It describes the range of conditions tolerated and used by a
198 given taxa. Taxa with high tolerance can persist under a wide range of environmental
199 conditions. They are generalists. Inversely, a low tolerance corresponds to specialists i.e. taxa
200 encountered under specific environmental conditions. Marginality (also known as niche
201 position) is the distance between the average conditions (or resources) used by a given taxa
202 and the average conditions (or resources) available in the study area. Taxa with high
203 marginality occupy a marginal realized ecological niche and occur in atypical habitats within
204 the study area. Inversely, taxa with low marginality occupy a non-marginal realized
205 ecological niche and occur in habitats commonly found in the study area. Residual tolerance

206 represents the part of variance that is not explained by marginality. It helps to determine
207 whether the dataset of environmental conditions used to perform the OMI analysis is relevant
208 to define the realized ecological niche of each taxa. The OMI analysis provides graphical
209 outputs which are described in the supplementary materials.

210 The WitOMI analysis uses the environmental space delimited by the OMI axes as a
211 reference. It decomposes the realized niche of each taxa into realized ecological sub-niches
212 (Karasiewicz et al., 2017). This analysis provides an estimation of niche shifts or
213 conservatism in the realized ecological niche of each taxa, under specific sub-environmental
214 conditions (called subsets) corresponding to a given time period or a sub-location within the
215 study area. For each subset studied, two additional marginalities are provided: $WitOMI_G$ and
216 $WitOMI_{GK}$. $WitOMI_G$ is the distance between the average conditions (or resources) used by
217 the taxa within the studied subset and the average conditions (or resources) available within
218 the whole sampling period or study area. $WitOMI_{GK}$ is the distance between the average
219 conditions (or resources) used by the taxa within the studied subset and the average conditions
220 (or resources) used by the community. Each of these marginalities is accompanied by an
221 index of tolerance ($Tol_{WitOMIG}$ and $Tol_{WitOMIGK}$) and residual tolerances. For each subset
222 considered, the WitOMI analysis provides a graphical representation of: 1) the environmental
223 conditions (or resources) available (sub-environmental space), 2) the potential sub-niche of
224 the taxa, 3) the realized ecological subniche of the taxa and 4) the biological constraints. The
225 potential sub-niche of the taxa is the intersection between the sub-environmental space within
226 the subset considered and the realized ecological niche defined by the OMI analysis. It
227 corresponds to the niche which could be occupied by the taxa in the absence of biotic
228 interactions. The realized ecological sub-niche is the niche currently occupied by the taxa.
229 The biological constraints correspond to the difference in size between the potential sub-niche
230 and realized ecological sub-niche, and represent the part of the niche that the taxa can't

231 occupy due to biotic interactions (Houliez et al., 2021). In the present study, the
232 environmental variables included in the OMI and WitOMI analyses were water temperature,
233 salinity, nutrient concentrations, turbulence and PAR. These factors are known to influence
234 harmful algal blooms and *Pseudo-nitzschia* spp. growth (e.g. Bates et al., 1998; Bates et al.,
235 2018; Lelong et al., 2012; Wells and Karlson, 2018). The WitOMI analysis was used to
236 decompose the realized ecological niche of *P. delicatissima* and *P. seriata* complexes by
237 considering two subsets corresponding to two contrasted periods based on their abundance.
238 For each *Pseudo-nitzschia* complex, the first subset corresponded to periods of low abundance
239 $< 10^3$ cells L⁻¹. The second subset corresponded to bloom periods. Bloom periods were
240 defined by using the French sanitary regulatory thresholds above which *Pseudo-nitzschia*
241 species are considered as producing blooms potentially harmful, and samples are collected for
242 domoic acid analysis in shellfish by the IFREMER REPHYTOX monitoring network (Belin
243 et al., 2021). This threshold was $\geq 10^5$ cells L⁻¹ for *P. seriata* complex and $\geq 3 \times 10^5$ cells L⁻¹
244 for *P. delicatissima* complex. A Mann-Whitney U test (Hollander et al., 2013) was used to
245 test the significance of differences in abiotic parameters between the blooms and periods of
246 low abundance of *P. delicatissima* and *P. seriata* complexes.

247

248 2.5.2 Phytoplankton community structure and biotic interactions

249

250 For both *P. delicatissima* and *P. seriata* complexes, the taxa contributing the most to
251 the dissimilarity in phytoplankton community structure between years with blooms and years
252 without bloom were studied with a SIMPER (SIMilarity PERcentage) analysis performed on
253 a data frame containing fourth root transformed phytoplankton species abundances using
254 PRIMER 6 (PRIMER-E ltd, Plymouth, UK) (Clarke and Warwick, 2001). When taxa

255 contribution was related to abundance changes, the significance of these changes was tested
256 with a Mann-Whitney U test (Hollander et al., 2013).

257 To highlight potential biotic interactions between the *Pseudo-nitzschia* complexes (*P.*
258 *delicatissima* and *P. seriata*) and the other members of the phytoplankton community, an
259 interaction network was built using the Chiquet et al. (2021)'s multivariate Poisson-lognormal
260 model (PLN model). This analysis was performed using the R PLNmodels package. PLN
261 models offer the possibility to distinguish pairs of species that are truly interacting from
262 indirect covariations due to similar response to environmental variables. From the matrix of
263 partial correlation coefficients obtained with the PLN model, a simplified version of the
264 network representing only the taxa interacting with *P. delicatissima* and *P. seriata* complexes
265 was represented by using Cytoscape v.3.8.2.

266

267 2.5.3 Niche overlaps

268

269 The realized ecological niche, potential sub-niche and realized ecological sub-niche of
270 *P. delicatissima* and *P. seriata* complexes were compared to the niches of the other taxa by
271 using the R hypervolume (Blonder et al., 2014) and BAT (Biodiversity Assessment Tools)
272 packages (Cardoso et al., 2021; Mammola, 2019). Niche hypervolumes were built by using
273 the function "hypervolume_svm" on a data frame containing the coordinates of the realized
274 ecological niche, potential sub-niche and realized ecological sub-niche along the first two
275 axes of the OMI and WitOMI analyses. The total volume of each niche and sub-niche was
276 calculated with the function "kernel.alpha" (Mammola and Cardoso, 2020). The function
277 "kernel.similarity" was used to compare the different niches (Mammola and Cardoso, 2020).
278 This function computes pairwise comparisons between kernel density niche hypervolumes of
279 multiple species and characterizes the similarity between pairs of species niches with pairwise

280 distance metrics (centroid and minimum distance) and similarity indices (intersection = niche
281 overlap, Jaccard similarity index and Soerensen-Dice similarity index) (see Mammola, 2019
282 for details). In the present study, only the niche overlaps were reported. They were expressed
283 as percentage of the volumes of the realized ecological niche, potential sub-niche and realized
284 ecological sub-niches of *P. seriata* or *P. delicatissima* complexes.

285

286 **3 Results:**

287 3.1 Bloom periods

288

289 *Pseudo-nitzschia delicatissima* and *Pseudo-nitzschia seriata* complexes are typically
290 present year round, but their bloom periods are different (Fig. 2 A&B). *P. delicatissima*
291 complex blooms mainly at the same time as *P. globosa* blooms from April to May. From
292 2009, *P. delicatissima* complex blooms were observed every year (data not shown). *P. seriata*
293 complex typically blooms from March to September but the blooms were more frequently
294 observed in June during the decline periods of low intensity *P. globosa* blooms. *P. seriata*
295 complex started to bloom either at the same time as *P. globosa* or with a small delay after the
296 start of *P. globosa* blooms. However in all cases, the peak of the blooms of *P. seriata*
297 complex was always reached during the decline of *P. globosa* blooms or shortly after. *P.*
298 *globosa* bloomed every year but it was not the case for *P. seriata* complex (data not shown).
299 During some years, low intensity *P. globosa* blooms were not accompanied by blooms of *P.*
300 *seriata* complex.

301

302

303

304 3.2 Realized ecological niches of *Pseudo-nitzschia* spp.

305

306 The OMI analysis revealed that *P. delicatissima* and *P. seriata* complexes occupied
307 different realized ecological niches and presented different affinities for abiotic environmental
308 conditions.

309 The first two axes of the OMI analysis explained 88.0% of total inertia (OMI1 =
310 70.3% and OMI2 = 17.6%, Fig. 3). OMI1 was mainly explained by $\text{NO}_3^- + \text{NO}_2^-$ and PAR
311 while OMI2 was mainly explained by water temperature (T). The OMI plane reflected the
312 seasonal variations of environmental conditions and delimited three main periods. The right
313 side of the OMI plane corresponded to autumn-winter conditions characterized by high
314 nutrient concentrations, well-mixed waters (high turbulence) and low PAR. The bottom left
315 side corresponded to spring conditions with low nutrient concentrations, high PAR and high
316 salinity. The top left side corresponded to summer conditions with also low nutrient
317 concentrations, high PAR and high salinity but with higher temperature. The realized
318 ecological niche center of gravity (marginality) of each taxa is positioned within this plane
319 according to their affinities for environmental conditions. The position of the marginality of
320 *P. delicatissima* and *P. seriata* complexes showed that *P. delicatissima* complex had affinity
321 for spring conditions while *P. seriata* complex had affinity for spring-summer conditions.
322 Along OMI2, the realized ecological niche of *P. seriata* complex was centered at a higher
323 temperature than the realized ecological niche of *P. delicatissima* complex. High abundances
324 of *P. delicatissima* complex were more frequently observed when temperature ranged from 11
325 to 14°C while high abundances of *P. seriata* complex were more frequently observed when
326 temperature ranged from 14 to 16°C (supplementary materials Fig. S2). Along OMI1, the
327 realized ecological niche of *P. seriata* complex was also centered at higher PAR than the
328 realized ecological niche of *P. delicatissima* complex. High abundances of *P. delicatissima*

329 **complex** were more frequently observed when PAR ranged from 25 to 45 einstein m⁻² day⁻¹
330 while high abundances of *P. seriata* **complex** were more frequently observed when PAR
331 ranged from 40 to 55 einstein m⁻² day⁻¹. *P. delicatissima* and *P. seriata* **complexes** also
332 differed in their affinity for NO₃⁻ + NO₂⁻ conditions. For both *P. delicatissima* and *P. seriata*
333 **complexes**, high abundances were more frequently observed when NO₃⁻ + NO₂⁻
334 concentrations were ≤ 1 μM. However, when NO₃⁻ + NO₂⁻ concentrations ranged from 5 to 12
335 μM, high abundances of *P. delicatissima* **complex** were more frequently observed than high
336 abundances of *P. seriata* **complex**.

337 *P. delicatissima* **complex** had a higher marginality and lower tolerance than *P. seriata*
338 **complex** (Table 1). In comparison to the other taxa composing the phytoplankton community,
339 *P. delicatissima* and *P. seriata* **complexes** were among the ten taxa with the lowest
340 marginality. *P. delicatissima* **complex** was the 17th taxa with the lowest tolerance while *P.*
341 *seriata* **complex** presented an intermediate tolerance (38th over the 74 diatoms with significant
342 realized niches).

343

344 3.3 Realized ecological sub-niches of *Pseudo-nitzschia* spp.

345 3.3.1 Environmental conditions

346

347 All abiotic environmental conditions differed between low abundance and **bloom**
348 periods of *P. delicatissima* **complex** (Fig. 4). During the **blooms** of *P. delicatissima* **complex**,
349 median water temperature, salinity, turbulence and nutrient concentrations (NH₄⁻, NO₂⁻ +
350 NO₃⁻, Si(OH)₄ and PO₄³⁻) were significantly lower and median PAR was significantly higher
351 than during its low abundance periods. By contrast, only median turbulence, NO₂⁻ + NO₃⁻
352 concentrations, Si(OH)₄ concentrations and PAR significantly differed between the **blooms**
353 and low abundance periods of *P. seriata* **complex**. Median turbulence, NO₂⁻ + NO₃⁻

354 concentrations and Si(OH)_4 concentrations were significantly lower while median PAR was
355 significantly higher during the blooms of *P. seriata* complex than during its low abundance
356 periods. During the years with blooms of *P. seriata* complex, Si(OH)_4 and $\text{NO}_2^- + \text{NO}_3^-$ winter
357 stocks were lower than during the years without blooms of *P. seriata* complex (supplementary
358 materials, Fig.S3).

