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Nicolas Mayot, Fabrizio d'Ortenzio, Vincent Taillandier, Louis Prieur, Orens Pasqueron de Fommervault, et al.. Physical and biogeochemical controls of the phytoplankton blooms in North-Western Mediterranean Sea: A multiplatform approach over a complete annual cycle (2012-2013 DEWEX experiment). *Journal of Geophysical Research. Oceans*, 2017, 122 (12), pp.9999-10019. 10.1002/2016JC012052 . hal-01630494

HAL Id: hal-01630494

<https://hal.science/hal-01630494>

Submitted on 15 Feb 2021

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1 **Physical and biogeochemical controls of the phytoplankton blooms in North Western**
2 **Mediterranean Sea: a multiplatform approach over a complete annual cycle (2012-**
3 **2013 DEWEX experiment)**

4
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17

18 **Key Points:**

- 19 • The initiation of the autumnal bloom is linked to the mixing of the shallowing summer
20 DCM
- 21 • Heat fluxes and restratification of the mixed layer control the spring bloom dynamics
- 22 • Deep winter convection events enhance the spring bloom's magnitude by favoring
23 diatoms development

24 Abstract

25 The North Western Mediterranean Sea exhibits recurrent and significant autumnal and spring
26 phytoplankton blooms. The existence of these two blooms coincide with typical temperate
27 dynamics. To determine the potential control of physical and biogeochemical factors on these
28 phytoplankton blooms, data from a multiplatform approach (combining ships, Argo and BGC-
29 Argo floats, and bio-optical gliders) were analyzed in association with satellite observations in
30 2012-2013. The satellite framework allowed a simultaneous analysis over the whole annual cycle
31 of *in situ* observations of mixed layer depth, photosynthetical available radiation, particle
32 backscattering, nutrients (nitrate and silicate) and chlorophyll-a concentrations. During the year
33 2012-2013, satellite ocean color observations, confirmed by *in situ* data, have revealed the
34 existence of two areas (or bioregions) with comparable autumnal blooms but contrasting spring
35 blooms. In both bioregions, the ratio of the euphotic zone (defined as the isolume 0.415 mol
36 photons $\text{m}^{-2} \text{d}^{-1}$, $Z_{0.415}$) and the MLD identified the initiation of the autumnal bloom, as well as
37 the maximal annual increase in [Chl-a] in spring. In fact, the autumnal phytoplankton bloom
38 might be initiated by mixing of the summer shallowing deep chlorophyll maximum, while the
39 spring restratification (when $Z_{0.415}/\text{MLD}$ ratio became > 1) might induce surface phytoplankton
40 production that largely overcomes the losses. Finally, winter deep convection events that took
41 place in one of the bioregions induced higher net accumulation rate of phytoplankton in spring
42 associated with a diatom-dominated phytoplankton community principally. We suggest that very
43 deep winter MLD lead to an increase in surface silicates availability, which favored the
44 development of diatoms.

45 1 Introduction

46 The seasonality of phytoplankton biomass in the North Western Mediterranean Sea (NWM)
47 follows a typical temperate pattern, with a spring bloom followed by summer oligotrophy and a
48 less intense secondary bloom in autumn [Morel and André, 1991; Bosc et al., 2004; Siokou-
49 Frangou et al., 2010; Estrada and Vaqué, 2014; Lavigne et al., 2015b]. Satellite data of
50 chlorophyll-a concentration ([Chl-a], in mg m^{-3} , considered as a proxy for phytoplankton
51 biomass) reveal that the temperate cycle found in the Gulf of Lion is different than in the rest of
52 the Mediterranean basin, which displays a typical subtropical cycle [D'Ortenzio and Ribera
53 d'Alcalà, 2009]. In addition, an autumnal bloom is also observed, and it can be related to the
54 deepening of the Mixed Layer Depth (MLD) after summer [Volpe et al., 2012; D'Ortenzio et al.,
55 2014; Mignot et al., 2014; Shabrang et al., 2015].

