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Realized niche analysis of phytoplankton communities involving HAB: *Phaeocystis* spp. as a case study

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Abstract :

The link between harmful algal blooms, phytoplankton community dynamics and global environmental change is not well understood. To tackle this challenging question, a new method was used to reveal how phytoplankton communities responded to environmental change with the occurrence of an harmful algae, using the coastal waters of the eastern English Channel as a case study. The great interannual variability in the magnitude and intensity of *Phaeocystis* spp. blooms, along with diatoms, compared to the ongoing gradual decrease in anthropogenic nutrient concentration and rebalancing of nutrient ratios; suggests that other factors, such as competition for resources, may also play an important role. A realized niche approach was used with the Outlying Mean Index analysis and the dynamics of the species' realized subniches were estimated using the Within Outlying Mean Indexes calculations under low (L) and high (H) contrasting *Phaeocystis* spp. abundance. The Within Outlying Mean Indexes allows the decomposition of the realized niche into realized subniches, found within the subset of habitat conditions and constrained by a subset of a biotic factor. The two contrasting scenarios were characterized by significantly different subsets of environmental conditions and diatom species (BV-step analysis), and different seasonality in salinity, turbidity, and nutrients. The subset L environmental conditions were potentially favorable for *Phaeocystis* spp. but it suffered from competitive exclusion by key diatom species such as *Skeletonema* spp., *Thalassiosira gravida*, *Thalassionema nitzschioides* and the *Pseudo-nitzschia seriata* complex. Accordingly, these diatoms species occupied 81% of *Phaeocystis* spp.'s existing fundamental subniche. In contrast, the greater number of diatoms, correlated with the community trend, within subset H exerted a weaker biological constraint and favored *Phaeocystis* spp. realized subniche expansion. In conclusion, the results strongly suggest that both abiotic and biotic interactions should be considered to understand *Phaeocystis* spp. blooms with greater consideration of the preceding diatoms. HABs needs must therefore be studied as part of the total phytoplankton community.

Highlights

► *Phaeocystis* spp.' has a smaller realized subniche in events of low abundance blooms. ► *Phaeocystis* spp.' small realized subniche is due to an important biological constraint. ► Higher diversity of the diatom community as a weaker biological constraint. ► The preceding key diatom community seemed controlled by the environment. ► The preceding diatom competitive ability controls the bloom of *Phaeocystis* spp.

Keywords : Harmful algae bloom, WitOMI, Subniche, Diatoms, Biotic interaction, Eastern English Channel

1. Introduction:

The unprecedented rate of global environmental change (Drijfhout et al., 2015), is potentially increasing the spread and impact of harmful algae blooms (HAB) worldwide (Fu et al., 2012; Hallegraeff, 2010; Wells et al., 2015). Attempts to link HABs or undesirable species and anthropogenically-altered environments have often been unclear and contradictory (Anderson, 2009; Davidson et al., 2012; Gowen et al., 2012; Wells et al., 2015). Moreover, the role of biotic interactions in shaping HABs, such as competition for resources, is still poorly studied. Yet, the variability in the magnitude and duration of reported HAB blooms emphasizes the idea that other factors, aside from abiotic variables, play an important role in driving HABs (Bianchi et al., 2000; Borkman et al., 2016; Yin, 2003). Previous research strategies, methods and hypotheses of how environmental pressures mechanistically affect HAB species (Wells et al., 2015) have used modelling (Passy et al., 2016), experiments (Veldhuis et al., 1991), *in situ* measurements (Houliet et al., 2013), and remote sensing imaging (Kurekin et al., 2014) to explore these links. The former studies were based on the hypothesis that HABs could be predicted from environmental variables only.

Hutchinson's niche concept (1991) allows studying the link between global changes and the phytoplankton community in relation to HABs. Among several multivariate methods available for niche analysis (Braak, 1986; *e.g.* Calenge et al., 2005; Ter Braak, 1987), Hernández-Fariñas et al. (2015) used the niche through using the Outlying Mean Index (OMI) (Dolédec et al., 2000), assessing the niche of 35 phytoplankton species, including diatoms, along the French coast. Recently, the Within Outlying Mean Index calculations (WitOMI; Karasiewicz et al., 2017) was developed as a refinement of the OMI analysis and provides estimations of niche shift and/or conservatism of a community under different subsets of habitat conditions (temporal and/or spatial). The WitOMI calculates the species' realized subniche dynamics (species' niche occupation within subset habitat conditions) within the realized niche resulting from the OMI analysis after selecting subsets. The realized subniches are, therefore, comparable under the same environmental gradients. The decomposition of the niche into subniches, with the WitOMI allows one to observe and measure the part of the existing fundamental subniche that is not used by the species despite being available. The unused part of the existing fundamental subniche is considered as the subset's biological constraints (*e.g.* competition, predation, mutualism, dispersal and colonization) (Karasiewicz et al., 2017). This last method deciphers the effect of selected environmental factors from unknown biotic factors and is fully adapted to explore the phytoplankton community response to climate change along with HABs.

29 The study aim was to use the Within Outlying Mean Indexes calculations (Karasiewicz et al., 2017) to understand
30 how the environment influences harmful species realized niches. The method should reveal how the phytoplankton
31 community before and/or during HABs, can influence the harmful algae realized niche. The estimation of the
32 biological constraint should reveal the impact of biological processes on the HAB, providing further insight into
33 the implications on potential competitors. This new method of HAB investigation will be tested with the case
34 study of *Phaeocystis* spp. in the Eastern English Channel. In these waters, the bulk of biomass is represented by
35 the diatom community and *Phaeocystis* spp. (Grattepanche et al., 2011). The genus *Phaeocystis* is one of the
36 most globally distributed marine haptophytes (Lancelot et al., 1994). Although non-toxic (Cadée and Hegeman,
37 2002), it is classified as undesirable because three species (*i.e.* *P. globosa*, *P. pouchetii* and *P. antarctica*) are
38 capable of forming large gelatinous colonies, creating impressive foam layers along beaches during bloom collapse
39 (Blauw et al., 2010). This accumulation of excessive organic matter could result in alteration both in the benthic
40 and pelagic compartments. More recently, Breton et al. (2017) suggested with a trait-based approach, that
41 competitive exclusion prevails during *Phaeocystis* spp.'s blooms. The diatoms' taxonomic level, however, was not
42 fine enough to reveal the potential resource competitors of *Phaeocystis* spp. (Breton et al. 2017). To date, no
43 studies have considered the competitive interactions as a possible HAB control.

44 2. Methods:

45 2.1. Data set:

46 The data were collected as part of the French REPHY-IFREMER (Réseau d'Observation de Surveillance du
47 Phytoplankton et des Phycotoxines) and the Regional Nutrients Monitoring Network (SRN, 2017). Water
48 samples were acquired from a fortnightly to monthly frequency from 1996-2012, between 0 and 1 m depth,
49 along with physical measurements, and were completed with chemical analyses. The environmental variables
50 measured included, seawater temperature ($^{\circ}\text{C}$), salinity (measured using the Practical Salinity Scale), turbidity
51 (NTU), inorganic nutrient concentrations (dissolved inorganic nitrogen, silicate, and phosphate in $\mu\text{mol.L}^{-1}$) and
52 photosynthetically active radiation (PAR, W.m^{-2}). Note that PAR is the cumulative sum over the five days
53 preceding phytoplankton sampling. In regards to the quantitative phytoplankton analyses, samples were fixed with
54 Lugol's solution and counted according to the Utermöhl method (Utermöhl, 1958). Organisms were identified to
55 the lowest possible taxonomic level. Taxa that are difficult to discriminate with optical microscopy were grouped
56 (*e.g.* *Pseudo-nitzschia seriata* complex). In addition, experts identified and counted (cells/L) phytoplankton taxa
57 bigger than 20 μm , and also smaller size species that create chain structures or form a colonies (*e.g.* *Phaeocystis*
58 *spp.*). Further details about sampling and processing of phytoplankton and physicochemical parameters are

59 available in the literature (Lefebvre et al., 2011; Belin and Neaud-Masson, 2012). Unlike Hernández-Fariñas et
60 al. (2015), this study focused on the coastal station 1 of Boulogne-sur-mer because the waters are known for
61 recurrent *Phaeocystis* blooms (Figure 1).

62 2.2. Subsets creation:

63 In order to understand the impact of biotic and abiotic factors on the *Phaeocystis* spp. realized niche, two data
64 subsets that gathered years of high and low *Phaeocystis* spp. annual mean abundance events were created (named
65 hereafter subset H and L for high and low respectively). The years of *Phaeocystis* spp. intermediate mean annual
66 abundance were left-out for the rest of the study. This methodology enables deciphering the conditions and the
67 potential resources used by the diatom community and *Phaeocystis* spp. in contrasted events. Each subset has its
68 own environmental habitat conditions and phytoplankton communities (n=53 sampling units for subset L and
69 n=71 for subset H). Additionally, a non-random BV-STEP analysis (Clarke et al., 2001) with 10000 reiterations
70 was performed to extract the species that correlated most with the entire diatom community during subsets L and
71 H. The diatom species best representing the community under both subsets were used to describe the succession
72 under each subset. Herein, the study does not try to determine the conditions under which the ecosystem is
73 dominated by *Phaeocystis* spp. (e.g., the ratio between diatoms species biomass and *Phaeocystis* spp.) as in
74 (Lefebvre et al., 2011), but rather the habitat conditions within which the species can reach high abundances.
75 The environmental habitat conditions are the environmental conditions measured at time t of the sampling.

76 2.3. Niche and subniche analysis:

77 An OMI analysis (Dolédec et al., 2000) was performed including all the sampling dates in order to reflect most of
78 the environmental variability within the OMI axes. Only the significant species identified by the BV step analysis
79 above were used further in the study. The subniche estimations within the subsets H and L (see below) were
80 calculated with the Within Outlying Mean Indexes calculations (WitOMI) (Karasiewicz et al., 2017). Species'
81 subniche dynamics were estimated by comparing the subniche parameters (marginality and tolerance) to the
82 origin G (WitOMI G and Tol), which is the representation of a uniformly distributed theoretical species that
83 would occur at all available habitat conditions (*i.e.* ubiquitous) (Dolédec et al., 2000). Second, the estimation
84 of the subniche parameters to the subset origin G_K (WitOMI G_K and Tol), which is the representation of the
85 subset mean habitat conditions used by a hypothetical species (Karasiewicz et al., 2017), revealing the species
86 distribution within the subset habitat conditions. The statistical significance of marginality was tested using a
87 Monte Carlo permutation procedure (Manly, 1997) with 10000 permutations.

88 *2.4. Biological constraint:*

89 The existing fundamental subniche, \mathbf{S}_P , corresponds to the realized niche, \mathbf{N}_R , which is reduced abiotically by the
 90 subset habitat conditions, \mathbf{K} . Therefore, \mathbf{S}_P includes the subset biotic factor, \mathbf{S}_B , reducing \mathbf{S}_P into the realized
 91 subniche, \mathbf{S}_R (Figure 2). In summary:

$$\mathbf{S}_R \cup \mathbf{S}_B = \mathbf{S}_P = \mathbf{K} \cap \mathbf{N}_R$$

92 \mathbf{S}_B represents negative biological interactions (e.g., predation, competition, parasitism, etc.), the species dispersal
 93 limitation (*i.e.*, lack of time for migration), or occupancy by another species (Peterson, 2011) (Figure 2). The \mathbf{S}_B
 94 unit is in percentage of \mathbf{S}_P , and represents the biological constraint exerted on the subniche. Therefore, under
 95 the subset habitat conditions H or L, the biological constraint exerted on *Phaeocystis* spp. subniches, and the
 96 effect of some other unselected abiotic variables, can be discussed.