359

360 3.3.2 WitOMI analysis

361

362 The WitOMI analysis showed that the sub-environmental space defined by the
363 available environmental conditions was narrower during the blooms of *P. delicatissima* and *P.*
364 *seriata* complexes than during their low abundance periods (Fig. 5). Consequently, the
365 realized ecological sub-niches of *P. delicatissima* and *P. seriata* complexes shifted during
366 their blooms. *P. delicatissima* and *P. seriata* complexes were both restricted by biological
367 constraints during their respective low abundance periods and they could not take up the
368 totality of their potential sub-niche. *P. delicatissima* and *P. seriata* complexes took up 63%
369 and 90% of their potential sub-niche respectively (Table 1). By contrast, during their blooms,
370 there was no biological constraint and they both took up the totality of their potential sub-
371 niche. However, the realized ecological sub-niche occupied was more marginal than during
372 their low abundance periods and their tolerance was lower.

373

374 3.4 Phytoplankton community structure and potential biotic interactions

375

376 To understand what were the biological constraints influencing the realized ecological
377 sub-niches of *P. delicatissima* and *P. seriata* complexes, the surrounding phytoplankton
378 community structure was compared between the years with blooms and years without bloom

379 to determine the taxa influencing the most the bloom periods of *P. delicatissima* and *P.*
380 *seriata* complexes. For both *P. delicatissima* and *P. seriata* complexes, the surrounding
381 phytoplankton community structure was significantly different between their blooming years
382 and the years without bloom (PERMANOVA, $p < 0.001$). For *P. delicatissima* complex, the
383 dissimilarity between the phytoplankton community present during the blooming years and
384 that present during the years without bloom equaled 68% (SIMPER analysis, supplementary
385 materials Table S1). Twenty-four taxa were identified as the most influential taxa explaining
386 this dissimilarity. Among them, *P. globosa* was the major contributor. For *P. seriata* complex,
387 the dissimilarity in phytoplankton community between the blooming years and years without
388 bloom equaled 71%. Twenty-three taxa were identified as the most influential and *P. globosa*
389 was also the major contributor to this dissimilarity.

390 However, contrasting interactions between *P. globosa* and each of the *Pseudo-*
391 *nitzschia* complexes (*P. delicatissima* and *P. seriata*) were observed. The interaction network
392 highlighted a positive interaction between *P. delicatissima* complex and *P. globosa* while
393 interaction between *P. seriata* complex and *P. globosa* was negative (Fig. 6). Positive
394 interactions between *P. seriata* complex and 5 other diatoms: *Guinardia delicatula*,
395 *Leptocylindrus danicus*, *Chaetoceros curvisetus* + *Chaetoceros debilis* and *Chaetoceros*
396 *danicus* were also highlighted. *P. globosa* abundance was thus significantly higher during the
397 blooms of *P. delicatissima* complex than during its low abundance periods (Fig. 7A) while the
398 opposite trend was observed during the blooms and low abundance periods of *P. seriata*
399 complex (Fig. 7B). *G. delicatula* (Fig. 7C), *C. curvisetus* + *C. debilis* (Fig. 7D) and *C.*
400 *danicus* (Fig. 7E) abundances were significantly higher during the blooming years of *P.*
401 *seriata* complex while for *L. danicus* (Fig. 7F), no significant difference was observed
402 between the blooming years of *P. seriata* complex and years without bloom. *G. delicatula*, *C.*
403 *curvisetus* + *C. debilis*, *C. danicus* and *L. danicus* were not present in high abundance at the

404 same period. *G. delicatula* was present in high abundance ($\geq 10^5$ cells L⁻¹) from March to
405 June during the blooms of *P. globosa* and *P. seriata* complex (Fig. 7G). *C. curvisetus* + *C.*
406 *debilis* high abundances ($\geq 10^5$ cells L⁻¹) were typically observed from March to October but
407 they were more frequently observed in March-April during the blooms of *P. globosa* and in
408 June during the blooms of *P. seriata* complex (Fig. 7H). *C. danicus* high abundances ($\geq 10^4$
409 cells L⁻¹) were more frequently observed from February to March during the first diatom
410 bloom and at the beginning of the *P. globosa* bloom period (Fig. 7I). *L. danicus* high
411 abundances ($\geq 10^5$ cells L⁻¹) were more frequently observed during the blooms of *P. seriata*
412 complex in June and July (Fig. 7J).

413

414 3.5 Realized ecological niches and sub-niches of the taxa interacting with *Pseudo-nitzschia*
415 spp. and niche overlaps

416

417 Overlaps between the realized ecological sub-niches of the taxa composing the
418 surrounding phytoplankton community and the realized ecological sub-niches of *P.*
419 *delicatissima* and *P. seriata* complexes were calculated to better understand the biological
420 constraints influencing the realized ecological sub-niches of *P. delicatissima* and *P. seriata*
421 complexes.

422 The number of other taxa present and showing a niche overlapping the realized
423 ecological sub-ecological niche of *P. delicatissima* complex was lower during the blooms of
424 *P. delicatissima* complex than during its low abundance periods. 113 other taxa were present
425 during low abundance periods of *P. delicatissima* complex vs. 74 during its blooms. 86% of
426 them had a realized ecological sub-niche overlapping the realized ecological sub-niche of *P.*
427 *delicatissima* complex during its low abundance periods vs. 77% during its blooms. The same
428 pattern was observed during low abundance periods and blooms of *P. seriata* complex. There

429 were 108 other taxa during the low abundance periods of *P. seriata* complex vs. 64 during its
 430 blooms. 92% of them had a realized ecological sub-niche overlapping the realized ecological
 431 sub-niche of *P. seriata* complex during its low abundance periods vs. 77% during its blooms.

432 Among these taxa, *P. globosa*, *G. delicatula*, *L. danicus*, *C. curvisetus* + *C. debilis*
 433 and *C. danicus* were the taxa interacting the most with *P. delicatissima* complex and/or *P.*
 434 *seriata* complex. The realized ecological niche and sub-niches of *P. globosa*, *G. delicatula*, *L.*
 435 *danicus*, *C. curvisetus* + *C. debilis* and *C. danicus* differed from the realized ecological niche
 436 and sub-niches of *P. delicatissima* and *P. seriata* complexes (Fig. 8 & Fig. 5). *C. curvisetus* +
 437 *C. debilis* presented a lower marginality than *P. delicatissima* and *P. seriata* complexes while
 438 *P. globosa*, *G. delicatula*, *L. danicus* and *C. danicus* had a higher marginality (Table 1).
 439 Among these five taxa, *P. globosa* was the least tolerant while *C. danicus* was the more
 440 tolerant. *C. danicus* had affinity for winter-spring conditions, *C. curvisetus* + *C. debilis* for
 441 spring-summer-autumn conditions, *P. globosa* for spring conditions and *L. danicus* and *G.*
 442 *delicatula* for spring-summer conditions (Fig. 3).

443 The realized ecological niche of *P. globosa* was more similar to the realized ecological
 444 niche of *P. delicatissima* complex than the realized ecological niche of *P. seriata* complex.
 445 The realized ecological niche of *P. globosa* overlapped 56 % of the realized ecological niche
 446 of *P. delicatissima* complex and 52 % of the realized ecological niche of *P. seriata* complex
 447 (Table 2). The realized ecological niche of *P. globosa* differed from realized ecological niches
 448 of *P. delicatissima* and *P. seriata* complexes mainly in the temperature, PAR and NO_2^- +
 449 NO_3^- conditions favoring its development (supplementary materials, Fig. S2). High *P. globosa*
 450 abundances were more frequently observed when PAR ranged from 30 to 45 einstein $\text{m}^{-2} \text{day}^{-1}$
 451 i.e. at values close to the PAR conditions favoring the development of *P. delicatissima*
 452 complex but at lower PAR than *P. seriata* complex. High *P. globosa* abundances were also
 453 more frequently observed at lower temperature (9-12°C) and higher NO_3^- + NO_2^-

454 concentrations than *P. delicatissima* and *P. seriata* complexes. Indeed, when $\text{NO}_3^- + \text{NO}_2^-$
455 concentrations were $> 10 \mu\text{M}$ high *P. globosa* abundances were more frequently observed
456 than high abundances of *P. delicatissima* and *P. seriata* complexes.

457 During low abundance periods of *P. delicatissima* complex, *P. globosa* occupied 49%
458 of its potential sub-niche (Table 1) and its realized ecological sub-niches were smaller than
459 the realized ecological sub-niches of *P. delicatissima* complex (Fig. 8A) *P. globosa* potential
460 and realized ecological sub-niches overlapped respectively 52% and 38% of the potential and
461 realized ecological sub-niches of *P. delicatissima* complex (Table 2). During the blooms of *P.*
462 *delicatissima* complex, the environmental conditions were different from its low abundance
463 periods. The realized ecological sub-niches of *P. delicatissima* complex and *P. globosa*
464 shifted (Fig. 5B & 8B). Consequently, the realized ecological sub-niches of *P. globosa*
465 overlapped a higher proportion of the potential and realized ecological sub-niches of *P.*
466 *delicatissima* complex (Table 2). Contrary to *P. delicatissima* complex that occupied the
467 totality of its potential sub-niche, *P. globosa* only occupied 87% of its potential sub-niche.

468 During low abundance periods of *P. seriata* complex, *P. globosa* occupied 74% of its
469 potential sub-niche and the sub-niches *P. globosa* were smaller than the sub-niches of *P.*
470 *seriata* complex (Fig. 8C). The potential and realized ecological sub-niches of *P. globosa*
471 overlapped respectively 57% and 43% of the potential and realized ecological sub-niches of
472 *P. seriata* complex. During low abundance periods of *P. seriata* complex, *P. globosa*
473 occupied a smaller proportion of its potential sub-niche due to stronger environmental and
474 biological constraints (Table 1, Fig. 8D). Its potential sub-niche became identical to the
475 potential sub-niche of *P. seriata* complex and the overlap between the realized ecological sub-
476 niches of *P. globosa* and *P. seriata* complex increased (Table 2).

477 Among the diatoms interacting with *P. seriata* complex, the realized ecological niche
478 of *G. delicatula* was the most similar to the realized ecological niche of *P. seriata* complex

479 and completely overlapped it (Fig. 8E & F, Table 2). The realized ecological niche of *P.*
480 *seriata complex* was however smaller than the realized ecological niche of *G. delicatula* (Fig.
481 8 & Fig.5) since high abundances of *G. delicatula* occurred over a larger range of
482 temperatures than high abundances of *P. seriata complex* (supplementary materials, Fig. S2).
483 The other diatoms were ranked as follows: *C. danicus*, *C. curvisetus* + *C. debilis* and *L.*
484 *danicus* with their realized ecological niches overlapping respectively 73%, 62% and 55% of
485 the realized ecological niche of *P. seriata complex* (Table 2). High abundances of *C. danicus*
486 were frequently observed over a larger range of $\text{NO}_3^- + \text{NO}_2^-$ concentrations than high
487 abundances of *P. seriata complex* and at lower temperature and PAR (supplementary
488 materials, Fig. S2). High abundances of *C. curvisetus* + *C. debilis* and *L. danicus* were
489 frequently observed at higher temperatures than high abundances of *P. seriata complex*.
490 However, high abundances of *C. curvisetus* + *C. debilis* were favored by lower PAR than *P.*
491 *seriata complex* while *L. danicus* and *P. seriata complex* were favored by relatively similar
492 PAR. High abundances of *C. curvisetus* + *C. debilis* were also observed over a larger range of
493 $\text{NO}_3^- + \text{NO}_2^-$ concentrations than *P. seriata complex* and *L. danicus*.

494 During low abundance periods of *P. seriata complex*, *C. curvisetus* + *C. debilis*
495 occupied the totality of its potential sub-niche while *G. delicatula*, *C. danicus* and *L. danicus*
496 occupied respectively 82%, 90% and 79% of their potential sub-niche (Fig. 8E, G, I, K &
497 Table 1). The sub-niches of *G. delicatula*, *C. curvisetus* + *C. debilis* and *C. danicus* were
498 larger than the sub-niches of *P. seriata complex* while the sub-niches of *L. danicus* were
499 smaller. The potential sub-niches of *L. danicus*, *C. curvisetus* + *C. debilis* and *C. danicus*
500 overlapped respectively 60%, 68%, and 96% of the potential sub-niche of *P. seriata complex*
501 while the potential sub-niche of *G. delicatula* overlapped the totality of the potential sub-
502 niche of *P. seriata complex* (Table 2). The realized ecological sub-niches of *L. danicus*, *C.*

503 *curvisetus* + *C. debilis*, *C. danicus* and *G. delicatula* overlapped respectively 37%, 77%, 99%
504 and 53% of the realized ecological sub-niche of *P. seriata* complex.