56 This winter deepening of the MLD in the NWM takes place mainly in a “mixed patch”, located
57 in the center of the general cyclonic circulation of the area, where open-ocean convective
58 activities occur due to atmospheric forcings [Millot, 1999]. Moreover, various (sub)mesoscale
59 processes are generally associated within the mixed patch (e.g. [Lévy et al., 1998, 1999; Testor
60 and Gascard, 2006; Waldman et al., submitted]), also generated by instabilities of the fronts and
61 the alongslope circulation (e.g. [Alberola et al., 1995; Font et al., 1995; Millot, 1999; Bosse et
62 al., 2015]). In spring, the water column is restratified by the shallowing of the MLD, followed by
63 a strong thermal stratification in summer that concludes the annual cycle of the MLD in the
64 NWM [D'Ortenzio et al., 2005; Houpert et al., 2014]. However, the winter deepening of the
65 MLD presents strong inter-annual variability. During some winters, events of open-ocean deep
66 convection occur, leading to the formation of the Western Mediterranean Deep Water (e.g.
67 [MEDOC Group, 1970; Marshall and Schott, 1999; Houpert et al., 2016]). In other terms, the

68 integrated effects of atmospheric forcings induce a widespread winter deepening of the MLD in
69 the NWM, but the reached maximal depths are greatly variable, depending on the spatiotemporal
70 variability of the atmospheric conditions and of the preconditioning before winter convection
71 [Houpert *et al.*, 2016; Somot *et al.*, 2016].

72 The variability of winter convective mixing leads to inter-annual variability in the intensity,
73 timing and spatial extent of phytoplankton spring blooms [Barale *et al.*, 2008; Marty and
74 Chiavérini, 2010; Olita *et al.*, 2011; Bernardello *et al.*, 2012; Volpe *et al.*, 2012; Herrmann *et*
75 *al.*, 2013; Lavigne *et al.*, 2013; Estrada *et al.*, 2014; Severin *et al.*, 2014; Mayot *et al.*, 2016].
76 However, these previous studies were generally restricted to a specific event (mostly on the basis
77 of cruise data, i.e., [Estrada *et al.*, 2014; Severin *et al.*, 2014]), or at a fixed site (i.e., at the
78 DYFAMED sampling site, [Marty and Chiavérini, 2010]), or using satellite data that are limited
79 to surface layer of the ocean (i.e., [Barale *et al.*, 2008; Olita *et al.*, 2011; Volpe *et al.*, 2012;
80 Lavigne *et al.*, 2013; Mayot *et al.*, 2016]). Therefore, the lack of *in situ* observations
81 simultaneously inferring the main physical and biogeochemical variables is certainly a major
82 obstacle to unify a consensual description of the variability of the phytoplankton spring bloom
83 and to elucidate the whole phytoplankton annual cycle (from summer to summer). For the
84 moment, and at a large regional scale, this was only achieved by coupling satellite data with
85 model and scarce *in situ* data (e.g. [Chiswell, 2011]).

86 The recent development of autonomous platforms equipped with biogeochemical sensors
87 provided an excellent source of *in situ* data, and enabled studying the phytoplankton blooms and
88 its annual cycle in more details. At the global scale, biogeochemical autonomous platforms now
89 comprise the majority of the *in situ* simultaneous observations of physical and biogeochemical
90 properties that is collected [Biogeochemical-Argo Planning Group, 2016]. However, they are
91 still too scarce to provide a complete reconstruction of the biogeochemical fields at the regional
92 scale. For this reason, they have to be accurately spatially and temporally aggregated, depending
93 on the variability of the processes being investigated.

94 In this context, satellite data represent a powerful tool to divide the ocean into spatial ecological
95 units (or bioregions), which could be then used to contextualize *in situ* data (e.g., [Devred *et al.*,
96 2007; Frajka-Williams and Rhines, 2010; Lavigne *et al.*, 2013; Lacour *et al.*, 2015]). In other
97 terms, they provide an excellent opportunity to determine how *in situ* data collected over
98 different periods of time in an area can be analyzed together.

99 In the NWM, the phytoplankton production exhibits a significant seasonal variability with a large
100 part of the production taking place during the spring bloom (e.g. [Marty and Chiavérini, 2002;
101 Uitz *et al.*, 2012]). Knowing that phytoplankton production is essential for marine ecosystems
102 and biogeochemical cycles, the environmental mechanisms controlling its spatiotemporal
103 variability have to be identified. Therefore, the objective of this study is to evaluate, over an
104 annual cycle, the environmental properties that influence the dynamics of the phytoplankton
105 biomass, in the NWM. We will focus on the autumnal and spring blooms, and elucidate the main
106 physical and biogeochemical control processes leading to the seasonal and spatial variability of
107 the phytoplankton biomass.