97 All analyses and graphical representations were performed using R software (R Core Team, 2013) with the packages
 98 “ade4” (Dray and Dufour, 2007) and “subniche” available for free on the CRAN repository www.cran.r-project.org
 99 and on GitHub www.github.com/KarasiewiczStephane/WitOMI.

100 **3. Results:**

101 *3.1. Subset habitat conditions:*

102 Low (<50 cells.L⁻¹) and high (>160 cells.L⁻¹) mean annual *Phaeocystis* spp. abundance events (named hereafter
 103 subset L and H) occurred on four and five occasions, respectively (L: 1996, 1997, 2000, and 2005, H: 2001, 2004,
 104 and 2010-2012; Figure 3). The non-random BV-step analysis revealed that 7 diatom species were correlated to
 105 the overall pattern of the community (Gud, Gus, Par, Pss, Ske, Thn, and Thg, with $\rho=0.97$; See code in Table
 106 1) in subset L, while 9 diatom species were relevant in subset H (Cha, Dyt, Gud, Gus, Led, Nit, Par, Ske, and
 107 Thn, with $\rho=0.96$). Five species, Gud, Gus, Par, Ske, Thn were common to the two contrasting environmental
 108 conditions, leading to 11 species of interest for the rest of the study. Two species occurred only in subset L (Thg
 109 and Pss) and four species occurred only in subset H (Dit, Cha, Led, and Nit)(See code in Table 1).

110 Although the two subsets showed similar increases in temperature and PAR, varying from 5.8 to 19.9°C and from
 111 8.5 to 6.1 10³.W.m² respectively (Figure 4A and 4B), the two subsets differed in turbidity, salinity and nutrient
 112 concentrations. Accordingly, subset L displayed higher turbidity but lower salinity than subset H (Figure 4C-D).
 113 Moreover, nutrient concentrations were significantly lower and decreased faster in subset H than in subset L

114 during late winter-early spring (Figure 2 E-H). Phosphate concentration had an overall higher concentration in
115 subset L (Figures 4F). The sum of nitrate and nitrite concentrations was similar in January and December in
116 both subset L and H, but the overall concentration was higher in subset L than in H (Figure 4G). The seasonal
117 trends of silicate concentration were similar in the two subsets, although it decreased faster the rest of the year
118 in subset H than in subset L (Figure 4H). The DIN:PO₄ followed a unimodal trend with a maximum in April
119 (DIN:PO₄: 88) and March (DIN:PO₄: 70) for subset L and H respectively (Figure 4I). The DIN:Si was higher in
120 subset L than in H with a maximum in April (DIN:Si: 59) and March (DIN:Si: 30) respectively.

121 3.2. Niche analysis (OMI):

122 The OMI analysis revealed that the realized niches of the 11 diatom species of interest, depicted by the BV-step
123 analysis, and of *Phaeocystis* spp. were significant (Table 1). The first two axis of the OMI analysis represented
124 87% of projected inertia, of which OMI1 represented 74%. OMI1 was mainly explained by nutrients and turbidity
125 (Figure 5C), while OMI2 was mainly explained by PAR, temperature and salinity. The seasonal effect can be
126 visualized by the environmental trajectories of subset H and L (Figure 5B). The environmental trajectory of
127 subset H had a higher position and better resembled a full cycle than subset L, which went “back on track”
128 (Figure 5B).

129 The species Ske, Thg and Thn were typical of late winter-early spring and were, as expected, low on the OMI1
130 axis (on the left side, Figure 5A). Their niches were explained by high nutrient concentrations and turbidity, but
131 low temperature, PAR and salinity. These three species have the highest niche breadth (Tol Ske: 3.52, Thn: 3.35,
132 Thg: 3.14) (Table1). The niches of Dit and Cha, Par and Nit were related to intermediate values of OMI1 (lower
133 values of nutrients and turbidity; Figure 5A). They distributed themselves vertically along the OMI2 by their
134 preferences for higher salinity, temperature and PAR (higher temperature and PAR downwards ; Figure 5A). The
135 species with the lowest marginality were Nit and Par (OMI: 0.06 and 0.09 for Nit and Par respectively). The
136 niches of Pss, Gud, Gus and Phae were characterized by low nutrient concentrations and turbidity but differed
137 from each other in salinity, PAR and temperature affinities. The niche position of Phae was characterized by
138 relatively high salinity but intermediate temperature and PAR, while the other species were rather defined by
139 lower salinity and higher temperature and PAR along the OMI2 axis. The niche of Led, which is typically a
140 summer diatom species was characterized by the lowest nutrient concentrations and turbidity, high salinity, and
141 intermediate temperature and PAR. As a result, Led was characterized by a high marginality (OMI: 2.231).

142 3.3. Subniche calculations (WitOMI):

143 *Phaeocystis* spp.'s subniche position significantly shifted and the subniche breadth expanded from subset L to
144 H (WitOMIG: 2.64 and 2.11; Tol: 0.59 and 0.64 for subset L and H respectively) (Figure 6). The marginality
145 (WitOMIG) showed that *Phaeocystis* spp. used a more common habitat in subset H than in L. This suggest
146 that the species has a preference for the environmental habitat conditions found in subset H over L (Figure 6).
147 Considering the subsets independently, the subniche position from the average subset habitat conditions, G_K was
148 much greater in subset L than H (WitOMIG $_K$: 3.24 and 0.59 from subset L and H respectively). In subset H,
149 *Phaeocystis* spp. used a more common habitat favoring its development (237 cells.L⁻¹, Table 2). On the other
150 hand, the habitat preference in subset L, which is atypical for the environmental habitat conditions within subset
151 L, is not well suited for *Phaeocystis* spp. (29 cells.L⁻¹, Table 2).

152 The different WitOMIG values for the common diatom species (Ske, Thn, Par, Gud, Gus), expressed a change
153 in subniche position (Table 2). Meanwhile, the tolerance from G increased for Gud, while it decreased for Gus,
154 Par, Ske and Thn (Table 2). The low WitOMIG $_K$ values in the environmental habitat conditions subset H were
155 preferable for Thn, Par, Gud, and Gus, compared to the environmental habitat conditions of subset L. The
156 opposite pattern occurred for Ske (Table 2). Ske had a preference for the environmental habitat conditions of
157 subset L, as the species' mean abundance, which was higher in subset L, likely reflected the species' habitat
158 suitability. The species Par and Thn had higher mean abundance in subset H, while Gud and Gus had stable
159 mean abundances (Table 2).

160 Concerning species that occurred in only one subset, Pss had one of the lowest marginalities and intermediate
161 tolerance (WitOMIG $_K$: 0.28 and Tol: 1.69), while Thg had an intermediate marginality with high tolerance
162 (WitOMIG $_K$:0.78 and Tol: 4.13), in subset L (Table 2). In subset H, marginality of low for Nit and Cha,
163 intermediate for Dit, and high for Led (WitOMIG $_K$: 0.14, 0.31, 0.58, and 2.05 for Nit, Cha, Dit and Led
164 respectively) (Table 2). Led had an intermediate tolerance while Nit, Cha and Dit had high tolerance in subset H
165 (Table 2).

166 The environmental habitat conditions of subset H enhanced the common diatoms and *Phaeocystis* spp. mean
167 abundances, as these species had greater affinities for these environmental habitat conditions. *Skeletonema*
168 spp. still managed to reach high abundance despite the increase of the relevant number of diatom species. *Skeletonema*
169 spp. was the only common diatom species that was disfavored by the change in environmental habitat conditions,
170 and better responded to the environmental habitat conditions of subset L.

171 A succession of the diatom subniche was observed in the two habitat subsets (Figure 7A and B), as expected
172 from the niche analysis (Figure 4). In subset L, the late-winter early-spring species (Ske, Thn and Thg) were

173 blooming first because they were affiliated with winter like conditions, *i.e.*, low temperature, PAR and salinity,
174 but high nutrient concentrations and turbidity. Then, Par was second to bloom followed by Pss, Gud, Gus and
175 Phae (Figure 7A). The first species to appear in subset H was Ske, while Thn, Cha, Dit, Par and Nit appeared
176 second. The succession of diatoms continued with Gud, Gus and Led (Figure 7B). In subset H, the subniche
177 of *Phaeocystis* spp. overlapped most of the diatoms' niche positions, but still managed to have a larger niche
178 breadth than in subset L. The diatom-*Phaeocystis* spp. succession did not take place in subset H, as *Phaeocystis*
179 spp. managed to develop concomitantly with the diatom species (Figure 7B).

180 3.4. Biological reducing factor:

181 The *Phaeocystis* spp. subniche in subset L occupied 19% of the existing fundamental subniche. Therefore the
182 biological constraint was equal to 81% (Figure 8B). The subniche occupation of *Phaeocystis* spp. in subset H
183 within the existing fundamental subniche, represented 75%. Thus, the subniche biological constraint was of 25%
184 of the existing fundamental subniche (Figure 8A). Therefore, the unused available conditions of the *Phaeocystis*
185 spp. existing fundamental subniche could have been occupied by competing diatom species, such as *Skeletonema*
186 spp., *Thalassionema nitzschioides*, *Thalassiosira gravida* and the *Pseudo-nitzschia seriata* complex (Figure 8A).
187 By contrast, the *Phaeocystis* spp. subniche overlapped the diatoms subniches in subset H (Figure 8B).

188 4. Discussion:

189 The OMI analysis revealed that nutrient concentrations (phosphate, silicate, nitrite, nitrate and ammonia)
190 played an important role in the diatom community distribution (Figure 5A and 5C). Subset H was characterized
191 both by lower nutrient concentrations and faster decreases than subset L (Figure 5E to 5H). Therefore, the
192 realized subniche of *Phaeocystis* spp. shifted in position and increased in breadth from subset L to H. The
193 diatom-*Phaeocystis* spp. succession occurred in subset L but not in H. The realized subniche of *Phaeocystis*
194 spp. seemed to be more controlled by the preceding diatom community than by the subset habitat conditions.
195 Furthermore, the increasing diversity in the diatom community exerted a lower biological constraint on the
196 *Phaeocystis* spp. realized subniche. The results suggest that key diatom species possibly competed for resources
197 with *Phaeocystis* spp., especially nitrogen, phosphate and light, but only when silicate was available. Hereafter,
198 the robustness of actual hypotheses related to the *Phaeocystis* spp. niche in the literature are discussed followed
199 by an examination of the possible biotic interaction explaining the fluctuating abundances.