505 During the blooms of *P. seriata* complex, the environmental conditions constrained
506 the realized ecological sub-niches of all the taxa interacting with *P. seriata* complex (Fig. 8F,
507 H, J & L). Consequently, all of them had the same potential sub-niche as *P. seriata* complex.
508 *G. delicatula* and *L. danicus* occupied almost the totality of their potential sub-niche while,
509 due to stronger biological constraints, *C. curvisetus* + *C. debilis* and *C. danicus* occupied a
510 smaller proportion of their potential sub-niche than during low abundance periods of *P.*
511 *seriata* complex (Table 1). Overlaps between the realized ecological sub-niche of *P. seriata*
512 complex and the realized ecological sub-niches of *C. curvisetus* + *C. debilis* and *C. danicus*
513 were thus reduced. By contrast, overlaps between the realized ecological sub-niche of *P.*
514 *seriata* complex and the realized ecological sub-niches of *G. delicatula* and *L. danicus*
515 increased (Table 2). Overlaps between the realized ecological sub-niche of *P. globosa* and the
516 realized ecological sub-niche of the other diatoms interacting with *P. seriata* complex were
517 also modified. Overlap between the realized ecological sub-niche of *P. globosa* and the
518 realized ecological sub-niche of *C. curvisetus* + *C. debilis* was reduced from 57% to 2%. By
519 contrast, overlaps between the realized ecological sub-niche of *P. globosa* and the realized
520 ecological sub-niches of *C. danicus* and *L. danicus* increased (*C. danicus*: from 56% to 71%,
521 *L. danicus*: from 43% to 81%).

522

523 4 Discussion

524

525 The complexes *Pseudo-nitzschia delicatissima* and *Pseudo-nitzschia seriata* are
526 typically present year round but they bloom at different periods and occupy different realized
527 ecological niches.

528 *P. delicatissima* complex showed affinity for spring conditions and blooms more
529 frequently from April to May at the same time as *P. globosa* blooms. *P. seriata* complex has
530 affinity for spring-summer conditions. *P. seriata* complex is able to bloom within a larger
531 seasonal window but its blooms are more frequently observed in June during the decline
532 period of low intensity *P. globosa* blooms. A similar succession in the bloom seasonality of
533 these two complexes has been observed by Fehling et al. (2006) in western Scottish coastal
534 waters and Delegrange et al. (2018) in the southern North Sea. High abundances of *P.*
535 *delicatissima* complex in spring have also been previously reported in the Skagerrak and
536 Norwegian coastal waters (Hasle et al., 1996) and in the southern North Sea (Delegrange et
537 al., 2018). This difference in seasonality can be explained by the two complexes occupying
538 different realized ecological niches. *P. delicatissima* complex occupies a more marginal niche
539 and is less tolerant than *P. seriata* complex. The realized ecological niches of *P. delicatissima*
540 and *P. seriata* complexes differ mainly in the temperature, light and $\text{NO}_2^- + \text{NO}_3^-$ conditions
541 allowing their growth and survival. High abundances of *P. seriata* complex are observed at
542 higher temperature and PAR than *P. delicatissima* complex but at lower $\text{NO}_2^- + \text{NO}_3^-$
543 concentrations. The abiotic conditions favoring the blooms of *P. delicatissima* and *P. seriata*
544 complexes also differ. The blooms of *P. delicatissima* complex are influenced by water
545 temperature, salinity, turbulence, PAR and nutrients (NH_4^+ , $\text{NO}_2^- + \text{NO}_3^-$, Si(OH)_4 and PO_4^{3-}
546 concentrations). By contrast, the blooms of *P. seriata* complex are not influenced by water
547 temperature, salinity and NH_4^+ and PO_4^{3-} concentrations.

548 In addition to environmental conditions, biotic interactions and niche shifts seem to
549 play an important role in the control of the blooms of *P. delicatissima* and *P. seriata*
550 complexes. During their respective low abundance periods, *P. delicatissima* and *P. seriata*
551 complexes were limited by strong biological constraints and they could not occupy the totality
552 of their potential sub-niche. For both complexes, the surrounding community structure was

553 different between their respective blooms and low abundance periods. The number of other
554 taxa present and proportions of taxa presenting a niche overlapping the niches of *P.*
555 *delicatissima* and *P. seriata* complexes were higher during their respective low abundance
556 periods, suggesting that *P. delicatissima* and *P. seriata* complexes had potentially to compete
557 with a higher number of other taxa during their respective low abundance periods than during
558 their blooms. *P. globosa* is the taxa that contributed the most to the dissimilarity in
559 community structure between these periods. *P. globosa* interacted positively with *P.*
560 *delicatissima* complex, but negatively with *P. seriata* complex. *P. globosa* also occupied
561 different sub-niches during the respective blooms and low abundance periods of *P.*
562 *delicatissima* and *P. seriata* complexes.

563 The positive interaction between *P. delicatissima* complex and *P. globosa* is in line
564 with observations frequently made in the eastern English Channel and southern North Sea. In
565 these areas, during *P. globosa* blooms, it is very frequent to observe *P. globosa* colonies
566 heavily colonized by *P. delicatissima* complex (e.g. Pannard et al., 2008; Sazhin et al., 2007).
567 Sazhin et al. (2007) observed up to 130 cells of *P. delicatissima* complex per *P. globosa*
568 colony. Cells of *P. delicatissima* complex associated with *P. globosa* colonies have also been
569 commonly observed in the Gulf of Maine (northwestern Atlantic Ocean) (Fernandes et al.,
570 2014). In the northern Adriatic Sea, Totti et al. (2005) observed higher proportions of *P.*
571 *delicatissima* complex in large mucilage aggregates than in the water column. The reasons for
572 the presence of *P. delicatissima* complex in mucilage aggregates and its association with *P.*
573 *globosa* are currently unknown. However, it is thought that *P. delicatissima* complex would
574 be able to use the organic substances contained in the mucus of *P. globosa* colonies and
575 mucilage aggregates (Sazhin et al., 2007). *P. globosa* colonies would thus provide a favorable
576 habitat for the growth of *P. delicatissima* complex (Sazhin et al., 2007). In accordance with
577 this hypothesis, Loureiro et al. (2009) observed that in laboratory cultures, *P. delicatissima* is

578 able to use organic nutrients to maintain its growth when inorganic nutrients are limiting. In
579 the present study, the blooms of *P. globosa* and *P. delicatissima* complex occurred after a first
580 diatom bloom that started to consume the nutrient stocks, and silicates were potentially
581 limiting for diatoms during this period. Like any other diatoms, *P. delicatissima* complex
582 requires silicate to grow. However, since *Pseudo-nitzschia* spp. have lightly silicified
583 frustules, they seem better adapted to low silicate conditions than many other diatoms
584 (Marchetti et al., 2004). Indeed, several laboratory studies showed that *Pseudo-nitzschia*
585 species were able to grow under low silicate concentrations (e.g. Fehling et al., 2004; Pan et
586 al., 1996a; Pan et al., 1996b). Natural blooms of *Pseudo-nitzschia* spp. have also been
587 repeatedly observed in association with depleted silicate concentrations and this genus has
588 often been found to outcompete other phytoplankton species during the late stage of a spring
589 diatom blooms (Anderson et al., 2006; Anderson et al., 2010; Bates et al., 1998; Davidson et
590 al., 2012; Dortch et al., 1997; Fehling et al., 2004; Marchetti et al., 2004; Pan et al., 1996a;
591 Pan et al., 1996b). It is thus frequent to find significant negative correlations between *Pseudo-*
592 *nitzschia* spp. blooms and silicate concentrations, Si:N or Si:P ratios (e.g. Anderson et al.,
593 2006; Anderson et al., 2010). In the present study, high abundances of *P. delicatissima*
594 complex were observed as associated with low Si:N ratios. Similar observations were made in
595 the southern North Sea in 2012 (Delegrange et al., 2018) and in the Bay of Seine (central
596 English Channel) in 2013 (Thorel et al., 2017). The capacity of *P. delicatissima* complex to
597 grow at low silicate concentrations associated with its potential ability to use organic
598 substances provided by *P. globosa* colonies mucus might be a competitive advantage over
599 other diatoms and might explain the positive interaction between the blooms of *P. globosa*
600 and *P. delicatissima* complex.

601 The negative interaction between *P. seriata* complex and *P. globosa* is more complex
602 since other diatoms: *C. curvisetus* + *C. debilis*, *C. danicus*, *L. danicus* and *G. delicatula* also

603 interacted with *P. globosa* and/or *P. seriata* complex. Interactions between *P. seriata*
604 complex, *L. danicus* and *G. delicatula* seem to have been direct, while interactions between *C.*
605 *curvisetus* + *C. debilis*, *C. danicus* and *P. seriata* seem to have been indirect because these
606 species were not present with high abundance at the same period of the year and were not
607 favored by the same environmental conditions. *P. seriata* complex was able to bloom after
608 that a sequence of events created conditions favorable to its growth. Its bloom periods were
609 accompanied by shifts in its realized ecological sub-niche but also in the realized ecological
610 sub-niches of its interacting taxa. *P. seriata* complex always bloomed during years of low
611 intensity *P. globosa* blooms. During the blooming years of *P. seriata* complex, the winter
612 stocks of $\text{NO}_2^- + \text{NO}_3^-$ and Si(OH)_4 were lower while PAR and abundances of *C. danicus* and
613 *C. curvisetus* + *C. debilis* were higher than during years without bloom of *P. seriata* complex.
614 High abundances of *C. danicus* and *C. curvisetus* + *C. debilis* were observed during the
615 diatom bloom preceding the blooms of *P. globosa*. During blooming years of *P. seriata*
616 complex, *C. danicus*, *C. curvisetus* + *C. debilis* and the other diatoms consumed prematurely
617 the winter stocks of $\text{NO}_2^- + \text{NO}_3^-$ and Si(OH)_4 , so that the $\text{NO}_2^- + \text{NO}_3^-$ stock left over after the
618 decline of this first diatom bloom was too low to support high intensity *P. globosa* blooms. In
619 spite of this, since *P. globosa* is an Haptophyte, it doesn't require Si(OH)_4 to grow, and it
620 managed to dominate the phytoplankton community when diatoms became limited by
621 Si(OH)_4 . It was the dominant species until temperature and PAR increased and became less
622 favorable to its growth. *P. globosa* and *P. seriata* complex did not occupy the same realized
623 ecological niches. Since *P. seriata* complex tolerates higher temperature and PAR than *P.*
624 *globosa*, it took advantage of this situation and started to bloom. In spite of their low
625 intensity, *P. globosa* blooms continued to consume the $\text{NO}_2^- + \text{NO}_3^-$ stock. Consequently,
626 $\text{NO}_2^- + \text{NO}_3^-$ concentrations left over during the decline of *P. globosa* blooms were lower than
627 during years without blooms of *P. seriata* complex. Different forms of nitrogen as well as

628 changes in the concentration of nitrogen and Si(OH)_4 can modify the competitive
629 relationships between diatoms species (e.g. van Ruth et al., 2012). In this study, nitrogen and
630 Si(OH)_4 appear to influence the ability of *P. seriata* complex to outcompete the other diatoms
631 present. When *P. seriata* complex bloomed, the Si(OH)_4 concentrations were still relatively
632 low, but since *P. seriata* complex is able to maintain viable cells under silicate limited
633 conditions and is a good competitor under low Si:N ratios (Fehling et al., 2004), it still
634 managed to grow. These blooms of *P. seriata* complex were accompanied by the presence of
635 *G. delicatula* and *C. danicus* that interacted positively with *P. seriata* complex. The
636 development of *P. globosa* blooms after *Chaetoceros* spp. blooms is common in the eastern
637 English Channel and southern North Sea (Grattepanche et al., 2011; Rousseau et al., 2002). It
638 was suggested that the winter nutrient stocks determines the composition of the first diatom
639 bloom, and this composition in turn influences the intensity of the blooms of *P. globosa*
640 through competitive relationships for nutrients (Karasiewicz et al., 2018). The association of
641 low intensity *P. globosa* blooms with low $\text{NO}_2^- + \text{NO}_3^-$ concentrations is in accordance with
642 observations made in the southern North Sea suggesting that *P. globosa* bloom intensity is
643 controlled by nitrate left over after the decline of the first diatom bloom (Rousseau et al., 2002
644 and references therein). The presence of *P. seriata* complex during years of low intensity *P.*
645 *globosa* blooms has been previously reported in a study examining the conditions favoring *P.*
646 *globosa* blooms in the eastern English Channel (Karasiewicz et al., 2018) and in a study
647 describing *Pseudo-nitzschia* spp. diversity and toxicity in 2012 in the southern North Sea
648 (Delegrange et al., 2018). As in the present study, the bloom of *P. seriata* complex in 2012 in
649 the southern North Sea was associated with low $\text{NO}_2^- + \text{NO}_3^-$ and Si(OH)_4 concentrations
650 (Delegrange et al., 2018). Negative relationships between the occurrence of *P. seriata*
651 complex and nitrate concentrations have also been previously reported in the western English
652 Channel (Downes-Tettmar et al., 2013) and western Scottish waters (Fehling et al., 2006)