108 For this, the role of several physical and biogeochemical properties in regulating the
109 phytoplankton blooms is assessed using year-round *in situ* observations from the whole NWM
110 area. The annual analysis presented here was possible thanks to the multiplatform approach
111 implemented in the DEWEX (DEep Water formation EXperiment) experiment, carried out

112 between July 2012 and July 2013 (for more details on DEWEX see *Testor et al., submitted*).
113 During DEWEX, five ship surveys were carried out at different periods of the year, with the
114 sampling strategy encompassing the whole NWM. During most of the periods and between ship
115 surveys, autonomous platform observations (i.e. profiling floats and gliders) were carried out.

116 The DEWEX experimental plan provided an exceptional density of *in situ* physical and
117 biogeochemical observations, which were analyzed in the context of large and consistent satellite
118 bioregions [*Mayot et al., 2016*] (as suggested by *The Mermex Group, [2011]*). Note that
119 bioregions are used here as a tool to generate time series of environmental properties from
120 dispersed and sparse *in situ* data. Such a large-scale approach, coupling satellite data with *in situ*
121 measurements, should highlight the large forcing factors affecting the phytoplankton
122 development, by averaging off the small-scale variabilities that might have an effect at a local
123 scale.

124 **2 Materials and Methods**

125 **2.1 Ship surveys**

126 Five ship surveys were carried out aboard the R/V *Le Suroît* and the R/V *Tethys II*: July 2012
127 (doi: 10.17600/12020030), September 2012 (doi: 10.17600/13450150), February 2013 (doi:
128 10.17600/13020010), April 2013 (doi: 10.17600/13020030) and July 2013 (doi:
129 10.17600/13450110). The station plan was identical for the five surveys, although the effective
130 number of stations differed between cruises (depending on weather conditions): 63 in
131 July/August 2012, 34 in September 2012, 54 in February 2013, 66 in April 2013 and 32 in July
132 2013 (**Fig. 1**).

133 Surface to bottom profiles of pressure, temperature, conductivity and chlorophyll fluorescence
134 were collected at each station. Profiles were derived from continuous measurements performed
135 with conductivity-temperature-depth sensors (CTD, SeaBird's 911plus) and a chlorophyll-*a*
136 measuring fluorometer (Chelsea AquaTrack). Discrete water samples were collected at 12
137 pressure levels with 12 L Niskin bottles, from which [Chla] (at 61 stations), particulate organic
138 carbon (POC, at 13 stations), nitrate (NO₃) and silicate (Si(OH)₄ at 121 stations) were measured.
139 Only the measurements from offshore stations (bathymetry greater than 1000 m) and that were
140 performed inside the studied bioregions (see Sect. 2.4) were used in the present study.

141 **2.2 Autonomous platforms: Argo floats, BGC-Argo floats and bio-optical gliders**

142 The ship surveys were supplemented by numerous autonomous platforms, which were deployed
143 to provide measurements between cruises. These include 13 Argo floats (between July 2012 and
144 July 2013, 493 profiles collected), five BGC-Argo floats (between September 2012 and July
145 2013, 292 profiles collected) and 10 bio-optical gliders (between September 2012 and July 2013,
146 2113 profiles collected) (**Fig. 1**).

147 Argo and BGC-Argo floats are autonomous profiling floats that drift at depth and collect
148 measurements during upward casts from 1000 m or 2000 m to the surface. These casts generally
149 take place at noon, every day or every five to ten days. Bio-optical gliders are steerable,
150 autonomous platforms that perform measurements in the water column along a saw-tooth
151 trajectory between the surface and a maximum depth of 1000 m, each profile being separated by
152 approximately 2–4 km and 2–4 h. For all these platforms, only profiles with measurements
153 obtained from the surface down to 1000 m were kept.