200 4.1. *Phaeocystis* spp. hypotheses:

201 The “silicate-*Phaeocystis* hypothesis” (Lancelot et al., 1987; Reid et al., 1990) has historically been a major
202 explanation in the appearance of *Phaeocystis* spp. Environmental silicate concentration may determine the
203 duration and stability of the diatom community. For instance, in both subsets, *Phaeocystis* spp. started to bloom
204 when the silicate concentration dropped below $1.5 \mu\text{mol.L}^{-1}$. This threshold was reached later, in April, for subset
205 L compared to March for subset H (see Figure 4). The “silicate-*Phaeocystis* hypothesis” (Lancelot et al., 1987;
206 Reid et al., 1990) was only partly verified since *Phaeocystis* spp. was already present in the subset H in January,
207 but did not bloom until the silicate concentration dropped below the threshold. The lower inorganic P demand
208 of *Phaeocystis* spp. compared to diatoms (Riegman et al., 1992) could explain the constant presence in subset
209 H, characterized by low phosphate concentration from January to June. On the contrary, the “eutrophication
210 hypothesis,” which stipulates that *Phaeocystis* spp. abundance increases with higher N concentration, was not
211 validated in this study. Subset L was characterized by higher concentrations of nitrite, nitrate and ammonia
212 than subset H, leading to a dominance of diatom species, but resulting in lower abundances of *Phaeocystis* spp.
213 Furthermore, even though in subset L, leftover N from diatoms remained high, *Phaeocystis* did not bloom as
214 much. *Phaeocystis* spp. might use the excess N leftover by the diatoms for growth, but this does not seem to
215 determine the outbreaks of high abundance bloom events. The hypotheses linking *Phaeocystis* spp. appearances
216 to N:Si (Tett et al., 1993; Tett and Walne, 1995) and N:P (Riegman et al., 1992) better at predicted the HAB
217 timing. The maximum in N:Si or N:P corresponded to the start of *Phaeocystis* spp. bloom in both habitat subset
218 conditions.

219 According to Borkman et al. (2016), higher salinity characterized the year of high *P. pouchetii* abundance and
220 could also explain the years of high *Phaeocystis* spp. abundance. The higher salinity also reflected a lower
221 precipitation flow rate from rivers and wind turbulence which can also take part in the turbidity level. Subset H
222 was characterized by higher salinity and lower turbidity than subset L. Photosynthetically active radiation and
223 temperature exhibited similar variations throughout the season. Temperature did not seem to impact *Phaeocystis*
224 spp. appearance, because in subset H, *Phaeocystis* spp. was present in January, the coldest month (6.5°C). The
225 higher turbidity level in subset L suggested that the real amount of photosynthetically active radiation reaching
226 the community was less than in subset H. Despite these conditions, *Phaeocystis* spp. still appeared under low
227 PAR. This contradicts the hypothesis suggesting that *Phaeocystis* spp. dominates over diatoms when conditions
228 resemble early summer along the Dutch coast (Peperzak, 1993).

229 4.2. Biotic interactions:

230 The unused available conditions in the *Phaeocystis* spp. existing fundamental subniche is considered as the subset
231 biotic reducing factor. Infection by viruses can also cause the biological constraint. Experimental results showed
232 that *P. pouchetii* cell mortality rates by virus infection can reach 0.8 d^{-1} (Brussaard et al., 2005) but viruses do
233 not infect healthy colonies (Bratbak et al., 1998).

234 Predation is a possible biological interaction that can affect *Phaeocystis* spp. forms. The high plasticity of
235 *Phaeocystis* spp. capacity to change life forms, single-cells and colonies in response to grazing is well known
236 (Nejstgaard et al., 2007). Furthermore, it can respond to different chemical cues released by different consumer
237 species (Wang et al., 2015). For instance, *Phaeocystis* spp. is capable of switching from single-cells to colonies
238 when grazed by ciliates (Long et al., 2007). Oppositely, when confronted by grazing copepods, *Phaeocystis* spp.
239 can significantly decrease its colony numbers by 60–90% (Long et al., 2007). Grazer abundances and diversity
240 with different *Phaeocystis* spp. life forms should be considered in future studies, as they can directly impact
241 HABs. The information on the different life-forms of *Phaeocystis* spp. and potential consumers were not available
242 in the used dataset.

243 Another appropriate biological constraint in this study appeared to be competition, as the diatom community
244 directly competes for resources with *Phaeocystis* spp. From late-winter to summer, the succession in blooms
245 of the diatoms and their appearance depends on their preferences regarding environmental habitat conditions,
246 further driving *Phaeocystis* spp. appearances and blooms. For instance, *Skeletonema* spp., *T. nitzschioides*,
247 and *T. gravida* are known to be bloom forming species (Pratt, 1959; Smayda, 1958). They are considered as
248 winter diatoms, according to their respective niche positions with preference for high nutrient concentrations and
249 turbidity in association with low temperature, PAR and salinity. Their leading appearance, bloom magnitude
250 and persistence determined the composition of the following community. The growth of *Skeletonema* spp. is
251 known to be 25% faster when on sustained ammonia than on nitrate (Suksomjit et al., 2009; Tada et al., 2009).
252 In addition, *T. nitzschioides* has also been shown to grow faster in ammonia and nitrate enriched conditions
253 (Mochamadkar et al., 2013). In subset L, the high concentration of ammonia could have potentially helped
254 *Skeletonema* spp., *T. nitzschioides* and *T. gravida*, which are pioneers, to grow faster and bloom, establishing their
255 dominance in the community (Suksomjit et al., 2009; Tada et al., 2009) (Figure 5B). Furthermore, the *P. seriata*
256 complex occurrence is also known to be nitrogen-limited, and more than capable of using ammonia (Fehling et
257 al., 2006). The growth of *Phaeocystis* spp. is faster on ammonia than on nitrate (Tungaraza et al., 2003), but
258 seemed to be out-competed by the diatoms in these environmental habitat conditions. Other factors, such as
259 silicate and phosphate were not limiting and favored the diatoms. The establishment of the diatom species, with
260 a preference for ammonia, possibly out-competed *Phaeocystis* spp., until the concentration of silicate became

261 limiting, succeeded by the *Phaeocystis* spp. bloom.

262 In subset H, *Phaeocystis* spp. managed to flourish despite the presence of the five same species (*Skeletonema* spp.,
263 *T. nitzschioides*, *Paralia sulcata*, *Guinardia delicatula* and *Guinardia striata*) and four other species (*Chaetoceros*
264 *danicus*, *Ditylum brightwellii*, *Nitzschia longissima* and *Leptocylindrus danicus*). The lower concentration of
265 phosphate favored *Phaeocystis* spp.'s presence over diatoms likely through *Phaeocystis* spp.'s capacity to store
266 phosphate within its colony matrix (Schoemann et al., 2001; Veldhuis et al., 1991) coupled with its lower P demand
267 (Riegman et al., 1992). Moreover, the strong competitive ability of *Phaeocystis* spp. to obtain nitrogen (Riegman,
268 1995), along with lower concentration of silicate, inhibited the diatom community from blooming as much as in
269 subset L. Silicate limitation is thought to have resulted in an increase in magnitude and continuity *Phaeocystis*
270 spp. blooms (Cadée and Hegeman, 1986; Lancelot, 1990; Lancelot et al., 1987). The silicate limitation dually
271 selected diatom species which are less silicified, such as *Leptocylindrus danicus*, *Chaetoceros danicus* and *Nitzschia*
272 *longissima* (Hasle et al., 1996). Furthermore, the N-source dependency of diatom silicate competitiveness, which
273 determines the dominant species of the community (Ruth, 2012), reinforced the idea that *Skeletonema* spp., *T.*
274 *nitzschioides*, *T. gravida* and *P. seriata* complex are decisive species for *Phaeocystis* spp. blooms.

275 The readjustment of nutrient concentrations rendered more than one resource limiting for the diatoms, resulting
276 in a biodiversity increase (Hillebrand et al., 2014), as shown with the BV-step analysis (7 to 11 species from
277 subset L to H). The niche expansion of *Phaeocystis* spp. (Tol: 0.59 and 0.64 for subset L and H respectively)
278 can be partly explained by a relaxation in biological constraints (Table 2). The possible decrease in diatom
279 competitive abilities resulted in the 25% of unused available environmental habitat conditions of the *Phaeocystis*
280 spp. existing fundamental subniche.

281 4.3. Further perspectives:

282 Further investigations on diatom competitive abilities can be done experimentally (Ruth, 2012), and with the
283 trait-based approach (Litchman and Klausmeier, 2008). The major components of the trait-based approach are
284 the species' traits, environmental gradients, species' interactions and performance currency, which determines
285 the species' niche within the community (McGill et al., 2006). In this study, the niche and subniche dynamics
286 within the overall environmental habitat and subset environmental habitat conditions were studied for the entire
287 community. Furthermore, the quantification of the biological constraints exerted on *Phaeocystis* spp.'s subniches
288 was made possible. The direct relationships between traits and the species' response to environmental conditions
289 (Lavorel and Garnier, 2002) can give us clues on the mechanisms driving community composition. In parallel, the
290 patterns of functional-trait distribution (Bello, 2009; Weiher et al., 1998) can help explain how the community
291 functional-traits controls the following *Phaeocystis* spp. bloom. Some methods, which link niche analysis and

292 trait-based approaches already exist. The OMI-GAM analysis (Kleyer et al., 2012) determines species' responses
293 to environmental conditions using the OMI analysis (Dolédéc et al., 2000), and additionally could explain these
294 responses using generalized additive models (GAM) with the traits as explanatory variables (Kleyer et al., 2012).
295 Such analyses can help solve the *Phaeocystis* spp. riddle and other HAB related issues. In future studies, more
296 precise ecological dynamics models could be built as the diatoms can be split into different functional groups.
297 Models, such as the MIRO model (Lancelot et al., 2014), which also studies the spring-diatom-*Phaeocystis*
298 bloom, considers diatoms as a large pool responding homogeneously to nutrient concentrations and/or ratios.
299 As shown in this study, the mechanism driving the bloom of *Phaeocystis* spp. is multifactorial, suggesting a
300 greater consideration of diatom diversity, including their respective traits and competitive abilities. Trait-based
301 understanding of plankton distribution started with the paradox of the plankton (Hutchinson, 1961). Margalef
302 was the first to understand the balance between the physical and nutritional forces relating to different life forms
303 of phytoplankton with the classical “mandala” (Margalef, 1978; Margalef et al., 1979). Since then, the concept of
304 the “mandala” has found its way into predicting HABs (Smayda and Reynolds, 2001) and nowadays incorporates
305 twelve dimensions (Glibert, 2016). Herein, the environmental trajectory can help predict the high abundance
306 events of *Phaeocystis* spp. in future “mandala” like models, by using the WitOMI calculations.

307 5. Conclusion:

308 The appearance of *Phaeocystis* spp. depends on multiple environmental factors, and moreover, on the preceding
309 diatom community, which first appear in late winter. Within both habitat subsets, *Phaeocystis* spp. could have
310 potentially realized a large subniche. The reduction and/or expansion of its subniche mostly depended on the
311 winter environmental conditions and on the biological constraints. The competitive ability of diatoms appearing
312 in late-winter are suspected to take part in the biological constraint of the *Phaeocystis* spp. subniche. The
313 establishment of the leading species in the bloom succession, here *Skeletonema* spp., *Thalassionema nitzschioides*
314 and *Thalassiosira gravida* seemed to be driven by nutrient concentration. Under non-limiting P environmental
315 conditions, competition among diatoms for silicate will be N-source dependent. The high concentration of
316 ammonia allowed a rapid growth and bloom of the later-winter diatoms (*i.e.* *Skeletonema* spp.) (Figure 3E), while
317 Si limited their bloom magnitude. The effect of winter conditions on the *Phaeocystis* spp. bloom requires further
318 investigation. The trait-based approach in relation with the community response to changing environmental
319 conditions could be a promising field for studying the future of Harmful Algae Bloom.