653 suggesting that *P. seriata* complex responds mainly to nitrate concentrations in surface waters
654 and is able to rapidly use nitrate when it becomes available. The capacity of *P. seriata*
655 complex to outcompete other diatoms when Si(OH)₄ concentrations are low is also in line
656 with competition experiments showing that in comparison with other diatoms, *Pseudo-*
657 *nitzschia pungens* (that belongs to the *Pseudo-nitzschia seriata* complex) is able to dominate
658 when Si:N ratios are relatively low (Sommer, 1994). The presence of *Leptocylindrus* species
659 and/or *Guinardia (Rhizosolenia) delicatula* at the same time as *Pseudo-nitzschia* spp. seems
660 to be recurrent. These taxa have been observed as associated with *Pseudo-nitzschia* spp. in the
661 Bay of Seine (eastern English Channel) (Thorel et al., 2017), in the western Scottish waters
662 (Fehling et al., 2006), on the Galician coasts (Casas et al., 1999), in the Adriatic Sea (Burić et
663 al., 2008; Totti et al., 2005) and in the Mediterranean Sea (Quiroga, 2006). This suggests
664 similarities in their environmental requirements. *G. delicatula* and *L. danicus* are often
665 observed together (Tomas, 1997). As *Pseudo-nitzschia* spp., *G. delicatula* and *L. danicus* are
666 lightly silicified chain forming diatoms (Conley et al., 1989; Davidson et al., 2012; Rousseau
667 et al., 2002; Schlüter et al., 2012). The presence of *G. delicatula* is also frequently observed
668 during periods of low Si(OH)₄ and nitrate concentrations since it generally appears after a
669 succession of blooms (Del Amo et al., 1997; Rousseau et al., 2002 and references therein). In
670 the present study, the OMI and WitOMI analyses showed that some similarities exist between
671 the realized ecological niches and sub-niches of *P. seriata* complex, *G. delicatula* and *L.*
672 *danicus*. They all have affinity for spring-summer conditions and tolerate higher temperature
673 and PAR than *P. globosa*. However, in spite of these similarities, *P. seriata* complex, *G.*
674 *delicatula* and *L. danicus* occupy different realized ecological niches and sub-niches. *G.*
675 *delicatula* and *L. danicus* occupy a more marginal niche and are less tolerant than *P. seriata*
676 complex.

677

678 **Conclusion**

679

680 This study showed that in the eastern English Channel and Southern North Sea, the
681 complexes *P. delicatissima* and *P. seriata* are typically present year round but their bloom
682 periods are different. This difference in seasonality can be explained by the two complexes
683 occupying different realized ecological niches. The necessity to investigate the surrounding
684 phytoplankton community in addition to the environmental conditions was also highlighted.
685 Indeed, niche shifts and biotic interactions played an important role in the control of the
686 blooms of *P. delicatissima* and *P. seriata* complexes. *P. globosa* interacted with the two
687 complexes but this interaction was positive with *P. delicatissima* complex and negative with
688 *P. seriata* complex. Other diatoms also influenced the blooms of *P. seriata* complex. The
689 positive interaction found between *P. delicatissima* complex and *P. globosa* is in accordance
690 with previous observations reporting cells of the *P. delicatissima* complex associated with *P.*
691 *globosa* colonies. However, the underlying processes explaining this association are currently
692 unresolved. Laboratory experiments with co-cultures of *P. globosa* and *Pseudo-nitzschia* may
693 help to better understand their relationships. The production of domoic acid associated with
694 the presence of the two *Pseudo-nitzschia* complexes and its potential impacts for the food web
695 have also not received adequate attention in this area.

696

697 **Authors' contribution**

698 EH: conceptualization, data analyses and wrote completely the first draft. All other authors
699 read, commented and approved the final version of the manuscript. EB and DS: identification
700 and count of phytoplankton species from the SNO-SOMLIT monitoring program. UK and FS:
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702

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 720

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Figure captions:

Fig. 1: Map of the eastern English Channel and southern North Sea showing the location of sampling stations (black points)

Fig. 2: Observation frequencies of A) *Pseudo-nitzschia delicatissima* complex (Pdel), B) *Pseudo-nitzschia seriata* (Pser) complex, C) all the other diatoms and D) *Phaeocystis globosa* (Phaeo) during the months of the year. Gray bars correspond to observation frequencies of the considered taxa whatever its abundance. Black bars correspond to observation frequencies of the bloom periods i.e. abundances $\geq 3 \times 10^5$ cells L⁻¹ for *P. delicatissima* complex and $\geq 10^5$ cells L⁻¹ for *P. seriata* complex, all the other diatoms and *P. globosa*

Fig. 3: Outlying Mean Index (OMI) analysis showing the projection of the environmental parameters (in black) and species niche marginality (in blue) along the two OMI axes (OMI1 and OMI2) delimiting the OMI plane. Dots are sampling units colored according to the seasons of the year. T = seawater temperature, par = photosynthetically active radiation, S = salinity, NH₄ = ammonium concentration, SIOH₄ = silicate concentration, PO₄ = phosphate concentration, Eps = turbulent dissipation rate, Pdel = *Pseudo-nitzschia delicatissima* complex, Pser = *Pseudo-nitzschia seriata* complex, Phaeo = *Phaeocystis globosa*, Gdel = *Guinardia delicatula*, Ldan = *Leptocylindrus danicus*, Ccur = *Chaetoceros curvisetus* + *Chaetoceros debilis* and Cdan = *Chaetoceros danicus*

Fig. 4: Boxplots representing A & B) seawater temperature (in °C), C & D) salinity, D & E) photosynthetically active radiation (PAR in einstein m⁻² day⁻¹), F & G) turbulent dissipation rate (epsilon in 10⁻³ W m⁻³), I & J) ammonium concentration (NH₄⁺ in μM), K & L) nitrite + nitrate concentration (NO₂⁻ + NO₃⁻ in μM), M & N) silicate concentration (Si(OH)₄ in μM) and phosphate concentration (PO₄³⁻ in μM) during the low abundance (LA) and bloom periods of *Pseudo-nitzschia delicatissima* complex (Pdel, left panel) and *Pseudo-nitzschia seriata* complex (Pser, right panel). P values are Mann-Whitney U test results. ns = non significant

Fig. 5: Within Outlying Mean Index (WitOMI) analysis. Sub-niches of A & B) *Pseudo-nitzschia delicatissima* complex and C & D) *Pseudo-nitzschia seriata* complex during their respective low abundance (left panel) and high abundance (right panel) periods. Grey polygon = environmental space, orange polygon = realized ecological niche (RN), blue polygon = sub-environmental space, yellow polygon = potential sub-niche (PS), green polygon = realized ecological sub-niche (RS). Red dot = WitOMI_G

Fig. 6: Interaction network based on a Poisson lognormal model (PLN) showing the taxa interacting with *Pseudo-nitzschia delicatissima* complex (Pdel) and *Pseudo-nitzschia seriata* complex (Pser). Phaeo = *Phaeocystis globosa*, Gdel = *Guinardia delicatula*, Ldan = *Leptocylindrus danicus*, Ccur = *Chaetoceros curvisetus* + *Chaetoceros debilis* and Cdan = *Chaetoceros danicus*. Solid lines represent positive interactions while dashed lines represent negative interactions. Lines width is proportional to interaction strength

Fig. 7: Abundance of *Phaeocystis globosa* (Phaeo) during low abundance (LA) and bloom periods of A) *Pseudo-nitzschia delicatissima* complex and B) *Pseudo-nitzschia seriata* complex. Abundance of C) *Guinardia delicatula* (Gdel), D) *Chaetoceros curvisetus* + *Chaetoceros debilis* (Ccur), E) *Chaetoceros danicus* (Cdan) and F) *Leptocylindrus danicus* (Ldan) during years of low intensity *Phaeocystis globosa* blooms without bloom of *Pseudo-*

nitzschia seriata complex (LA Phaeo) vs. years when the blooms of *Pseudo-nitzschia seriata* complex accompanied the low intensity *Phaeocystis globosa* blooms (LA Phaeo + Pser bloom). Observation frequencies of G) Gdel, H) Ccur, I) Cdan and J) Ldan during the months of the year. Gray bars correspond to observation frequencies of the considered taxa whatever its abundance. Black bars correspond to observation frequencies of high abundances

Fig. 8: Sub-niches of *Phaeocystis globosa* during the low abundance A) and B) bloom periods of *Pseudo-nitzschia delicatissima* complex. Sub-niches of C & D) *Phaeocystis globosa*, E & F) *Guinardia delicatula* (Gdel), G & H) *Chaetoceros curvisetus* + *Chaetoceros debilis* (Ccur), J & J) *Chaetoceros danicus* (Cdan) and K & L) *Leptocylindrus danicus* (Ldan) during the low abundance (left panel) and bloom (right panel) periods of *Pseudo-nitzschia seriata* complex. Grey polygon = environmental space, orange polygon = realized ecological niche (RN), blue polygon = sub-environmental space, yellow polygon = potential sub-niche (PS), green polygon = realized ecological sub-niche (RS). Red dot = WitOMI_G

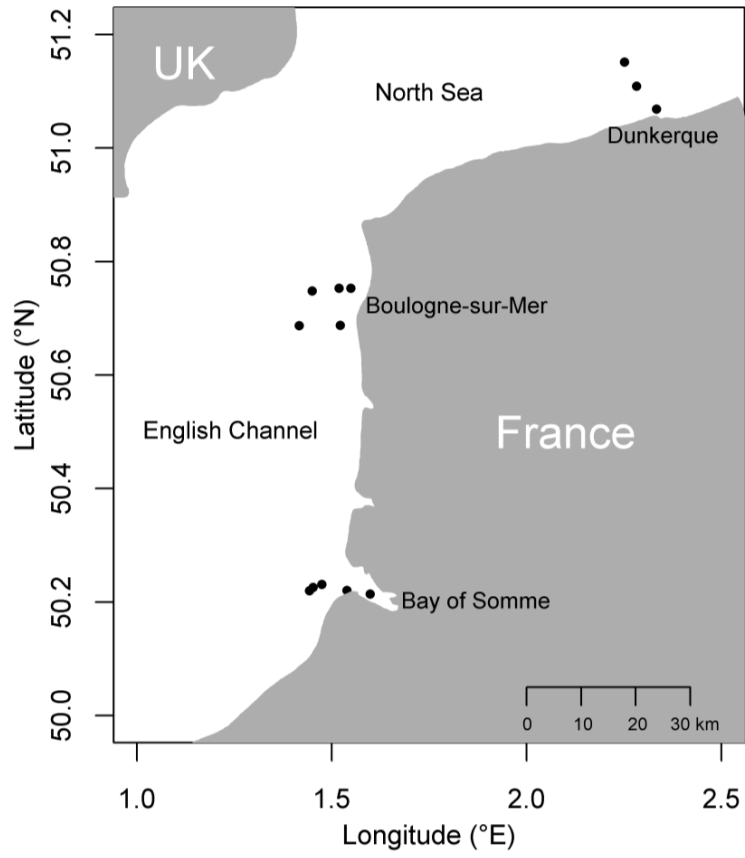


Fig. 1: Map of the eastern English Channel and southern North Sea showing the location of sampling stations (black points)