154 All the autonomous platforms were equipped with CTD sensors (MedArgo Program, [Poulain *et*
155 *al.*, 2007]). Some platforms also carried biogeochemical sensors. Four BGC-Argo floats [Le
156 Traon *et al.*, 2012; Barnard and Mitchell, 2013] and the 10 bio-optical gliders [Niewiadomska *et*
157 *al.*, 2008; Testor *et al.*, 2010] were equipped with a chlorophyll-*a* measuring fluorometer. Three
158 of the BGC-Argo floats were also equipped with an optical backscattering at 700 nm and a
159 multispectral ocean color radiometer for measuring photosynthetically available radiation (PAR,
160 integrated over 400–700 nm, [Organelli *et al.*, 2016]), and one of them carried also a nitrate
161 sensor [Le Traon *et al.*, 2012; Pasqueron de Fommervault *et al.*, 2015a]. A fifth BGC-Argo float
162 only had a nitrate sensor [D’Ortenzio *et al.*, 2012].

163 **2.3 Retrieval of physical and biogeochemical properties**

164 Among all the variables measured during the DEWEX experiment, only temperature, salinity,
165 [Chl-*a*], NO₃, Si(OH)₄, PAR and the optical particle backscattering coefficients (b_{bp} , converts to
166 POC) were specifically analyzed. The choice of these parameters is based on the fact that most
167 of them were measured from both ships and autonomous platforms, which dramatically
168 increased the number of available observations.

169 **2.3.1 Mixed layer depth (MLD)**

170 The shipborne temperature and conductivity sensors were corrected for possible drifts, assessed
171 between pre-cruise and post-cruise calibration baths. For the temperature and conductivity
172 sensors of bio-optical gliders, an offset per deployment was estimated by comparing the
173 measurements performed in the deep layers (700-1000 m) with nearby CTD casts collected by
174 the ship or mooring line (the bio-optical glider CTD calibration is fully presented in [Bosse *et al.*,
175 2015]). A similar method was used here to calibrate the BGC-Argo float CTD sensors. For Argo
176 floats, only data flagged “good” after a Coriolis data center quality control (www.coriolis.eu.org)
177 were considered.

178 The potential density was then derived from pressure, temperature and conductivity. For each
179 available density profile, the MLD was estimated with a density criterion of 0.01 kg m⁻³ (using
180 the 10 m data as reference). Indeed, Houpert *et al.* [2016] argued that a fine criterion is needed to
181 better represent the winter deep mixed layer of the Gulf of Lion due to its weak stratification.
182 When a profile was found to be completely homogeneous according to this criterion, the MLD as
183 associated to the maximal depth of the profile (i.e., 1000 m) even though it might have been
184 deeper.

185 **2.3.2 Chlorophyll-*a***

186 The [Chl-*a*] was evaluated in the discrete water samples collected with Niskin bottles. For this,
187 between 0.62 L and 3.2 L of water samples were filtered onto glass fiber filters (GF/F *Whatman*
188 25 mm), that were then stored at -80°C until further analysis at the Oceanography Laboratory of
189 Villefranche-sur-mer. The phytoplankton pigments, including the chlorophyll-*a*, were extracted
190 from the filters in 100% methanol, disrupted by sonication and clarified by filtration (GF/F
191 *Whatman* 0.7 μm) and finally separated and quantified by High-Performance Liquid
192 Chromatography (HPLC, for further details see [Ras *et al.*, 2008]).

193 The [Chl-*a*] was also estimated with chlorophyll-*a* measuring fluorometers mounted on a CTD-
194 rosette, BGC-Argo floats and bio-optical gliders. For this, the factory calibrations were firstly
195 applied to all fluorometers so as to convert the fluorescence signal into a nominal [Chl-*a*].

196 Secondly, a three-step post-processing procedure was applied to all profiles. The first step of the
197 post-processing consisted in the estimation of a deep offset, corresponding to the median value
198 of fluorescence over the 950-1000 m range. Except for deep mixing conditions, the deep
199 chlorophyll-*a* fluorescence was expected to be null, hence the offset could be removed from the
200 whole profile. The second step consisted in removing spikes by using a median filter. The third
201 and last step corrected the fluorescence profile for non-photochemical quenching, following the
202 procedure of [Xing *et al.*, 2012]. Exclusively for bio-optical gliders, only night profiles (between
203 22 pm and 2 am) were used in order to avoid non-photochemical quenching. These night profiles
204 were also averaged to remove small-scale variabilities.