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328 References:

- 329 Anderson, D.M., 2009. Approaches to monitoring, control and management of harmful algal blooms (habs).
330 *Ocean & Coastal Management* 52, 342–347. doi:<http://dx.doi.org/10.1016/j.ocecoaman.2009.04.006>
- 331 Bello, D., 2009. Partitioning of functional diversity reveals the scale and extent of trait convergence and divergence
332 475–486.
- 333 Belin, C., and Neaud-Masson, N. 2012. *Cahier de Procédures REPHY 2012–2013*. Ifremer, Nantes. 81 pp.
- 334 Bianchi, T.S., Engelhaupt, E., Westman, P., Andrén, T., Rolff, C., Elmgren, R., 2000. Cyanobacterial blooms in the
335 Baltic Sea: Natural or human-induced? *Limnology and Oceanography* 45, 716–726. doi:[10.4319/lo.2000.45.3.0716](https://doi.org/10.4319/lo.2000.45.3.0716)
- 336 Blauw, A.N., Los, F.J., Huisman, J., Peperzak, L., 2010. Nuisance foam events and *Phaeocystis glo-*
337 *bosa* blooms in Dutch coastal waters analyzed with fuzzy logic. *Journal of Marine Systems* 83, 115–126.
338 doi:[10.1016/j.jmarsys.2010.05.003](https://doi.org/10.1016/j.jmarsys.2010.05.003)
- 339 Borkman, D.G., Libby, P.S., Mickelson, M.J., Turner, J.T., Jiang, M., 2016. Variability of Winter-Spring Bloom
340 *Phaeocystis pouchetii* Abundance in Massachusetts Bay. *Estuaries and Coasts* 39, 1084–1099. doi:[10.1007/s12237-](https://doi.org/10.1007/s12237-016-0065-5)
341 [016-0065-5](https://doi.org/10.1007/s12237-016-0065-5)
- 342 Braak, C.J.F.T., 1986. Canonical correspondence analysis: A new eigenvector technique for multivariate direct
343 gradient analysis. *Ecology* 67, 1167–1179.
- 344 Bradley, P.B., Sanderson, M.P., Nejstgaard, J.C., Sazhin, A.F., Frischer, M.E., Killberg-Thoreson, L.M., Verity,
345 P.G., Campbell, L., Bronk, D.A., 2010. Nitrogen uptake by phytoplankton and bacteria during an induced

- 346 *Phaeocystis pouchetii* bloom, measured using size fractionation and flow cytometric sorting. *Aquatic Microbial*
347 *Ecology* 61, 89–104. doi:[10.3354/ame01414](https://doi.org/10.3354/ame01414)
- 348 Bratbak, G., Jacobsen, a, Heldal, M., 1998. Viral lysis of *Phaeocystis pouchetii* and bacterial secondary production.
349 *Aquatic Microbial Ecology* 16, 11–16. doi:[10.3354/ame016011](https://doi.org/10.3354/ame016011)
- 350 Breton, E., Christaki, U., Bonato, S., Didry, M., Artigas, L., 2017. Functional trait variation and nitrogen use
351 efficiency in temperate coastal phytoplankton. *Marine Ecology Progress Series* 563, 35–49. doi:[10.3354/meps11974](https://doi.org/10.3354/meps11974)
- 352 Brussaard, C.P.D., Kuipers, B., Veldhuis, M.J.W., 2005. A mesocosm study of *Phaeocystis globosa* population
353 dynamics: I. Regulatory role of viruses in bloom control. *Harmful Algae* 4, 859–874. doi:[10.1016/j.hal.2004.12.015](https://doi.org/10.1016/j.hal.2004.12.015)
- 354 Cadée, G.C., Hegeman, J., 1986. Seasonal and annual variation in *phaeocystis pouchetii* (haptophyceae) in the
355 westernmost inlet of the Wadden Sea during the 1973 to 1985 period. *Netherlands Journal of Sea Research* 20,
356 29–36. doi:[10.1016/0077-7579\(86\)90058-X](https://doi.org/10.1016/0077-7579(86)90058-X)
- 357 Cadée, G.C., Hegeman, J., 2002. Phytoplankton in the marsdiep at the end of the 20th century; 30 years
358 monitoring biomass, primary production, and *phaeocystis* blooms. *Journal of Sea Research* 48, 97–110.
359 doi:[https://doi.org/10.1016/S1385-1101\(02\)00161-2](https://doi.org/10.1016/S1385-1101(02)00161-2)
- 360 Calenge, C., Dufour, A.B., Maillard, D., 2005. K-select analysis: A new method to analyse habitat selection in
361 radio-tracking studies. *Ecological Modelling* 186, 143–153. doi:[10.1016/j.ecolmodel.2004.12.005](https://doi.org/10.1016/j.ecolmodel.2004.12.005)
- 362 Clarke, K., Warwick, R., Laboratory, P.M., 2001. Change in marine communities: An approach to statistical
363 analysis and interpretation. PRIMER-E Limited.
- 364 Davidson, K., Gowen, R.J., Tett, P., Bresnan, E., Harrison, P.J., McKinney, A., Milligan, S., Mills, D.K., Silke, J.,
365 Crooks, A.M., 2012. Harmful algal blooms: How strong is the evidence that nutrient ratios and forms influence
366 their occurrence? *Estuarine, Coastal and Shelf Science* 115, 399–413. doi:[10.1016/j.ecss.2012.09.019](https://doi.org/10.1016/j.ecss.2012.09.019)
- 367 Dolédec, S., Chessel, D., Gimaret-Carpentier, C., 2000. Niche separation in community analysis: A new method.
368 *Ecology* 81, 2914. doi:[10.1890/0012-9658\(2000\)081\[2914:NSICAA\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2000)081[2914:NSICAA]2.0.CO;2)
- 369 Dray, S., Dufour, A.B., 2007. The ade4 Package: Implementing the Duality Diagram for Ecologists. *Journal of*
370 *Statistical Software* 22, 1–20. doi:[10.1.1.177.8850](https://doi.org/10.1.1.177.8850)
- 371 Drijfhout, S., Bathiany, S., Beaulieu, C., Brovkin, V., Claussen, M., Huntingford, C., Scheffer, M., Sgubin, G.,
372 Swingedouw, D., 2015. Catalogue of abrupt shifts in Intergovernmental Panel on Climate Change climate models.
373 *Proceedings of the National Academy of Sciences* 201511451. doi:[10.1073/pnas.1511451112](https://doi.org/10.1073/pnas.1511451112)
- 374 Egge, J.K., Aksnes, D.L., 1992. Silicate as regulating nutrient in phytoplankton competition. *Marine Ecology*

- 375 Progress Series 83, 281–289. doi:[10.3354/meps083281](https://doi.org/10.3354/meps083281)
- 376 Fehling, J., Davidson, K., Bolch, C., Tett, P., 2006. Seasonally of *Pseudo-nitzschia* spp. (Bacillariophyceae) in
377 western Scottish waters. Marine Ecology Progress Series 323, 91–105. doi:[10.3354/meps323091](https://doi.org/10.3354/meps323091)
- 378 Fu, F.X., Tatters, A.O., Hutchins, D.A., 2012. Global change and the future of harmful algal blooms in the ocean.
379 Marine Ecology Progress Series 470, 207–233. doi:[10.3354/meps10047](https://doi.org/10.3354/meps10047)
- 380 Glibert, P.M., 2016. Margalef revisited: A new phytoplankton mandala incorporating twelve dimensions, including
381 nutritional physiology. Harmful Algae 55, 25–30. doi:[10.1016/j.hal.2016.01.008](https://doi.org/10.1016/j.hal.2016.01.008)
- 382 Gowen, R., Tett, P., Bresnan, E., Davidson, K., McKinney, A., Harrison, P., Milligan, S., Mills, D., Silke, J.,
383 Crooks, A.-M., 2012. Anthropogenic nutrient enrichment and blooms of harmful phytoplankton, in: Oceanography
384 and Marine Biology: An Annual Review. pp. 65–126. doi:[10.1201/b12157-3](https://doi.org/10.1201/b12157-3)
- 385 Grattepanche, J.D., Breton, E., Brylinski, J.M., Lecuyer, E., Christaki, U., 2011. Succession of primary producers
386 and micrograzers in a coastal ecosystem dominated by *Phaeocystis globosa* blooms. Journal of Plankton Research
387 33, 37–50. doi:[10.1093/plankt/fbq097](https://doi.org/10.1093/plankt/fbq097)
- 388 Hallegraeff, G.M., 2010. Ocean climate change, phytoplankton community responses, and harmful algal blooms:
389 A formidable predictive challenge1. Journal of Phycology 46, 220–235. doi:[10.1111/j.1529-8817.2010.00815.x](https://doi.org/10.1111/j.1529-8817.2010.00815.x)
- 390 Hamm, C. E., Simson, D. A., Merkel, R., and Smetacek, V. (1999). Colonies of *Phaeocystis globosa* are protected
391 by a thin but tough skin. Marine Ecology Progress Series, 187:101–111.
- 392 Hasle, G.R., Lange, C.B., Syvertsen, E.E., 1996. A review of *Pseudo-nitzschia*, with special reference to the skager-
393 rak, north atlantic, and adjacent waters. Helgoländer Meeresuntersuchungen 50, 131–175. doi:[10.1007/BF02367149](https://doi.org/10.1007/BF02367149)
- 394 Hernández-Fariñas, T., Bacher, C., Soudant, D., Belin, C., Barillé, L., 2015. Assessing phytoplankton realized
395 niches using a French national phytoplankton monitoring network. Estuarine, Coastal and Shelf Science 159,
396 15–27. doi:[10.1016/j.ecss.2015.03.010](https://doi.org/10.1016/j.ecss.2015.03.010)
- 397 Hillebrand, H., Cowles, J.M., Lewandowska, A., Van de Waal, D.B., Plum, C., 2014. Think ratio! A sto-
398 ichiometric view on biodiversity–ecosystem functioning research. Basic and Applied Ecology 15, 465–474.
399 doi:[10.1016/j.baae.2014.06.003](https://doi.org/10.1016/j.baae.2014.06.003)
- 400 Houliez, E., Lizon, F., Artigas, L.F., Lefebvre, S., Schmitt, F.G., 2013. Spatio-temporal variability of phytoplank-
401 ton photosynthetic activity in a macrotidal ecosystem (the Strait of Dover, eastern English Channel). Estuarine,