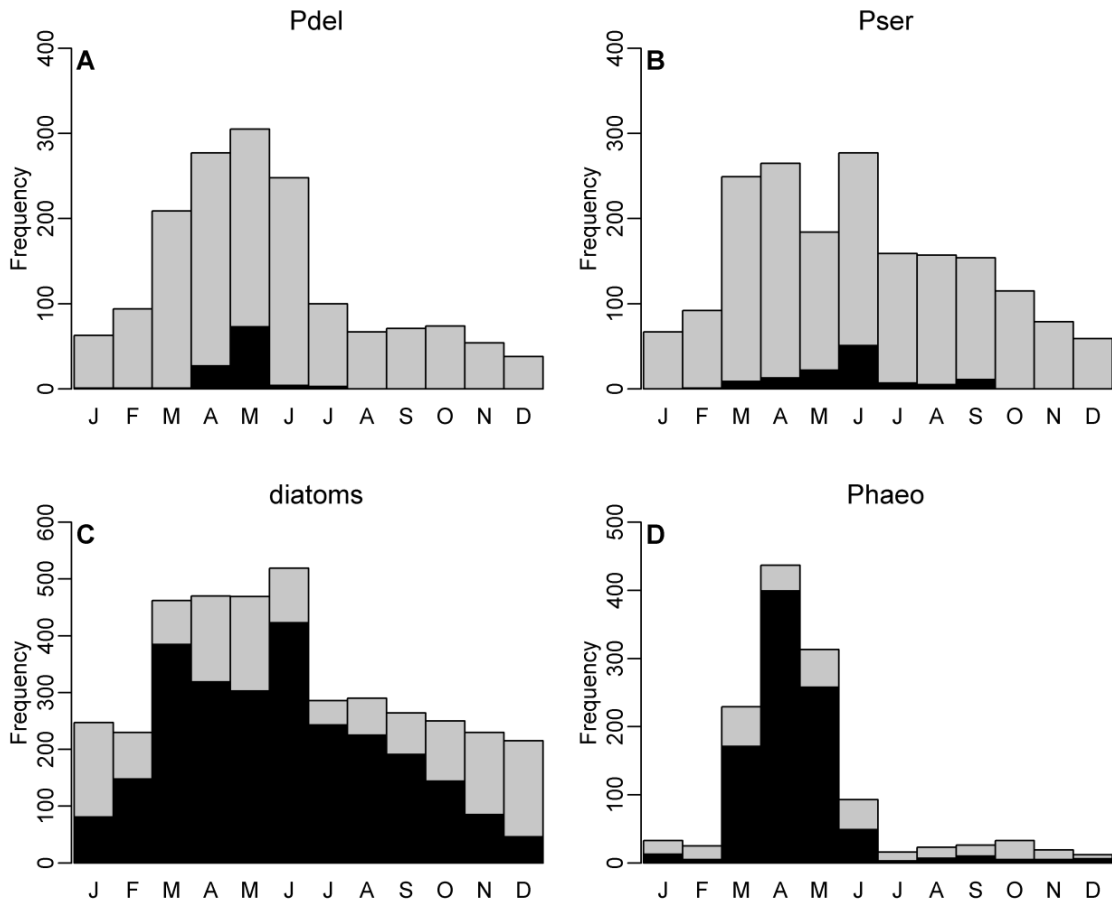


Fig. 2: Observation frequencies of A) *Pseudo-nitzschia delicatissima* complex (Pdel), B) *Pseudo-nitzschia seriata* (Pser) complex, C) all the other diatoms and D) *Phaeocystis globosa* (Phaeo) during the months of the year. Gray bars correspond to observation frequencies of the considered taxa whatever its abundance. Black bars correspond to observation frequencies of the bloom periods i.e. abundances $\geq 3 \times 10^5$ cells L^{-1} for *P. delicatissima* complex and $\geq 10^5$ cells L^{-1} for *P. seriata* complex, all the other diatoms and *P. globosa*

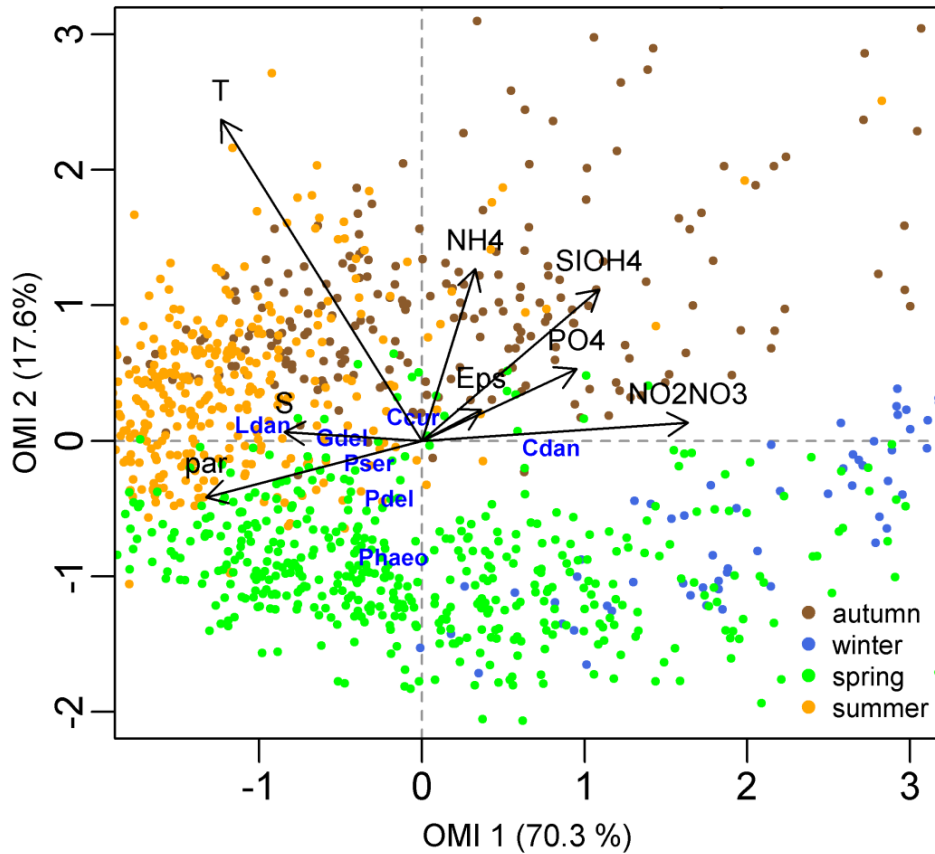


Fig. 3: Outlying Mean Index (OMI) analysis showing the projection of the environmental parameters (in black) and species niche marginality (in blue) along the two OMI axes (OMI1 and OMI2) delimiting the OMI plane. Dots are sampling units colored according to the seasons of the year. T = seawater temperature, par = photosynthetically active radiation, S = salinity, NH₄ = ammonium concentration, SIOH₄ = silicate concentration, PO₄ = phosphate concentration, Eps = turbulent dissipation rate, Pdel = *Pseudo-nitzschia delicatissima* complex, Pser = *Pseudo-nitzschia seriata* complex, Phaeo = *Phaeocystis globosa*, Gdel = *Guinardia delicatula*, Ldan = *Leptocylindrus danicus*, Ccur = *Chaetoceros curvisetus* + *Chaetoceros debilis* and Cdan = *Chaetoceros danicus*

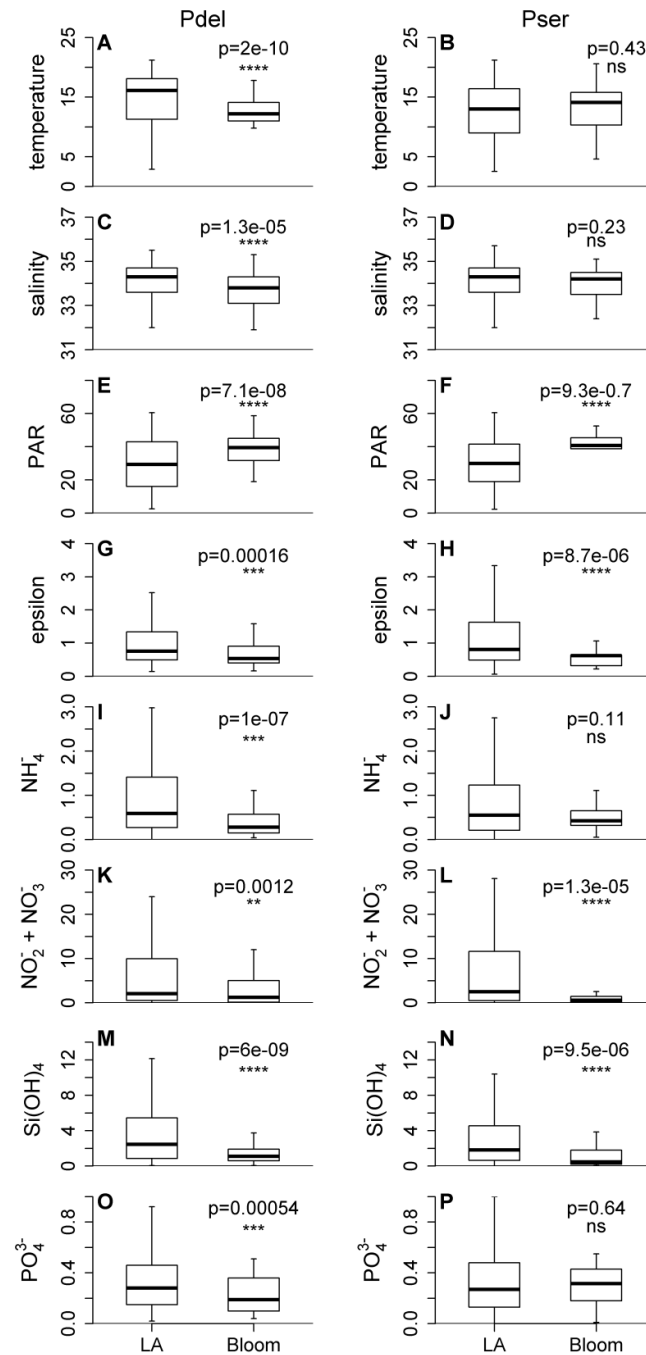


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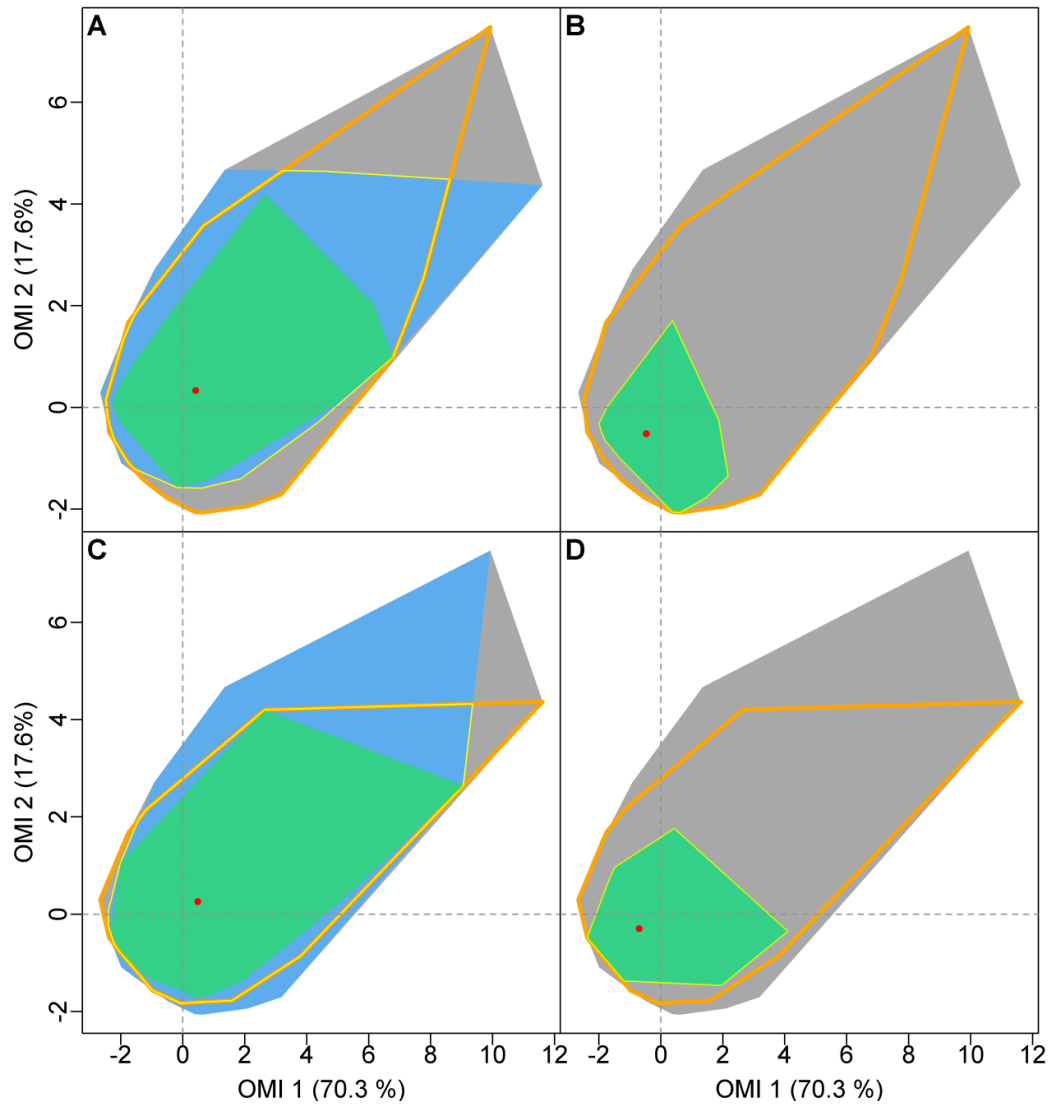


Fig. 5: Within Outlying Mean Index (WitOMI) analysis. sub-niches of A & B *Pseudo-nitzschia delicatissima* complex and C & D *Pseudo-nitzschia seriata* complex during their respective low abundance (left panel) and bloom (right panel) periods. Grey polygon = environmental space, orange polygon = realized ecological niche (RN), blue polygon = sub-environmental space, yellow polygon = potential sub-niche (PS), green polygon = realized ecological sub-niche (RS). Red dot = WitOMI_G