205 Finally, each individual platform fluorometer was calibrated with all available simultaneous
206 bottle measurements of [Chl-*a*] (i.e. HPLC estimations) using a least-square linear regression.
207 For shipborne fluorometers, the fluorescence measurements at the time of the bottle samplings
208 were used for the linear regression. For autonomous platforms, only fluorescence profiles
209 performed on the same day as the water sampling cast, and within a spatial radius lesser than 35
210 km, were retained for the regression. On average, the spatiotemporal lag between the
211 fluorescence profiles and the sampling casts were 13 h and 12.5 km. It is noteworthy that the
212 fluorescence values around the depth of available bottle samples (± 5 m) were averaged and
213 kept for the linear regression only when the densities measured from both platforms at the given
214 depth were similar (a density difference lesser than 0.03 kg.m^{-3} , or 0.01 kg.m^{-3} for winter mixing
215 conditions). The linear regression provided two coefficients: a scale factor (the slope) and a dark
216 value (the intercept). For each linear regression, the dark value was systematically null (i.e., not
217 statistically different from zero, t-test, *p-value* <0.001), as an offset had already been applied to
218 the fluorescence profiles during the post-processing steps. Thus, only the scale factor needed to
219 be applied in order to calibrate the fluorometer (**Table 1**).

220 When simultaneous measurements of [Chl-*a*] and fluorescence were unavailable to align the
221 platform fluorometer with the bottle measurements, a calibration method using satellite ocean
222 color data was used instead [Lavigne *et al.*, 2012]. This was only the case for bio-optical glider
223 fluorometers. The calibration obtained from this method was tested against the one using the
224 bottle measurements. To do so, the calibration of Lavigne *et al.* [2012] was applied to the whole
225 dataset of fluorescence profiles and compared to the bottle measurements associated with these
226 fluorescence profiles. Both calibrations gave satisfying and similar results (MADP of 23% with
227 HPLC and MADP of 38% with satellite), thus supporting the use of the method of Lavigne *et al.*,
228 [2012] when direct comparison with *in situ* data was not possible.

229 **2.3.3 Nitrate and Silicate**

230 To evaluate NO_3 ($\pm 0.02 \text{ }\mu\text{M}$) and $\text{Si}(\text{OH})_4$ ($\pm 0.05 \text{ }\mu\text{M}$) concentrations (as detailed in [Severin
231 *et al.*, 2014]), 20 mL of seawater were immediately filtered on board (using $0.45 \text{ }\mu\text{m}$ cellulose
232 acetate filters) and stored in 20 ml polyethylene vials at -20°C until analysis. In the laboratory,
233 samples were rapidly thaw and analyzed by colorimetry on a Seal-Bran-Luebbe autoanalyzer
234 AA3 HR, according to Aminot and K erouel, [2007].

235 Two BGC-Argo floats were equipped with a nitrate sensor (SUNA), which measured the *in situ*
236 $[\text{NO}_3]$ by measuring the UV absorption spectrum over the 217-240 nm range [Johnson and
237 Coletti, 2002]. Several possible algorithms exist for deconvoluting $[\text{NO}_3]$ from the observed UV
238 absorption spectrum (e.g., [Johnson and Coletti, 2002; Sakamoto *et al.*, 2009; Zielinski *et al.*,
239 2011]). For the first BGC-Argo float (PROVOR-SUNA), only the processed data were

240 transmitted (i.e. $[\text{NO}_3]$ computed by the manufacturer algorithm), and a specific calibration was
 241 developed that accounted for temperature and salinity corrections (fully explained in [D'Ortenzio
 242 *et al.*, 2014]). For the second BGC-Argo float, $[\text{NO}_3]$, as well as raw data (i.e. absorbance
 243 spectrum) were transmitted, allowing for data reprocessing with the modified Sakamoto
 244 algorithm [Pasqueron de Fommervault *et al.*, 2015a]. The two sensors were then calibrated by
 245 using *in situ* data, and resulted in a detection limit of $\sim 1 \mu\text{M}$ (see [D'Ortenzio *et al.*, 2014;
 246 Pasqueron de Fommervault *et al.*, 2015a] for details). The $[\text{NO}_3]$ in the MLD was averaged
 247 ($[\text{NO}_3]_{\text{MLD}}$) by using the corresponding MLD values.

248 2.3.4 Particulate Organic Carbon

249 For 13 stations performed during DEWEX cruises, POC concentration ($[\text{POC}]$) was estimated
 250 from the discrete bottle samples. For this, POC was collected on precombusted (24 h, 450 C)
 251 glass fiber filters (Whatman GF/F, 25 mm). Filters were dried in an oven at 50°C and stored in
 252 ashed glass vial and in a dessicator until analysis in laboratory on a CHN autoanalyser.