- 402 Coastal and Shelf Science 129, 37–48. doi:[10.1016/j.ecss.2013.06.009](https://doi.org/10.1016/j.ecss.2013.06.009)
- 403 Hutchinson, G.E., 1961. The paradox of the plankton. *The American Naturalist* 95, 137–145.
- 404 Jahnke, J., 1989. The light and temperature dependence of growth rate and elemental composition of *Phaeocystis*
405 *globosa* scherffel and *P. pouchetii* (har.) lagerh. in batch cultures. *Netherlands Journal of Sea Research* 23, 15–21.
406 doi:[http://dx.doi.org/10.1016/0077-7579\(89\)90038-0](http://dx.doi.org/10.1016/0077-7579(89)90038-0)
- 407 Jakobsen, H. H. and Tang, K. W., 2002. Effects of protozoan grazing on colony formation in *Phaeocystis globosa*
408 (prymnesiophyceae) and the potential costs and benefits. *Aquatic Microbial Ecology*, 27(3):261–273.
- 409 Karasiewicz, S., Dolédec, S., Lefebvre, S., 2017. Within outlying mean indexes: Refining the omi analysis for the
410 realized niche decomposition. *PeerJ*. doi:[10.7717/peerj.3364](https://doi.org/10.7717/peerj.3364)
- 411 Kleyer, M., Dray, S., Bello, F., Lepš, J., Pakeman, R.J., Strauss, B., Thuiller, W., Lavorel, S., 2012. Assessing
412 species and community functional responses to environmental gradients: which multivariate methods? *Journal of*
413 *Vegetation Science* 23, 805–821. doi:[10.1111/j.1654-1103.2012.01402.x](https://doi.org/10.1111/j.1654-1103.2012.01402.x)
- 414 Kurekin, A.A., Miller, P.I., Van der Woerd, H.J., 2014. Satellite discrimination of *Karenia mikimotoi* and
415 *Phaeocystis* harmful algal blooms in European coastal waters: Merged classification of ocean colour data. *Harmful*
416 *Algae* 31, 163–176. doi:[10.1016/j.hal.2013.11.003](https://doi.org/10.1016/j.hal.2013.11.003)
- 417 Lacroix, G., Ruddick, K., Gypens, N., Lancelot, C., 2007. Modelling the relative impact of rivers
418 (Scheldt/Rhine/Seine) and Western Channel waters on the nutrient and diatoms/*Phaeocystis* distributions in
419 Belgian waters (Southern North Sea). *Continental Shelf Research* 27, 1422–1446. doi:[10.1016/j.csr.2007.01.013](https://doi.org/10.1016/j.csr.2007.01.013)
- 420 Lancelot, C., 1990. *Phaeocystis* blooms in the continental coastal areas of the Channel and the North Sea. In C.
421 Lancelot, G. Billen, & H. Barth (Eds.). *Eutrophication and algal blooms in the North Sea coastal zones, the*
422 *Baltic and adjacent areas : prediction and assessment of preventive actions* 27–54.
- 423 Lancelot, C., Billen, G., Sournia, A., Weisse, T., Colijn, F., Veldhuis, M.J.W., Davies, A., Wassman, P., 1987.
424 *Phaeocystis* blooms and nutrient enrichment in the continental coastal zones of the North Sea. *Ambio* 16, 38–46.
- 425 Lancelot, C., Passy, P., Gypens, N., 2014. Model assessment of present-day *Phaeocystis* colony blooms in the
426 Southern Bight of the North Sea (SBNS) by comparison with a reconstructed pristine situation. *Harmful Algae*
427 37, 172–182. doi:[10.1016/j.hal.2014.05.017](https://doi.org/10.1016/j.hal.2014.05.017)
- 428 Lancelot, C., Wassmann, P., Barth, H., 1994. Ecology of *Phaeocystis*-dominated ecosystems. *Journal of Marine*
429 *Systems* 5, 1–4. doi:[http://dx.doi.org/10.1016/0924-7963\(94\)90012-4](http://dx.doi.org/10.1016/0924-7963(94)90012-4)
- 430 Lavorel, S., Garnier, E., 2002. Predicting changes in community composition and ecosystem functioning from

- 431 plant traits : Functional Ecology 16, 545–556.
- 432 Lefebvre, A., Guiselin, N., Barbet, F., Artigas, F.L., 2011. Long-term hydrological and phytoplankton monitoring
433 (19922007) of three potentially eutrophic systems in the eastern English Channel and the Southern Bight of the
434 North Sea. ICES Journal of Marine Science 68, 2029–2043. doi:[10.1093/icesjms/fsr149](https://doi.org/10.1093/icesjms/fsr149)
- 435 Levasseur, M., Keller, M.D., Bonneau, E., D'Amours, D., Bellows, W.K., 1994. Oceanographic basis of a
436 dms-related atlantic cod (*Gadus morhua*) fishery problem: Blackberry feed. Canadian Journal of Fisheries and
437 Aquatic Sciences 51, 881–889. doi:[10.1139/f94-087](https://doi.org/10.1139/f94-087)
- 438 Litchman, E., Klausmeier, C.a., 2008. Trait-Based Community Ecology of Phytoplankton. Annual Review of
439 Ecology, Evolution, and Systematics 39, 615–639. doi:[10.1146/annurev.ecolsys.39.110707.173549](https://doi.org/10.1146/annurev.ecolsys.39.110707.173549)
- 440 Long, J. D., Smalley, G. W., Barsby, T., Anderson, J. T., and Hay, M. E., 2007. Chemical cues induce consumer-
441 specific defenses in a bloom-forming marine phytoplankton. Proceedings of the National Academy of Sciences,
442 104(25):10512–10517.
- 443 Lundgren, V., Granéli, E., 2010. Grazer-induced defence in *Phaeocystis globosa* (Prymnesiophyceae): Influence of
444 different nutrient conditions. Limnology and Oceanography 55, 1965–1976. doi:[10.4319/lo.2010.55.5.1965](https://doi.org/10.4319/lo.2010.55.5.1965)
- 445 Manly, B.F.J., 1997. Randomization, bootstrap and monte carlo methods in biology. Chapman & Hall, London.
- 446 Margalef, R., 1978. Life-forms Phytoplankton as survival alternatives in an unstable environment. Oceanologica
447 Acta 1, 463–509. doi:[10.1007/BF00202661](https://doi.org/10.1007/BF00202661)
- 448 Margalef, R., Estrada, M., Blasco, D., 1979. Functional morphology of organisms involved in red tides, as adapted
449 to decaying turbulence. Elsevier.
- 450 McGill, B.J., Enquist, B.J., Weiher, E., Westoby, M., 2006. Rebuilding community ecology from functional traits.
451 Trends in Ecology and Evolution 21, 178–185. doi:[10.1016/j.tree.2006.02.002](https://doi.org/10.1016/j.tree.2006.02.002)
- 452 Mochemadkar, S., Gauns, M., Pratihary, A., Thorat, B., Roy, R., Pai, I.K., Naqvi, S.W.A., 2013. Response of
453 phytoplankton to nutrient enrichment with high growth rates in a tropical monsoonal estuary - Zuari estuary,
454 India. Indian Journal of Marine Sciences 42, 314–325.
- 455 Nejstgaard, J. C., Tang, K. W., Steinke, M., Dutz, J., Koski, M., Antajan, E., and Long, J. D., 2007. Zooplankton
456 grazing on phaeocystis: a quantitative review and future challenges. Biogeochemistry, 83(1-3):147–172.
- 457 Passy, P., Le Gendre, R., Garnier, J., Cugier, P., Callens, J., Paris, F., Billen, G., Riou, P., Romero, E., 2016.
458 Eutrophication modelling chain for improved management strategies to prevent algal blooms in the Bay of Seine.

- 459 Marine Ecology Progress Series 543, 107–125. doi:[10.3354/meps11533](https://doi.org/10.3354/meps11533)
- 460 Peperzak, L., 1993. Daily irradiance governs growth rate and colony formation of *Phaeocystis* (Prymnesiophyceae).
461 Journal of Plankton Research 15, 809–821. doi:[10.1093/plankt/15.7.809](https://doi.org/10.1093/plankt/15.7.809)
- 462 Peperzak, L., Colijn, F., Gieskes, W.W.C., Peeters, J.C.H., 1998. Development of the diatom-*Phaeocystis* spring
463 bloom in the Dutch coastal zone of the North Sea: the silicon depletion versus the daily irradiance threshold
464 hypothesis. Journal of Plankton Research 20, 517–537. doi:[10.1093/plankt/20.3.517](https://doi.org/10.1093/plankt/20.3.517)
- 465 Peterson, A.T., 2011. Ecological niches and geographic distributions (mpb-49). Princeton University Press.
- 466 Pratt, D.M., 1959. The Phytoplankton of Narragansett Bay. Limnology and Oceanography 4, 425–440.
- 467 R Core Team, 2013. R Core Team. R: A language and environment for statistical computing. R Foundation for
468 Statistical Computing, Vienna, Austria.
- 469 Reid, P.C., Lancelot, C., Gieskes, W.W.C., Hagmeier, E., Weichart, G., 1990. Phytoplankton of the North Sea
470 and its dynamics: a review. Netherlands Journal of Sea Research 26, 295–331. doi:[10.1016/0077-7579\(90\)90094-w](https://doi.org/10.1016/0077-7579(90)90094-w)
- 471 Riegman, R., 1995. Nutrient-related selection mechanisms in marine phytoplankton communities and
472 the impact of eutrophication on the planktonic food web. Water Science and Technology 32, 63–75.
473 doi:[http://dx.doi.org/10.1016/0273-1223\(95\)00682-6](http://dx.doi.org/10.1016/0273-1223(95)00682-6)
- 474 Riegman, R., Noordeloos, A.A.M., Cadée, G.C., 1992. *Phaeocystis* blooms and eutrophication of the continental
475 coastal zones of the north sea. Marine Biology 112, 479–484. doi:[10.1007/BF00356293](https://doi.org/10.1007/BF00356293)
- 476 Rogers, S., Lockwood, S., 1990. Observations on coastal fish fauna during a spring bloom of *Phaeocystis pouchetii*
477 in the eastern irish sea. Journal of the Marine Biological Association of the United Kingdom 70, 249–253.
478 doi:[10.1017/S0025315400035360](https://doi.org/10.1017/S0025315400035360)
- 479 Ruth, P.D. van, 2012. Size Dependent Competition in Centric Diatoms as a Function of Nitrogen and Silicon
480 Availability. Open Journal of Marine Science 02, 33–42. doi:[10.4236/ojms.2012.21005](https://doi.org/10.4236/ojms.2012.21005)
- 481 Schoemann, V., Wollast, R., Chou, L., Lancelot, C., 2001. Effects of photosynthesis on the accumulation of Mn
482 and Fe by *Phaeocystis* colonies. Limnology and Oceanography 46, 1065–1076. doi:[10.4319/lo.2001.46.5.1065](https://doi.org/10.4319/lo.2001.46.5.1065)
- 483 Smayda, T.J., 1958. Biogeographical Studies of Marine Phytoplankton. Oikos 9, 158–191.
- 484 Smayda, T.J., Reynolds, C.S., 2001. Community assembly in marine phytoplankton: application of recent models
485 to harmful dinoflagellate blooms. Journal of Plankton Res. 23, 447–461. doi:[10.1093/plankt/23.5.447](https://doi.org/10.1093/plankt/23.5.447)
- 486 SRN - Regional Observation and Monitoring program for Phytoplankton and Hydrology in the eastern English
487 Channel (2017). SRN dataset - Regional Observation and Monitoring Program for Phytoplankton and Hydrology