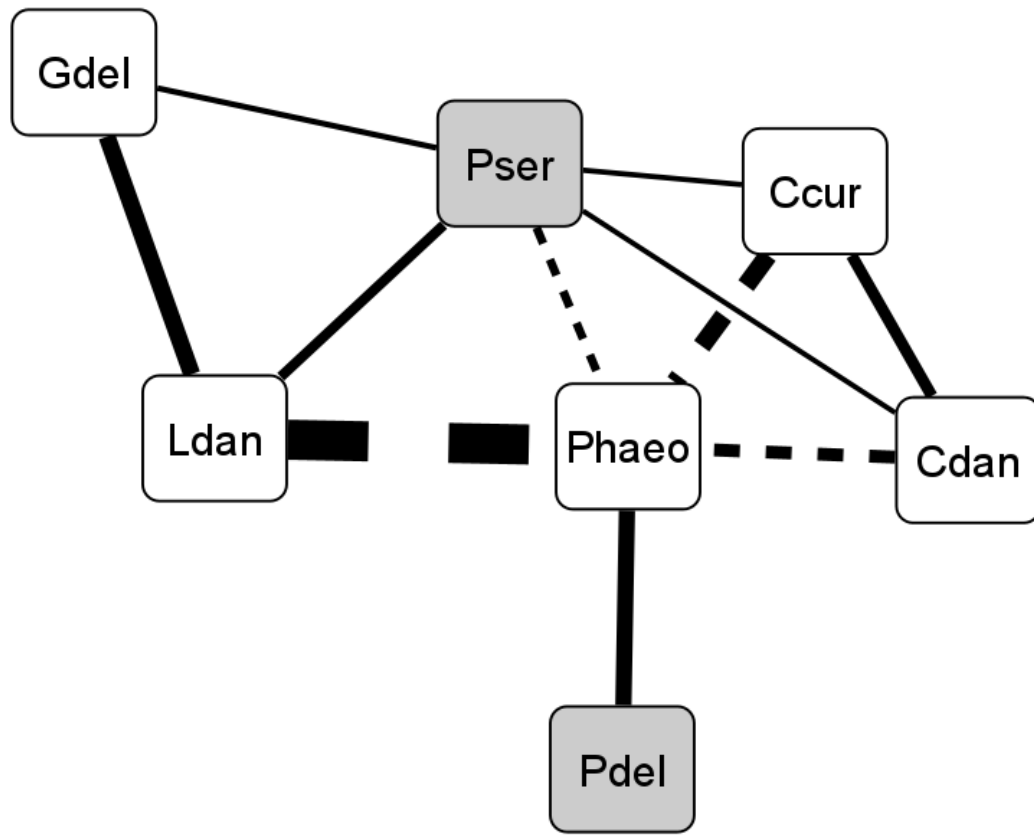


Fig. 6: Interaction network based on a Poisson lognormal model (PLN) showing the taxa interacting with *Pseudo-nitzschia delicatissima* complex (Pdel) and *Pseudo-nitzschia seriata* complex (Pser). Phaeo = *Phaeocystis globosa*, Gdel = *Guinardia delicatula*, Ldan = *Leptocylindrus danicus*, Ccur = *Chaetoceros curvisetus* + *Chaetoceros debilis* and Cdan = *Chaetoceros danicus*. Solid lines represent positive interactions while dashed lines represent negative interactions. Lines width is proportional to interaction strength

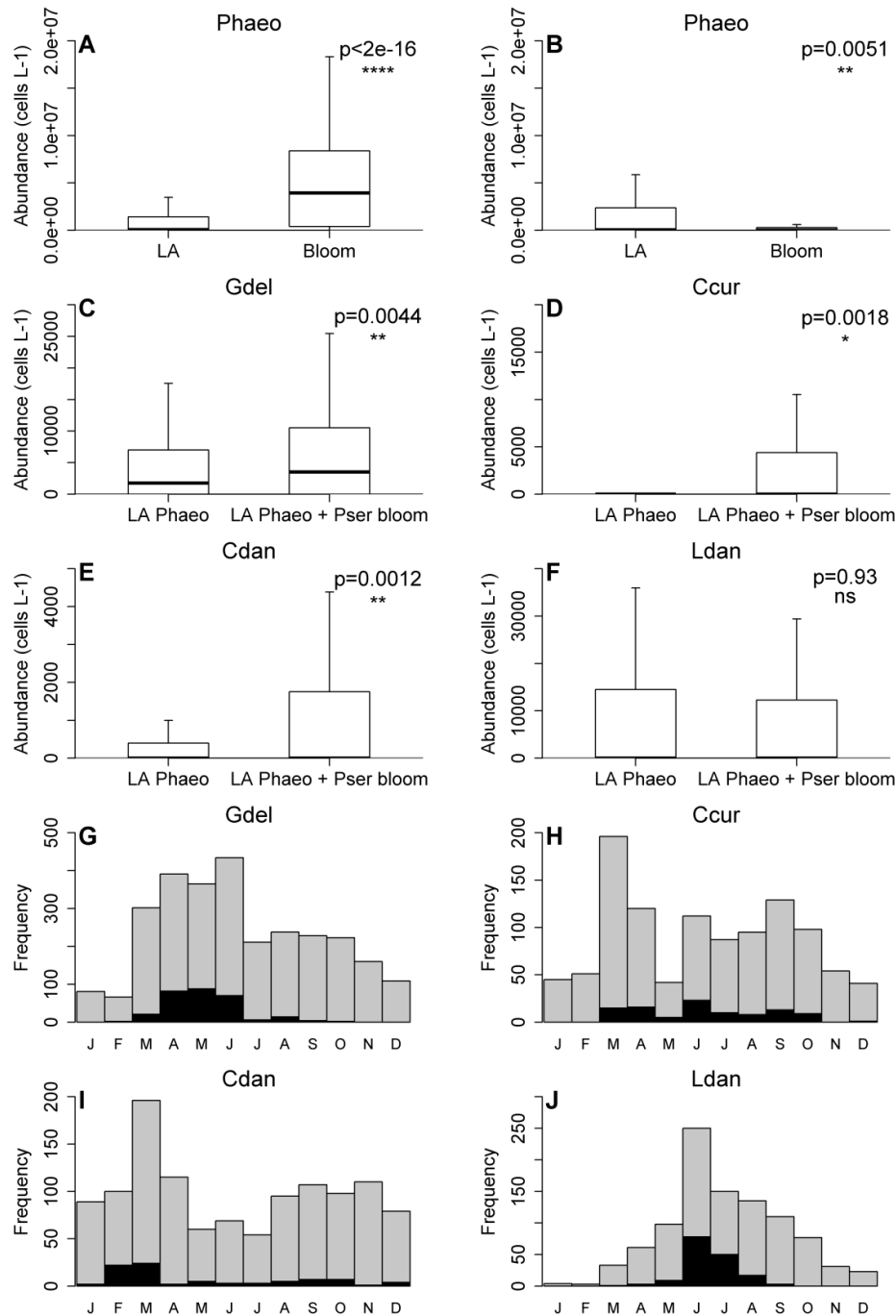


Fig. 7: Abundance of *Phaeocystis globosa* (Phaeo) during low abundance (LA) and bloom periods of A) *Pseudo-nitzschia delicatissima* complex and B) *Pseudo-nitzschia seriata* complex. Abundance of C) *Guinardia delicatula* (Gdel), D) *Chaetoceros curvisetus* + *Chaetoceros debilis* (Ccur), E) *Chaetoceros danicus* (Cdan) and F) *Leptocylindrus danicus* (Ldan) during years of low intensity *Phaeocystis globosa* blooms without bloom of *Pseudo-nitzschia seriata* complex (LA Phaeo) vs. years when the blooms of *Pseudo-nitzschia seriata* complex accompanied the low intensity *Phaeocystis globosa* blooms (LA Phaeo + Pser bloom). Observation frequencies of G) Gdel, H) Ccur, I) Cdan and J) Ldan during the months of the year. Gray bars correspond to observation frequencies of the considered taxa whatever its abundance. Black bars correspond to observation frequencies of high abundances

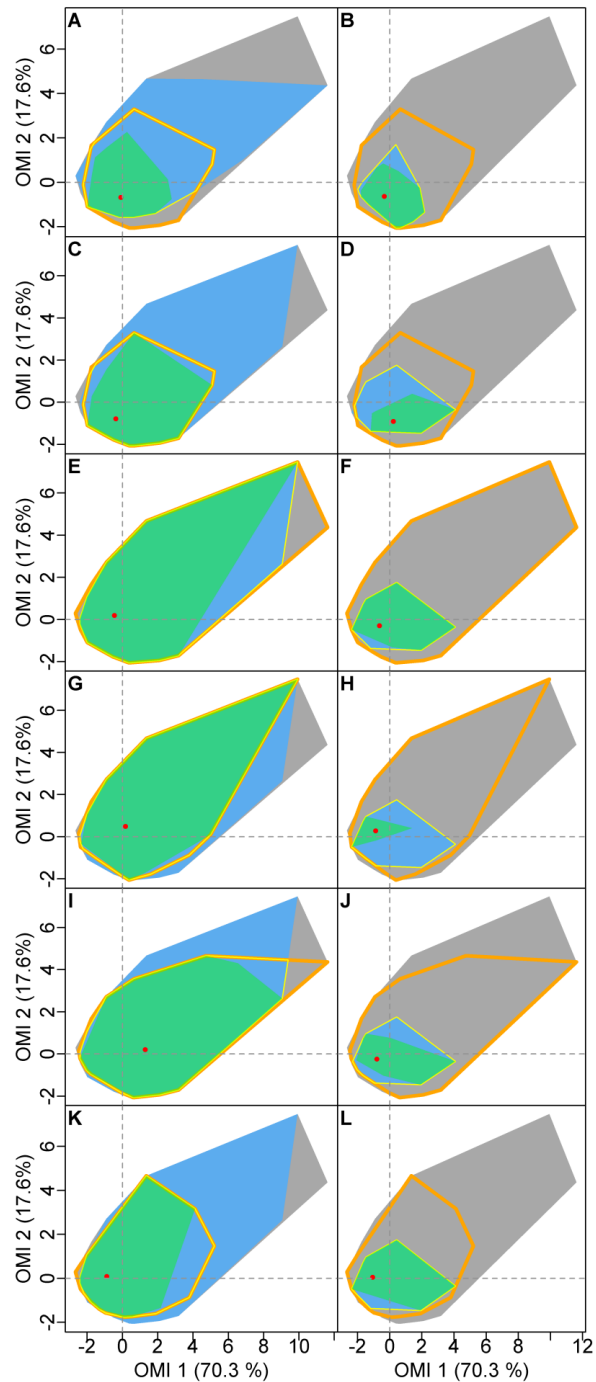


Fig. 8: Sub-niches of *Phaeocystis globosa* during the low abundance A) and B) bloom periods of *Pseudo-nitzschia delicatissima* complex. Sub-niches of C & D) *Phaeocystis globosa*, E & F) *Guinardia delicatula* (Gdel), G & H) *Chaetoceros curvisetus* + *Chaetoceros debilis* (Ccur), J & J) *Chaetoceros danicus* (Cdan) and K & L) *Leptocylindrus danicus* (Ldan) during the low abundance (left panel) and bloom (right panel) periods of *Pseudo-nitzschia seriata* complex. Grey polygon = environmental space, orange polygon = realized ecological niche (RN), blue polygon = sub-environmental space, yellow polygon = potential sub-niche (PS), green polygon = realized ecological sub-niche (RS). Red dot = WitOMI_G

Table 1: Realized ecological niche and sub-niches parameters of *Pseudo-nitzschia delicatissima* complex (Pdel), *Pseudo-nitzschia seriata* complex (Pser), *Phaeocystis globosa* (Phaeo), *Guinardia delicatula* (Gdel), *Leptocylindrus danicus* (Ldan), *Chaetoceros curvisetus* + *Chaetoceros debilis* (Ccur) and *Chaetoceros danicus* (Cdan)