253 Several studies demonstrated that the $[\text{POC}]$ can also be estimated from b_{bp} (e.g. [Loisel *et al.*,
 254 2001; Cetinić *et al.*, 2012]). Therefore, from optical backscattering mounted on BGC-Argo
 255 floats, the b_{bp} was computed following the protocol of [Schmechtig *et al.*, 2015] to estimate POC.
 256 Spikes from the resulting b_{bp} profiles were firstly removed with a 5-points median filter followed
 257 by a 7-points moving average [Briggs *et al.*, 2011]. Following the same procedure as the
 258 chlorophyll-*a* measured by the BGC-Argo fluorometers (see Sect. 1.3.2), b_{bp} was converted into
 259 POC with factors of calibration obtained by comparing b_{bp} data with simultaneous bottle
 260 measurements of $[\text{POC}]$, using a least-square linear regression. For this, data from all BGC-Argo
 261 floats were used together to obtain a unique linear regression: $\text{POC} = 54463 \times b_{\text{bp}} - 1.19$ ($n = 33$
 262 and $r^2 = 0.82$, $p\text{-value} < 0.001$).

263 2.3.5 The euphotic zone

264 The euphotic zone was defined as the isolume depth $0.415 \text{ mol photons m}^{-2} \text{ d}^{-1}$ ($Z_{0.415}$), because
 265 phytoplankton photosynthesis is assumed to be impossible below $0.415 \text{ mol photons m}^{-2} \text{ d}^{-1}$
 266 [Letelier *et al.*, 2004; Boss and Behrenfeld, 2010; Brody and Lozier, 2014; Cetinić *et al.*, 2015].
 267 This definition is used instead of the depth where the downward PAR irradiance equal 1% of the
 268 surface value ($Z_{1\%}$), which only depends on the transparency of the water column.

269 For this, the daily average PAR irradiance at the surface (PAR_0 , measured from MODIS AQUA
 270 satellite at 8 days and 9 km of resolution) is used with a diffuse attenuation coefficient for the
 271 downward PAR irradiance (K_{PAR}) derived from MODIS AQUA satellite [Chl-*a*] values ($[\text{Chl-}$
 272 $\text{a}]_{\text{sat}}$, at 8 days and 9 km of resolution, see the equation 10 in [Morel *et al.*, 2007]):

$$273 \quad Z_{0.415} = \log\left(\frac{0.415}{\alpha \times \text{PAR}_0}\right) \left(\frac{1}{K_{\text{PAR}}}\right) \quad (1)$$

274 where α is the factor correcting the PAR_0 values for transmission through the air-sea interface
 275 [Mobley *et Boss*, 2012]. An *in situ* evaluation of this $Z_{0.415}$ estimate was also performed by
 276 combining PAR_0 with the PAR profiles recorded by BGC-Argo floats ($\text{PAR}_{\text{float}}$) and following
 277 the same approach as Letelier *et al.*, [2004]:

$$278 \quad \text{PAR}(z) = \alpha \times \text{PAR}_0 \times \left(\frac{\text{PAR}_{\text{float}}(z)}{\text{PAR}_{\text{float}}(0)}\right) \quad (2)$$

279 where $PAR(z)$ is the PAR value for a specific depth and PAR_{float} the instantaneous PAR
 280 measured by a BGC-Argo float. For this, PAR_0 data at 1 day and 9 km of resolutions from
 281 MODIS AQUA satellite are used.

282 The interplay between $Z_{0.415}$ and the MLD was investigated using their ratio ($Z_{0.415}/MLD$). In
 283 addition, the “penetration depth” (Z_{pd}), i.e. the depth encompassing 90% of the satellite-
 284 measured signal [Gordon and McCluney, 1975], is derived as $Z_{pd} = Z_{1\%} \times 4.6$ [Morel and
 285 Berthon, 1989].

286 **2.4 A satellite-based bioregionalization of the NWM**

287 *In situ* observations of physical and biogeochemical properties are sparse and dispersed over a
 288 large region (**Fig. 1**). They were thus grouped selectively over biogeochemical-coherent areas in
 289 order to generate unique time-series for each of them. For this, a satellite-based
 290 bioregionalization was used.