- 488 in the eastern English Channel. 1992-2016. SEANOE. doi:[10.17882/50832](https://doi.org/10.17882/50832)
- 489 Suksomjit, M., Ichimi, K., Hamada, K.I., Yamada, M., Tada, K., Harrison, P.J., 2009. Ammonium accelerates
490 the growth rate of *Skeletonema* spp. in the phytoplankton assemblage in a heavily eutrophic embayment, Dokai
491 Bay, Japan. *La mer* 47, 89–101.
- 492 Tada, K., Suksomjit, M., Ichimi, K., Funaki, Y., Montani, S., Yamada, M., Harrison, P.J., 2009. Diatoms grow
493 faster using ammonium in rapidly flushed eutrophic Dokai Bay, Japan. *Journal of Oceanography* 65, 885–891.
494 doi:[10.1007/s10872-009-0073-1](https://doi.org/10.1007/s10872-009-0073-1)
- 495 Tang, K. W. ,2003. Grazing and colony size development in *Phaeocystis globosa* (Prymnesiophyceae): the role of
496 a chemical signal. *Journal of Plankton Research*, 25(7):831–842.
- 497 Ter Braak, C.J.F., 1987. The analysis of vegetation-environment relationships by canonical correspondence
498 analysis. *Vegetatio* 69, 69–77. doi:[10.1007/BF00038688](https://doi.org/10.1007/BF00038688)
- 499 Tett, A.P.B., Joint, I.R., Purdie, D.A., Baars, M., Oosterhuis, S., Daneri, G., Mills, D.K., Plummer, D., Pomroy,
500 A.J., Walne, A.W., Witte, H.J., Howarth, M.J., Lankester, R., 1993. Biological Consequences of Tidal Stirring
501 Gradients in the North Sea [and Discussion] Biological consequences of tidal stirring gradients in the North Sea.
502 *Philosophical Transactions: Physical Sciences and Engineering* 343, 493–508. doi:[10.1098/rsta.1993.0061](https://doi.org/10.1098/rsta.1993.0061)
- 503 Tett, P., Walne, A., 1995. Observations and simulations of hydrography, nutrients and plankton in the southern
504 north sea. *Ophelia* 42, 371–416. doi:[10.1080/00785326.1995.10431514](https://doi.org/10.1080/00785326.1995.10431514)
- 505 Tungaraza, C., Rousseau, V., Brion, N., Lancelot, C., Gichuki, J., Baeyens, W., Goeyens, L., 2003. Contrasting
506 nitrogen uptake by diatom and *Phaeocystis*-dominated phytoplankton assemblages in the North Sea. *Journal of*
507 *Experimental Marine Biology and Ecology* 292, 19–41. doi:[10.1016/S0022-0981\(03\)00145-X](https://doi.org/10.1016/S0022-0981(03)00145-X)
- 508 Utermöhl, H. 1958. Zur Vervollkommnung der quantitativen Phytoplankton-Methodik. *Mitteilungen Interna-*
509 *tionale Vereinigung Theoretische und Angewandte Limnologie*, 9: 1–38.
- 510 Veldhuis, M.J.W., Colijn, F., Admiraal, W., 1991. Phosphate Utilization in *Phaeocystis pouchetii* (*Haptophyceae*).
511 *Marine Ecology Pubblicazioni Della Stazione Zoologica Di Napoli I* 12, 53–62.
- 512 Wang, X., Wang, Y., Ou, L., He, X., and Chen, D., 2015. Allocation costs associated with induced defense in
513 *Phaeocystis globosa* (prymnesiophyceae): the effects of nutrient availability. *Scientific reports*, 5.
- 514 Weiher, E., Clarke, G.D.P., Keddy, P.A., 1998. Community assembly rules, morphological dispersion, and the
515 coexistence of plant species. *Oikos* 81, 309–322.
- 516 Wells, M.L., Trainer, V.L., Smayda, T.J., Karlson, B.S.O., Trick, C.G., Kudela, R.M., Ishikawa, A., Bernard, S.,

- 517 Wulff, A., Anderson, D.M., Cochlan, W.P., 2015. Harmful algal blooms and climate change: Learning from the
518 past and present to forecast the future. *Harmful Algae* 49, 68–93. doi:[10.1016/j.hal.2015.07.009](https://doi.org/10.1016/j.hal.2015.07.009)
- 519 Yin, K., 2003. Influence of monsoons and oceanographic processes on red tides in Hong Kong waters. *Marine*
520 *Ecology Progress Series* 262, 27–41. doi:[10.3354/meps262027](https://doi.org/10.3354/meps262027)

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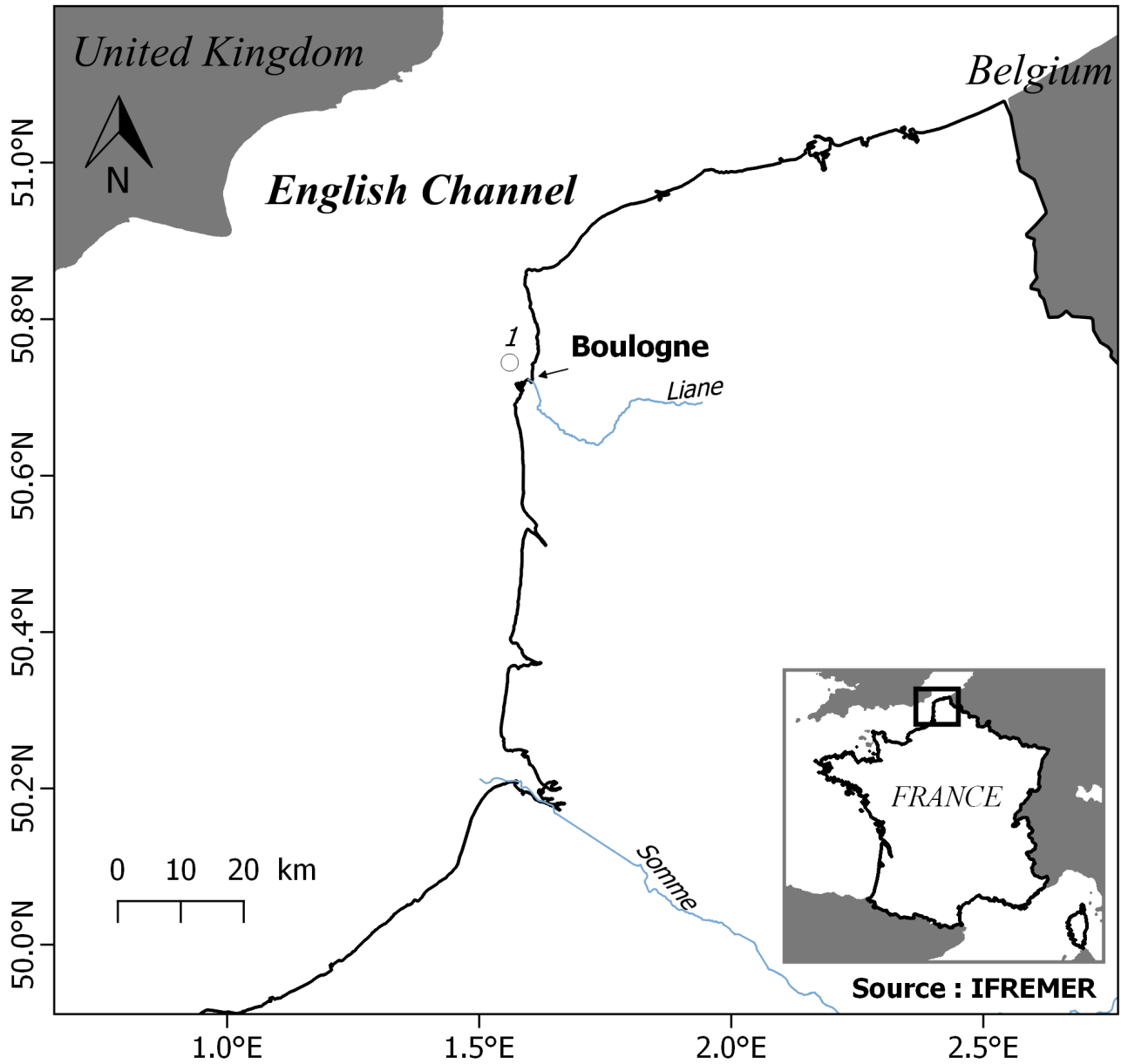


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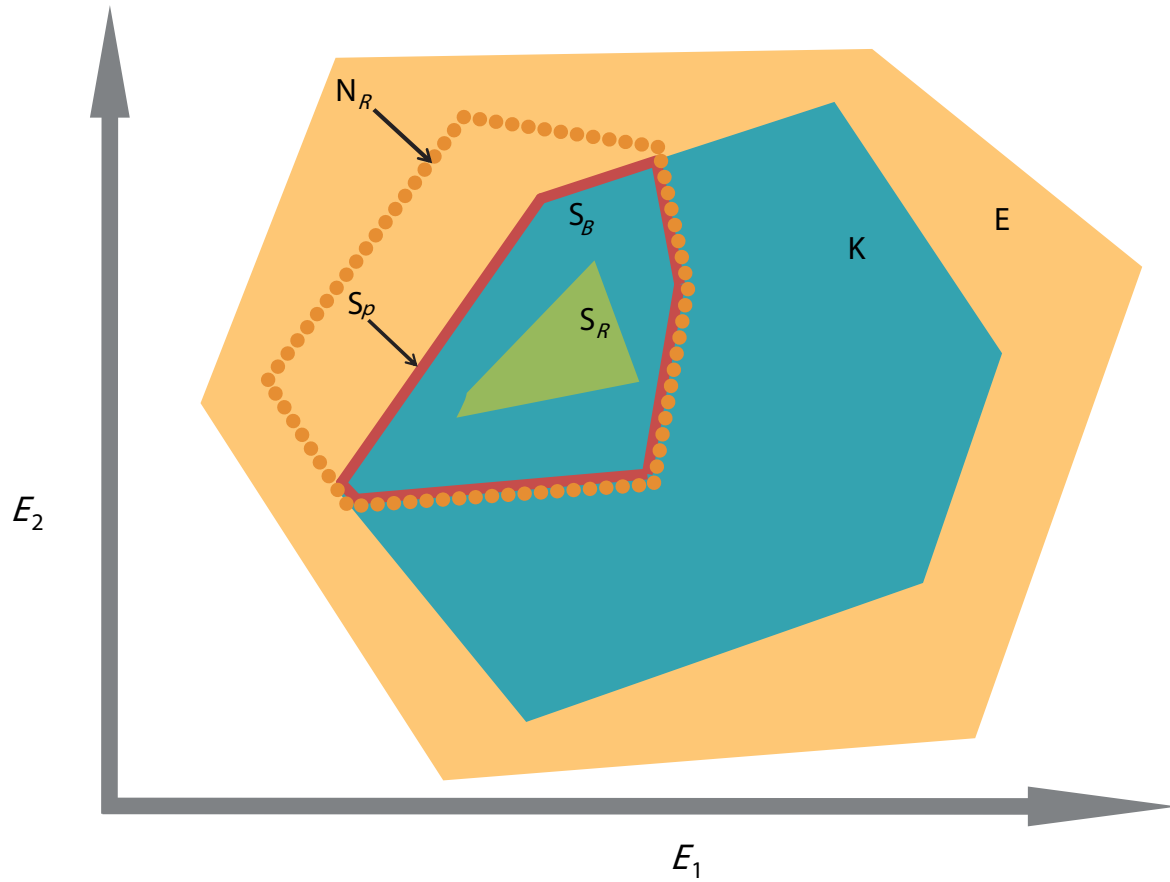