Taxa	Niche parameters (OMI analysis)		Sub-niche parameters (WitOMI analysis)				
	Marginality	Tolerance	Periods	Marginality (WitOMIG)	Tolerance (Tol _{WitOMIG})	Biological constraints	% PS occupied
Pdel	0.23	0.95	Pdel LA Pdel blooms	0.35 0.84	4.19 0.25	37 0	63 100
Pser	0.15	1.81	Pser LA Pser blooms	0.33 0.95	4.30 0.77	10 0	90 100
Phaeo	0.77	0.37	Pdel LA Pdel blooms Pser LA Pser blooms	0.58 0.92 0.76 1.21	0.84 0.21 0.40 0.11	51 13 26 44	49 87 74 56
Gdel	0.25	1.78	Pser LA Pser blooms	0.27 0.88	1.12 0.69	18 7	82 93
Ldan	1.08	0.99	Pser LA Pser blooms	0.85 1.72	0.84 0.87	21 5	79 95
Ccur	0.12	0.79	Pser LA Pser blooms	0.41 1.95	2.27 0.13	0 81	100 19
Cdan	0.68	3.24	Pser LA Pser blooms	1.77 1.16	3.83 0.67	10 27	90 73

OMI = Outlying Mean Index, WitOMI = Within Outlying Mean Indexes, Biological constraints = part of the potential sub-niche volume that could not be occupied due to biological constraints, % PS occupied = percentage of the potential sub-niche volume occupied by the realized ecological sub-niche, Pdel LA = low abundance periods of *Pseudo-nitzschia delicatissima* complex, Pdel blooms = blooms of *Pseudo-nitzschia delicatissima* complex, Pser LA = low abundance periods of *Pseudo-nitzschia seriata* complex, Pser blooms = blooms of *Pseudo-nitzschia seriata* complex

Table 2: Overlap percentages between the realized ecological niche, potential sub-niche and realized ecological sub-niches of *Pseudo-nitzschia delicatissima* complex, *Pseudo-nitzschia seriata* complex and their interacting taxa

	Pdel RN	Pser RN		Pdel PS		Pser PS			Pdel RS		Pser RS	
				LA	Blooms	LA	Blooms		LA	Blooms	LA	Blooms
Phaeo RN	56	52	Phaeo PS	52	96	57	100	Phaeo RS	38	80	43	87
Gdel RN		100	Gdel PS			100	100	Gdel RS			53	87
Ldan RN		55	Ldan PS			60	100	Ldan RS			37	86
Ccur RN		62	Ccur PS			68	100	Ccur RS			77	17
Cdan RN		73	Cdan PS			96	100	Cdan RS			99	60

RN = realized ecological niche, PS = potential sub-niche, RS = realized ecological sub-niche, Pdel= *Pseudo-nitzschia delicatissima* complex, Pser = *Pseudo-nitzschia seriata* complex, Phaeo = *Phaeocystis globosa*, Gdel = *Guinardia delicatula*, Ldan = *Leptocylindrus danicus*, Ccur = *Chaetoceros curvisetus* + *Chaetoceros debilis*, Cdan = *Chaetoceros danicus*, LA = low abundance period

Supplementary materials

On the conditions promoting *Pseudo-nitzschia* spp. blooms in the eastern English Channel and southern North Sea

Emilie Houliez, François G. Schmitt, Elsa Breton, Dimitra-Ioli Skouroliakou, Urania Christaki

Supplementary Materials and Methods

Realized ecological niche and sub-niches

Hutchinson's niche concept

Hutchinson (1957) describes the species ecological niche as a n-dimensional hypervolume delimited by a set of favorable environmental conditions (biotic and abiotic) under which a species can maintain nonnegative growth rates, survive and reproduce. Each of these conditions is referred to as a "niche axis". Distinction is made between the fundamental and realized components of the species ecological niche. The fundamental ecological niche corresponds to the hypervolume of conditions under which a species can sustain nonnegative growth rates and persist in the absence of immigration and competition. This definition has been updated to also assume the absence of different other biotic interactions including the absence of predation, pathogens, facultative mutualists or facilitations (Bruno et al., 2003; Carscadden et al., 2020; Holt, 2009). A species may fail to occupy a portion of its fundamental ecological niche because these conditions (or resources) do not exist at a specific time in the study area or because interspecific biotic interactions have excluded the species from locations where those conditions occur (Carscadden et al., 2020). The hypervolume of conditions actually occupied by the species is thus called the realized ecological niche. It is a subset of its fundamental ecological niche that corresponds to the conditions under which the species can persist and be observed given the presence of other species competing for the same resources and/or in the presence of other kinds of biotic interactions (predation, presence of pathogens or mutualistic and facilitation relationships) (Brun et al., 2015).

Outlying Mean Index (OMI) and Within Outlying mean Index (WitOMI)

The OMI and WitOMI analyses were both based on a principal component analysis (PCA). They were performed with two data frames. The first data frame contained the environmental variables and included water temperature, salinity, nutrient concentrations, turbulence and PAR data. The second data frame contained fourth root transformed phytoplankton species abundances. The fourth root transformation down-weight the importance of the highly abundant species for a proper characterization of the realized

ecological niches of not only the less common (“mid-range”) species but also of the rarer species (Clarke and Warwick, 2001).

The OMI analysis is a multivariate analysis defining the realized ecological niche (RN) of each taxa within a given environmental space. It characterizes the RN of each taxa with three parameters: marginality, tolerance and residual tolerance. The OMI analysis is accompanied by a Monte Carlo permutation test defining the statistical significance of the marginality. It compares the observed marginality to the distribution of 1000 random marginality values obtained by permutations under the null hypothesis that the taxonomic unit is indifferent to its environment. If the observed marginality is greater or lower than marginality values obtained by permutations, the null hypothesis can be rejected. The OMI analysis provides several graphics. The first graphic represents the projection of the environmental variables on the OMI axes. The second graphic represents the projection of the marginality of each taxa on the OMI axes. The third graphic represents with polygons the RN of each taxa within the environmental space (previously called “realized environmental space” in Karasiewicz et al., 2017) on the plane defined by the OMI axes (Fig. S1).

The WitOMI analysis uses the environmental space delimited by the OMI axes as a reference. It decomposes the RN of each taxa into realized ecological sub-niches (RS) corresponding to a given time period of interest or a sub-location within the study area. For each subset studied, two additional marginalities, two tolerance indexes and two residual tolerances are provided. Associated Monte Carlo permutation tests define the significance of WitOMI_G and WitOMI_{GK} (see Karasiewicz et al., 2017 for more details).

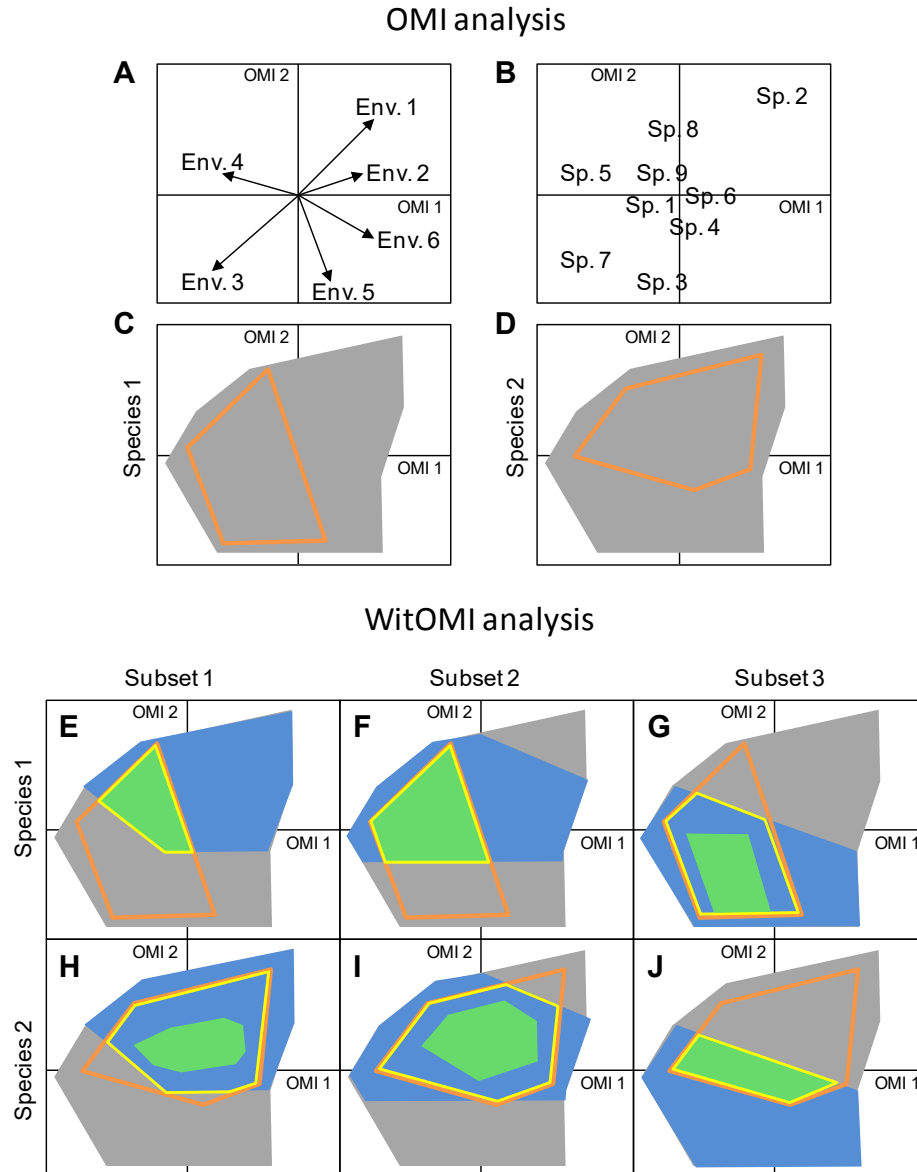


Fig. S1: Schematic representation of the OMI and WitOMI analyses results. (A) Projection of the environmental variables on the first two axes of the OMI (OMI 1 and OMI2). Env. = environmental variable. (B) Projection of the niche position of each taxa on the first two axes of the OMI. Sp. = species. Realized ecological niches of species 1 (C) and species 2 (D). Realized ecological sub-niches of species 1 (E, F, G) and species 2 (H, I, J) in the first subset (first column), second subset (second column) and third subset (third column). Grey polygon = environmental space. Orange polygon = realized ecological niche. Blue polygon = sub-environmental space. Yellow polygon = potential sub-niche. Green polygon = realized ecological sub-niche. In G, H, I, the realized ecological sub-niche of species 1 and 2 is smaller than their respective potential sub-niche due to biotic interactions. The blue area inside the yellow polygon and around the green polygon represents thus the biological constraints. In E, F, J, the size of the realized ecological sub-niche of species 1 and species 2 is not reduced by biotic interactions and they occupy the totality of their potential sub-niche. Their realized ecological sub-niche has thus the same size as their potential sub-niche. Figure adapted from Karasiewicz et al. (2017) and Karasiewicz et al., 2020).