291 Here, the recent bioregionalization of the Mediterranean basin based on $[Chl-a]_{sat}$ was chosen
 292 [Mayot *et al.*, 2016]. More precisely, this bioregionalization considered a climatological analysis
 293 [D’Ortenzio and Ribera d’Alcalà, 2009] to provide bioregions at the annual time scale. The
 294 positions of the bioregions present in the NWM according to Mayot *et al.*, [2016], between July
 295 2012 and July 2013, were extracted (**Fig. 2a**), in addition to their associated mean annual time-
 296 series of $[Chl-a]_{sat}$ (**Fig. 2b**, data at 8 days and 9 km of resolutions from MODIS AQUA).

297 This bioregionalization of Mayot *et al.*, [2016] (determined on the basis of the shape of the
 298 annual cycle of surface $[Chl-a]$) is used under the hypothesis that similar patterns of surface
 299 $[Chl-a]$ reflect comparable variations of physical and biogeochemical properties of the water
 300 column. Therefore, all available *in situ* data of physical and biogeochemical properties (i.e.,
 301 MLD, $[Chl-a]$, $[NO_3]$, $[Si(OH)_4]$, $[POC]$ and PAR) were spatially assembled into bioregions
 302 according to their location. We prefer grouping *in situ* observations on the basis of these
 303 bioregions rather than using spatial criteria or using intensively statistical interpolations and
 304 analysis methods applied to our datasets.

305 The availability of density, fluorescence, $[NO_3]$, $[POC]$ and PAR profiles throughout the year
 306 used to reconstruct these time-series of physical and biogeochemical properties is summarized in
 307 **figure 3**. The period of maximum availability of *in situ* profiles throughout the year extended
 308 from January to June 2013 (**Fig. 3**). Before January 2013, the availability of observations was
 309 restricted to the ship survey periods (in August and September 2012) and to the bio-optical glider
 310 transects (in December 2012). For the nitrate and POC profiles, data were essentially available
 311 after February 2013, through the profiles collected during the two DEWEX cruises (in February
 312 and April) and by some BGC-Argo floats that operated in between. The nine profiles from one
 313 BGC-Argo float that were performed in a cyclonic eddy in late April were removed: indeed, as
 314 the platform undertook measurements when there was a low availability of biogeochemical
 315 observations (**Fig. 3a**), a structure completely different from the surrounding environment may
 316 have led to a misinterpretation. Data were daily averaged and a five days median filter was
 317 finally applied on the reconstructed time-series.

318 **2.5 Dates of the phytoplankton bloom initiation**

319 The initiation date of the phytoplankton blooms was determined through three different
 320 phenological metrics. Different metrics were used because the inherent variability between them
 321 could highlight different periods of the year [Brody *et al.*, 2013; Ferreira *et al.*, 2014].

322 The first metric was based on the air-sea heat flux (“Heat Flux” criterion, [Ferrari *et al.*, 2015]).
 323 According to this criterion, the phytoplankton bloom is initiated with the warming of the ocean
 324 (a positive air-sea heat flux). To determine this date, daily air-sea flux data at $0.125^\circ \times 0.125^\circ$
 325 resolution from ECMWF ERA-interim reanalysis were used [Dee *et al.*, 2011; Donlon *et al.*,
 326 2012]. A time-series for each bioregion was then generated by averaging data with a 7-days
 327 median filter. After the date of the winter minimum negative heat flux, the date of the onset of
 328 the phytoplankton bloom corresponded to the first day with positive air-sea heat fluxes. To
 329 discuss the potential influence of the wind, time-series of daily wind speed for each bioregion
 330 was also generated from data available from ECMWF ERA-interim reanalysis, at the same
 331 spatial resolution.

332 The second phenological metric determined the start date as the day when the $[\text{Chl-a}]_{\text{sat}}$ time-
 333 series exceeds a certain threshold. Two different thresholds were used here: 1) the semi-annual
 334 (i.e., from July 2012 to the date of the $[\text{Chl-a}]_{\text{sat}}$ maximum) median value plus 5% (“median +
 335 5%” criterion, [Siegel *et al.*, 2002; Brody *et al.*, 2013; Hopkins *et al.*, 2015]); 2) the 15% of the
 336 cumulative sum of the annual $[\text{Chl-a}]_{\text{sat}}$ (“15% cum. sum.” criterion, [Brody *et al.*, 2013]).