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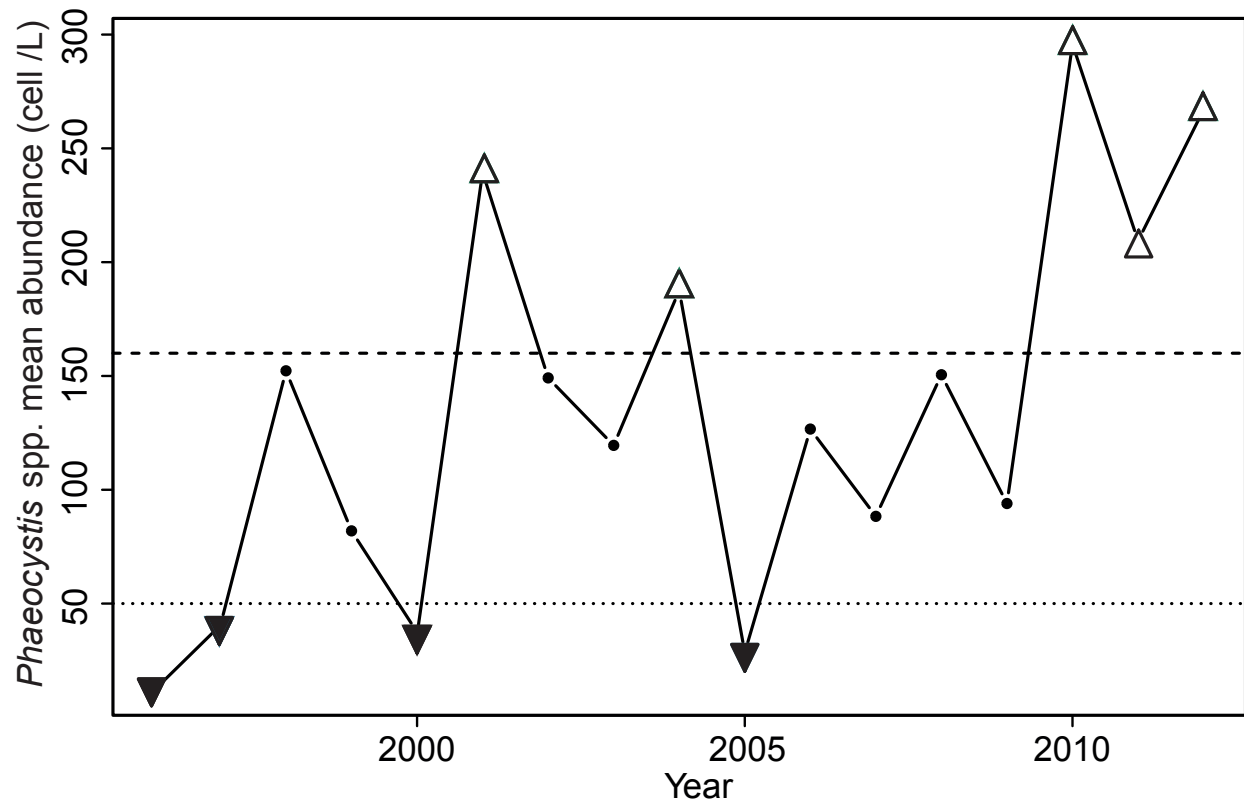


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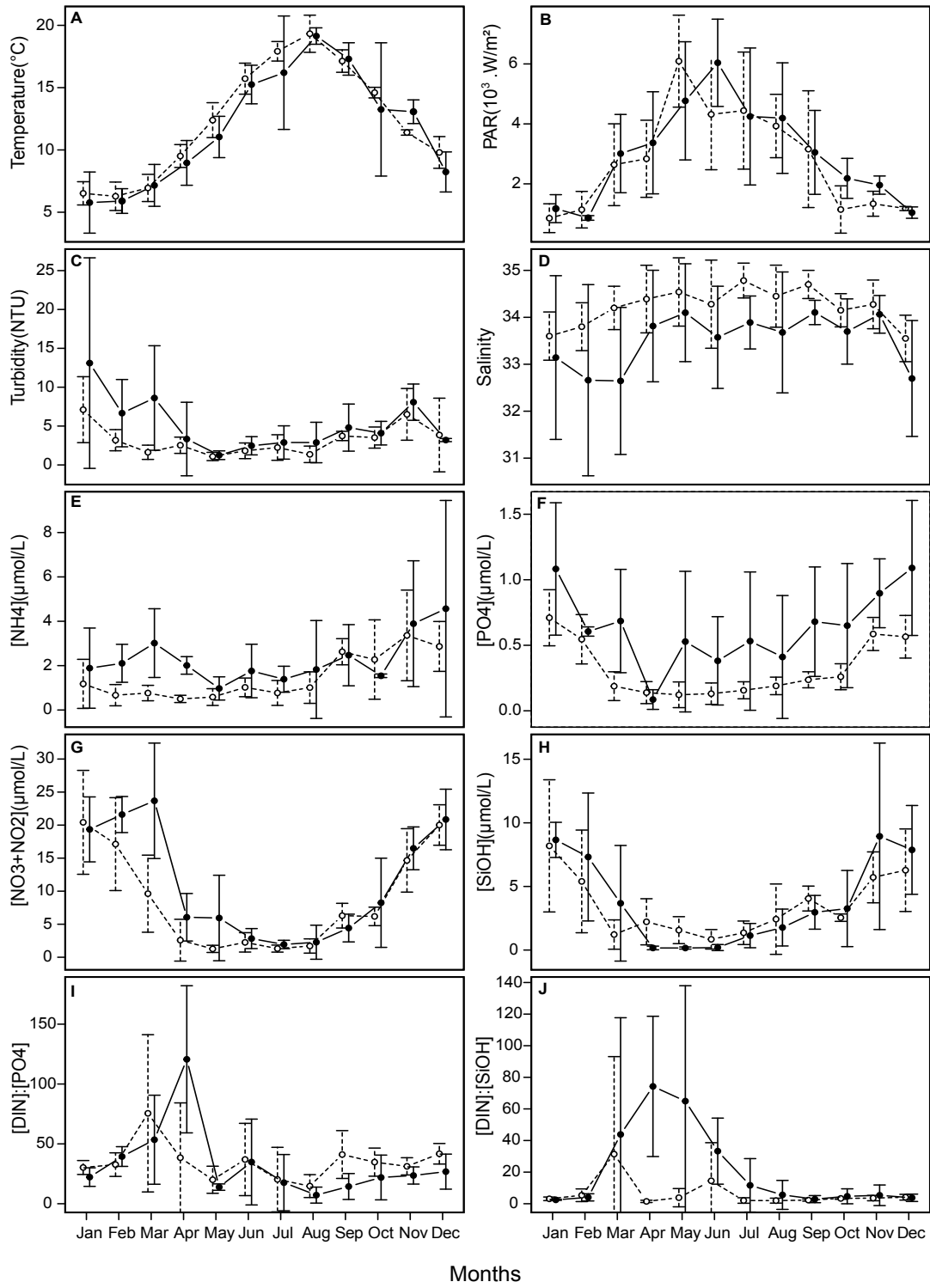


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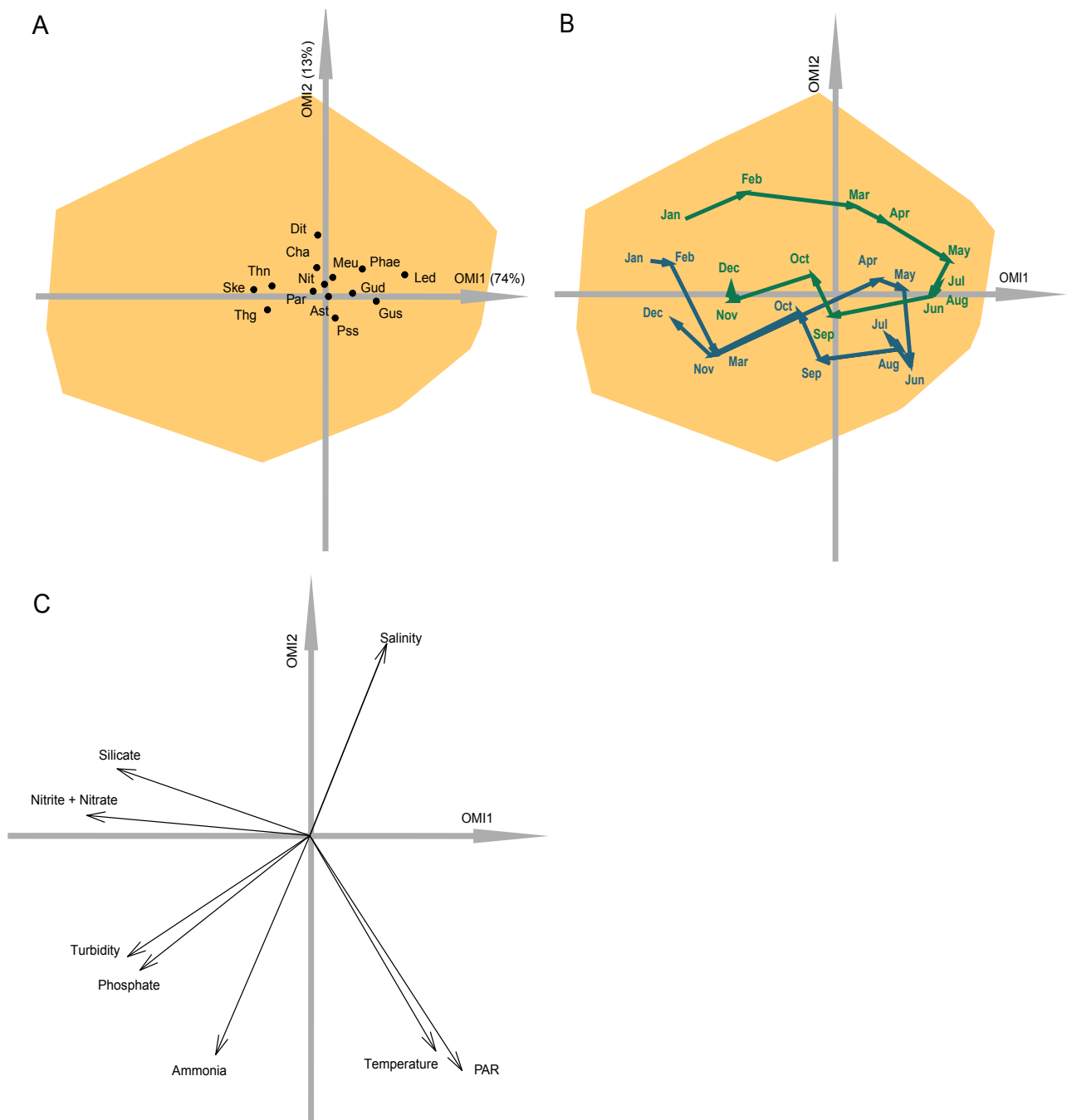