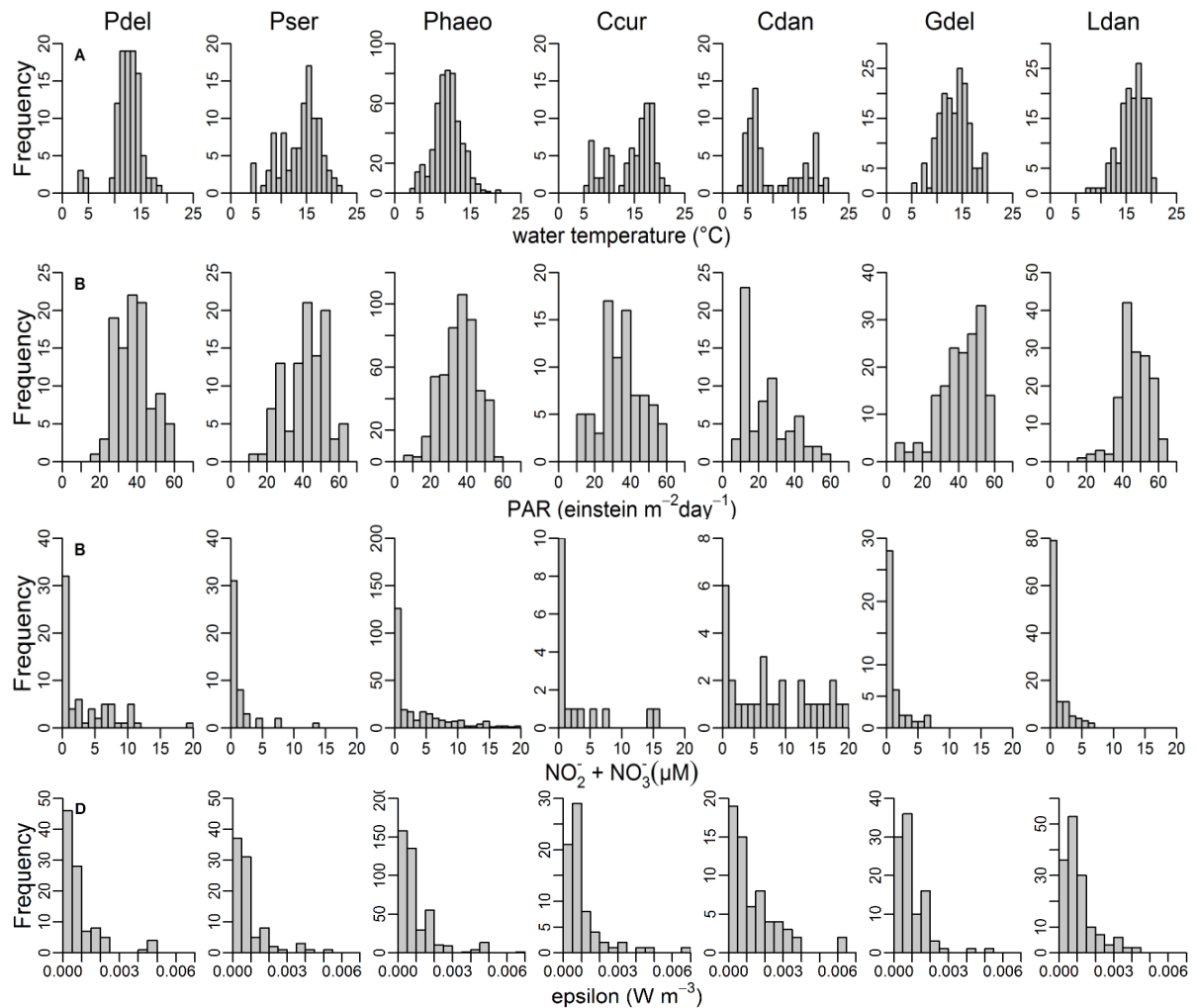


Figure S2: Observation frequencies of high abundances of *Pseudo-nitzschia delicatissima* complex (Pdel), *Pseudo-nitzschia seriata* complex (Pser), *Phaeocystis globosa* (Phaeo), *Chaetoceros curvisetus* (Ccur), *Chaetoceros danicus* (Cdan), *Guinardia delicatula* (Gdel) and *Leptocylindrus danicus* (Ldan) against water temperature (A), PAR (B), NO₂⁻ + NO₃⁻ concentrations (C) and turbulence (D)

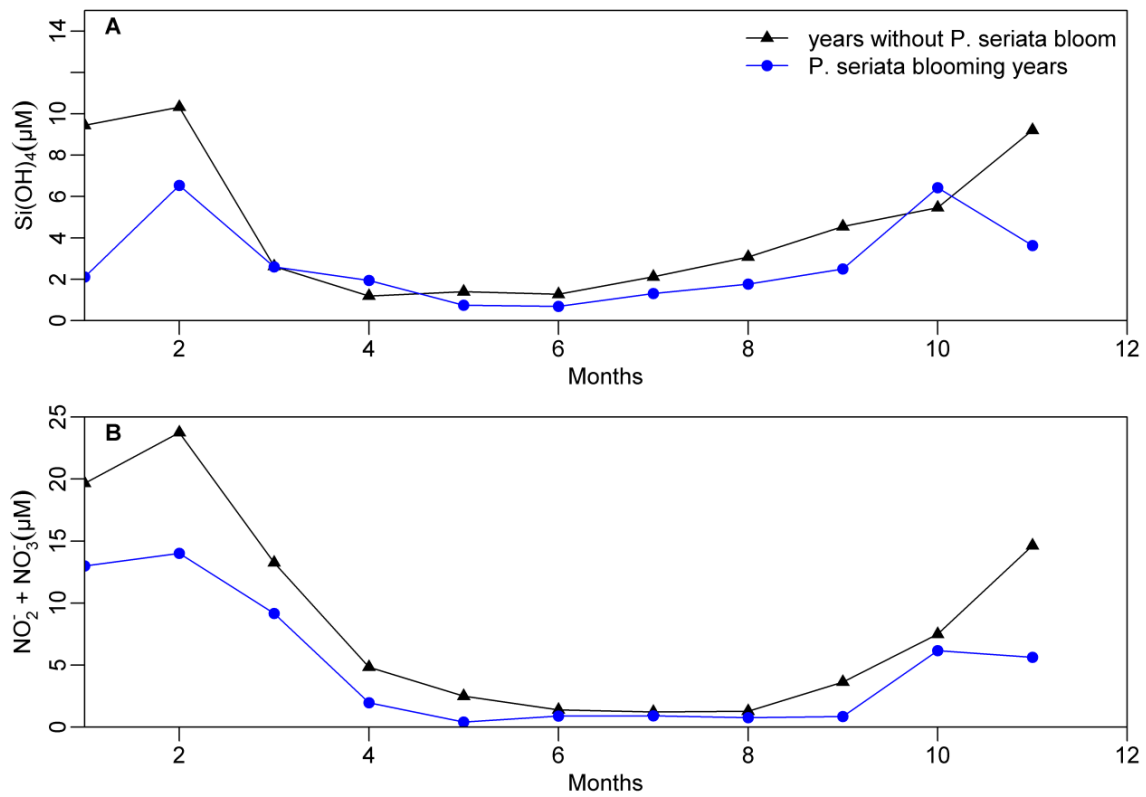


Fig. S3: A) silicate and B) nitrate + nitrite concentrations during *Pseudo-nitzschia seriata* blooming years (blue curve) and years without *P. seriata* bloom (black curve)

Table S1: SIMPER analysis identifying the main taxa contributing to the dissimilarity between the phytoplankton community present during blooming years and years without bloom of *Pseudo-nitzschia delicatissima* complex (Pdel) and *Pseudo-nitzschia seriata* complex (Pser)

Pdel: blooming years vs. years without bloom

Average dissimilarity = 68.05

Taxa	Class	Code	Years without bloom	Blooming years	Average dissimilarity	Contribution %
			Average abundance (cells L ⁻¹)	Average abundance (cells L ⁻¹)		
<i>Phaeocystis globosa</i>	Haptophyceae	Phaeo	3x10 ⁵	9x10 ⁵	9.22x10 ⁻²	13.55
<i>Asterionellopsis glacialis</i>	Bacillariophyceae	Agla	2x10 ³	8x10 ³	2.98x10 ⁻²	4.37
<i>Guinardia delicatula</i>	Bacillariophyceae	Gdel	1x10 ⁴	1x10 ³	2.85x10 ⁻²	4.18
<i>Rhizosolenia hebetata</i>	Bacillariophyceae	Rheb	4x10 ³	8x10 ³	2.63x10 ⁻²	3.87
<i>Pseudo-nitzschia seriata</i> complex	Bacillariophyceae	Pser	418	2x10 ³	2.29x10 ⁻²	3.35
<i>Chaetoceros</i> spp.	Bacillariophyceae	Cspp	556	155	1.91x10 ⁻²	2.80
<i>Paralia sulcata</i>	Bacillariophyceae	Psul	734	2x10 ³	1.90x10 ⁻²	2.79
<i>Chaetoceros socialis</i> + <i>Chaetoceros socialis</i> f. <i>radians</i>	Bacillariophyceae	Csoc	208	204	1.88x10 ⁻²	2.76
<i>Eucampia striata</i>	Bacillariophyceae	Gstri	567	91	1.85x10 ⁻²	2.72
<i>Synedra nitzschoides</i> f. <i>nitzschoides</i>	Bacillariophyceae	Tnit	502	191	1.78x10 ⁻²	2.62
<i>Lauderia</i> spp. + <i>Schroederella</i> spp.	Bacillariophyceae	Lann	263	119	1.70x10 ⁻²	2.50
<i>Skeletonema</i> spp.	Bacillariophyceae	Ske	53	222	1.69x10 ⁻²	2.48
<i>Thalassiosira</i> spp.	Bacillariophyceae	Thsp	153	265	1.68x10 ⁻²	2.47
<i>Thalassiosira gravida</i>	Bacillariophyceae	Tgra	59	231	1.58x10 ⁻²	2.32
<i>Nitzschia longissima</i>	Bacillariophyceae	Nlon	237	534	1.58x10 ⁻²	2.32
<i>Raphoneis</i> spp. + <i>Delphineis</i>	Bacillariophyceae	Rha	253	374	1.56x10 ⁻²	2.30

spp.							
<i>Chaetoceros curvisetus</i> + <i>Chaetoceros debilis</i>	Bacillariophyceae	Ccur	75	64	1.42×10^{-2}	2.08	
<i>Ditylum brightwellii</i>	Bacillariophyceae	Dbri	1	214	1.26×10^{-2}	1.86	
<i>Rhizosolenia setigera</i>	Bacillariophyceae	Rset	131	10	1.18×10^{-2}	1.72	
<i>Rhizosolenia fragilissima</i> f. <i>fragilissima</i>	Bacillariophyceae	Dfra	8	46	1.16×10^{-2}	1.71	
<i>Guinardia</i> spp.	Bacillariophyceae	Gui	63	1	1.11×10^{-2}	1.64	
<i>Cerataulina</i>	Bacillariophyceae	Cer	90	0	1.08×10^{-2}	1.59	
spp.							
<i>Navicula</i> spp. + <i>Fallacia</i> spp. + <i>Haslea</i> spp.	Bacillariophyceae	Navi	35	53	1.08×10^{-2}	1.58	
<i>Leptocylindrus danicus</i>	Bacillariophyceae	Ldan	1	36	1.08×10^{-2}	1.58	

Pser: blooming years vs. years without bloom

Average dissimilarity = 71.00

Taxa	Class	Code	Years without bloom	Blooming years	Average dissimilarity	Contribution %
			Average abundance (cells L ⁻¹)	Average abundance (cells L ⁻¹)		
<i>Phaeocystis globosa</i>	Haptophyceae	Phaeo	3×10^4	8×10^4	7.22×10^{-2}	10.16
<i>Asterionellopsis glacialis</i>	Bacillariophyceae	Agla	3×10^3	5×10^3	3.25×10^{-2}	4.58
<i>Pseudo-nitzschia delicatissima</i> complex	Bacillariophyceae	Pdel	2×10^3	2×10^3	3.07×10^{-2}	4.32
<i>Guinardia delicatula</i>	Bacillariophyceae	Gdel	4×10^3	6×10^3	2.89×10^{-2}	4.07
<i>Rhizosolenia hebetata</i>	Bacillariophyceae	Rheb	4×10^3	4×10^3	2.87×10^{-2}	4.05
<i>Chaetoceros socialis</i> + <i>Chaetoceros socialis</i> f. <i>radians</i>	Bacillariophyceae	Csoc	348	603	2.46×10^{-2}	3.46
<i>Eucampia striata</i>	Bacillariophyceae	Gstri	1×10^3	755	2.42×10^{-2}	3.41
<i>Chaetoceros</i>	Bacillariophyceae	Cspp	654	885	2.33×10^{-2}	3.29

<i>spp.</i>						
<i>Leptocylindrus danicus</i>	Bacillariophyceae	Ldan	151	177	2.14×10^{-2}	3.02
<i>Paralia sulcata</i>	Bacillariophyceae	Psul	1×10^3	2×10^3	1.92×10^{-2}	2.70
<i>Synedra nitzschioides f. nitzschioides</i>	Bacillariophyceae	Tnit	282	230	1.80×10^{-2}	2.54
<i>Thalassiosira spp.</i>	Bacillariophyceae	Thsp	149	267	1.79×10^{-2}	2.52
<i>Skeletonema spp.</i>	Bacillariophyceae	Ske	141	63	1.71×10^{-2}	2.40
<i>Nitzschia longissima</i>	Bacillariophyceae	Nlon	301	622	1.67×10^{-2}	2.36
<i>Raphoneis spp. + Delphineis spp.</i>	Bacillariophyceae	Rha	154	381	1.64×10^{-2}	2.31
<i>Chaetoceros curvisetus + Chaetoceros debilis</i>	Bacillariophyceae	Ccur	71	99	1.61×10^{-2}	2.26
<i>Lauderia spp. + Schroederella spp.</i>	Bacillariophyceae	Lann	56	151	1.57×10^{-2}	2.21
<i>Thalassiosira gravida</i>	Bacillariophyceae	Tgra	66	113	1.53×10^{-2}	2.15
<i>Leptocylindrus spp.</i>	Bacillariophyceae	Lep	4	101	1.43×10^{-2}	2.02
<i>Cerataulina spp.</i>	Bacillariophyceae	Cer	21	52	1.32×10^{-2}	1.86
<i>Guinardia spp.</i>	Bacillariophyceae	Gui	25	35	1.31×10^{-2}	1.85
<i>Navicula spp. + Fallacia spp. + Haslea spp.</i>	Bacillariophyceae	Navi	107	103	1.26×10^{-2}	1.78
<i>Rhizosolenia setigera</i>	Bacillariophyceae	Rset	37	59	1.26×10^{-2}	1.77

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