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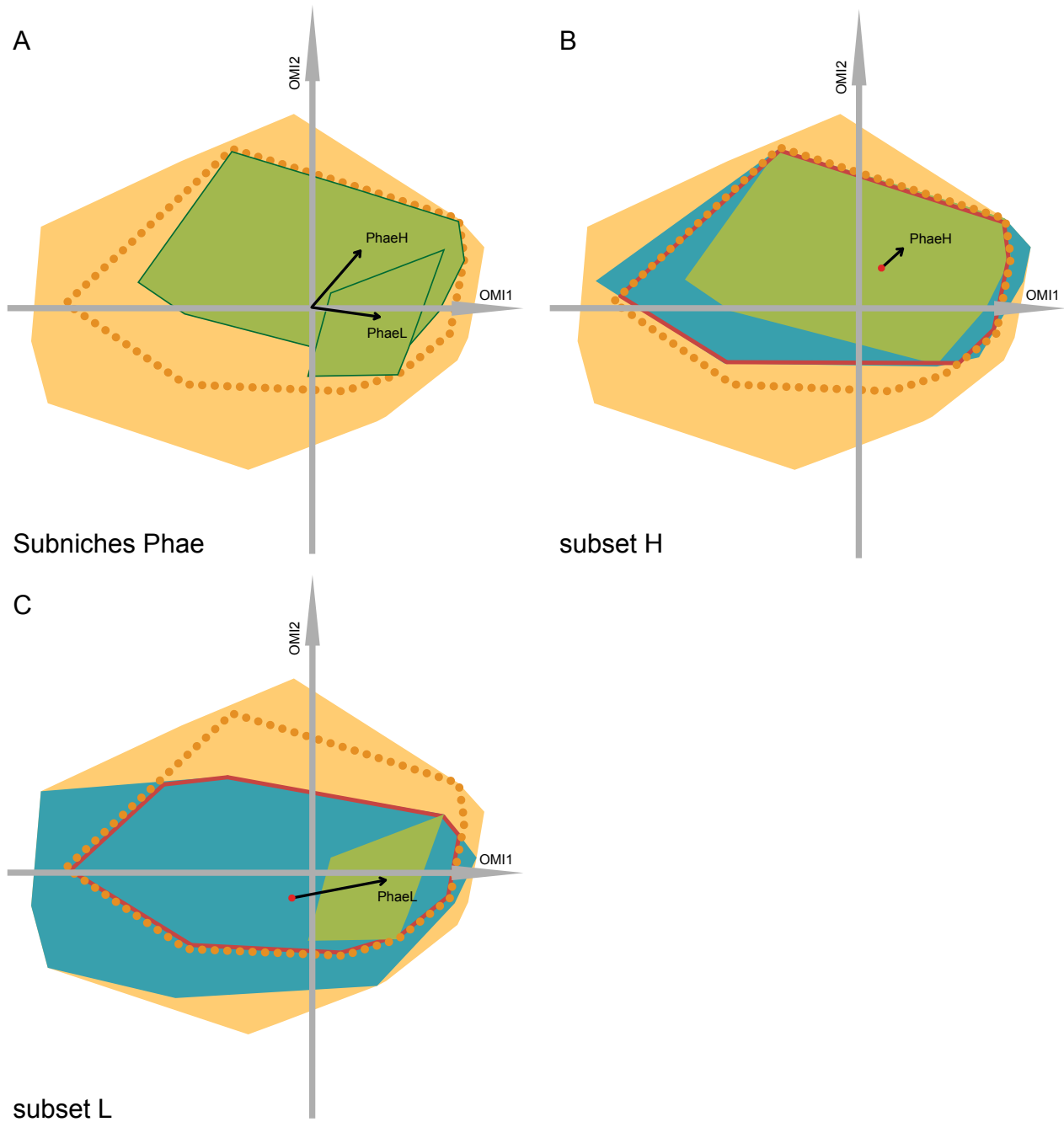


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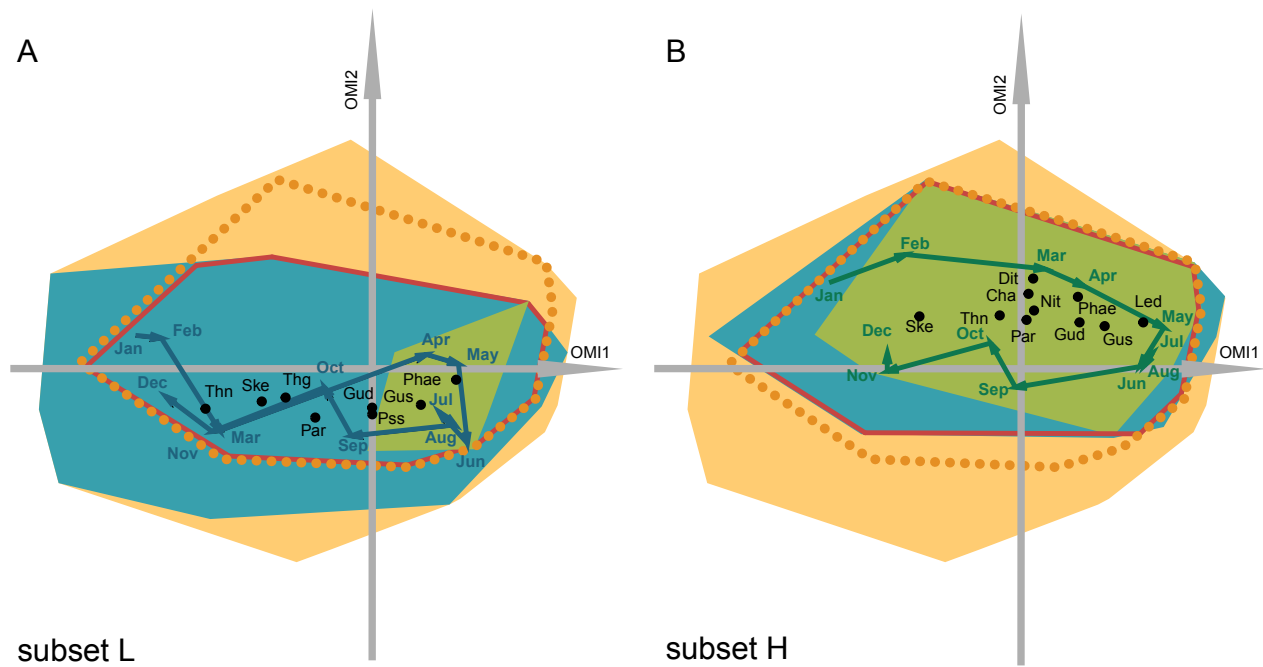


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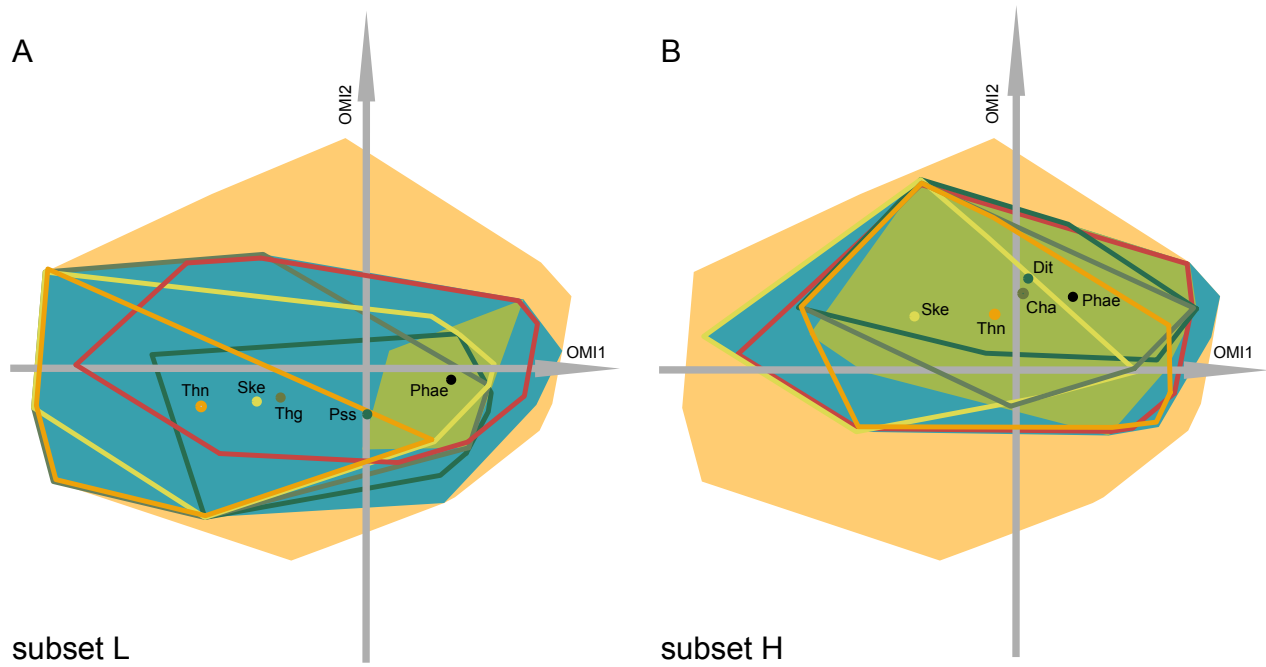


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Table 1: Niche parameters calculated with the OMI analysis for 11 diatoms species and *Phaeocystis* spp. The parameters are the inertia, the marginality (OMI), the tolerance (Tol) and the residual tolerance (Rtol). The P values were calculated with 1000 permutations, see methods for further details.

Species	Code	Inertia	OMI	Tol	Rtol	P
<i>Chaetoceros danicus</i>	Cha	7.09	0.36	0.98	5.76	0.03
<i>Ditylum brightwellii</i>	Dit	7.48	1.07	1.14	5.26	0.00
<i>Guinardia delicatula</i>	Gud	7.28	0.22	2.51	4.56	<0.001
<i>Guinardia striata</i>	Gus	6.65	0.79	1.62	4.24	<0.001
<i>Leptocylindrus danicus</i>	Led	6.61	2.23	1.31	3.07	<0.001
<i>Nitzschia longissima</i>	Nit	7.73	0.06	0.77	6.89	0.05
<i>Paralia sulcata</i>	Par	7.82	0.09	2.24	5.49	0.00
<i>Pseudo – nitzschia seriata</i> complex	Pss	7.25	0.20	0.96	6.09	0.01
<i>Skeletonema</i> spp.	Ske	10.12	1.64	3.52	4.96	<0.001
<i>Thalassionema nitzschioides</i>	Thn	9.02	0.93	3.35	4.74	<0.001
<i>Thalassiosira gravida</i>	Thg	9.23	1.15	3.14	4.95	<0.001
<i>Phaeocystis</i> spp.	Phae	6.58	0.83	1.36	4.39	<0.001

Table 2: Subniche parameters of the 11 diatom species of interest and *Phaeocystis* spp. The marginality (WitOMI), tolerance (TOL) and mean abundance were calculated under the two subsets, L and H. The niche parameters were calculated from G and G_K . For code see Table 1. All subniches were significant ($P \leq 0.001$). - not applicable means that the species were absent in one of the two subsets, or not significant with the BV step analysis. For further details see Materials and Methods.

Code Origin	WitOMI				Tol				Mean abundance (cells.L ⁻¹)	
	G		G_K		G		G_K		L	H
Data subset	L	H	L	H	L	H	L	H	L	H
Cha	-	1.34	-	0.31	-	0.56	-	1.95	-	111
Dit	-	1.93	-	0.58	-	0.45	-	1.26	-	100
Gud	0.6	1.26	0.2	0.16	0.62	1.28	2.97	1.97	295	298
Gus	1.09	2.07	1.3	0.65	1.43	0.91	2.05	1.49	226	222
Led	-	4.11	-	2.05	-	0.61	-	0.65	-	118
Nit	-	0.86	-	0.14	-	0.58	-	2.14	-	268
Par	1.48	0.63	0.52	0.16	1.73	0.45	1.68	2.85	138	284
Pss	0.83	-	0.28	-	0.6	-	1.69	-	173	-
Ske	3.17	2.88	1.71	3.85	3.83	2.14	3.86	2.45	206	126
Thn	6.61	0.77	4.36	0.63	2.17	1.19	2.22	3.03	163	197
Thg	2.02	-	0.78	-	3.83	-	4.13	-	139	-
Phae	2.64	2.11	3.24	0.59	0.59	0.64	0.67	0.46	29	237