337 The third and last phenological metric established the bloom start date as the day displaying the
 338 maximal accumulation of phytoplankton biomass (using the $[\text{Chl-a}]_{\text{sat}}$ as a proxy of the
 339 phytoplankton biomass) in the period preceding the date of the $[\text{Chl-a}]_{\text{sat}}$ maximum. Therefore,
 340 the net phytoplankton biomass accumulation rates (r , also referred to as the rate of phytoplankton
 341 biomass changes, e.g. [Behrenfeld and Boss, 2014]) is used and calculated using the mean $[\text{Chl-}$
 342 $\text{a}]_{\text{sat}}$ time-series (as in [Lacour *et al.*, 2015]):

$$343 \quad r = \log \left(\frac{[\text{Chl-a}]_{\text{sat}}(t+\Delta t)}{[\text{Chl-a}]_{\text{sat}}(t)} \right) \times \frac{1}{\Delta t} \quad (3)$$

344 where Δt corresponds to the time interval (here 8 days).

345 **3 Results**

346 **3.1 Two distinct bioregions in the NWM**

347 For the 2012-2013 period, two main bioregions are identified in the NWM, the “High Bloom”
 348 bioregion, located in the center of the NWM, and the “Bloom” bioregion, located at its periphery
 349 (**Fig. 2a**). These bioregions are characterized by similar patterns in $[\text{Chl-a}]_{\text{sat}}$ temporal evolution
 350 (**Fig. 2b**). Low mean values of $[\text{Chl-a}]_{\text{sat}}$ are observed during the summer ($< 0.25 \text{ mg m}^{-3}$)
 351 followed by a slight increase in autumn (in November/December, $0.3\text{-}0.4 \text{ mg m}^{-3}$). Low winter
 352 values ($< 0.3 \text{ mg m}^{-3}$) are then observed, before a subsequent increase from March to mid-April.
 353 The main difference between the two time-series can be observed during this last period, with the
 354 spring maximal value in $[\text{Chl-a}]_{\text{sat}}$ clearly lower in the “Bloom” (1.3 mg m^{-3}) than in the “High
 355 Bloom” bioregion (2.9 mg m^{-3}). After the spring maximum, both bioregions are characterized by
 356 a progressive return to a summer oligotrophy (in May, **Fig. 2b**).

357 For both bioregions, the phenological metrics based on threshold criteria (i.e., “median + 5%”
 358 and “15% cum. sum.”) show that the phytoplankton bloom starts in autumn
 359 (November/December, **Fig 2c**). The “Heat Flux” and the “max. ROC” criteria point out a
 360 phytoplankton bloom in spring (**Fig 2c**). However, the “max ROC” criteria indicated a spring
 361 bloom one month earlier in the “Bloom” bioregion (2 March \pm 4 days) than in the “High Bloom”
 362 bioregion (3 April \pm 4 days).

363 3.2 Time series of physical and biogeochemical properties in the two bioregions

364 3.2.1 Heat flux and wind speed

365 The mean time-series of the net heat flux and of the surface wind speed, calculated for the two
 366 bioregions, are comparable (**Fig. 4a-b**). In summer positive net heat flux ($\sim 100 \text{ W m}^{-2}$) are
 367 associated with relatively low wind speed values ($< 8 \text{ m s}^{-1}$), while recurrent strong negative net
 368 heat flux ($< -200 \text{ W m}^{-2}$) and wind burst events ($> 8 \text{ m s}^{-1}$) are observed in winter. During the
 369 transitional periods of spring and autumn, net heat flux values are marked by multiple positive to
 370 negative changes around zero, and wind speed is around 8 m s^{-1} .

371 Beyond these similar seasonal trends between the two bioregions, the average intensity in winter
 372 of surface heat losses and wind speed are higher in the “High Bloom” bioregion (-176 W m^{-2} and
 373 8 m s^{-1} , with daily maximum at -376 W m^{-2} and 11.9 m s^{-1}) than in the “Bloom” bioregion (-142
 374 W m^{-2} and 7.2 m s^{-1} , with daily maximum at -325 W m^{-2} and 10.1 m s^{-1}). Interestingly, the
 375 winter-spring transition is marked by a first event of positive net heat flux the 5th March,
 376 followed by a short event of strong surface heat losses, mainly in the “High Bloom” bioregion ($-$
 377 149.8 W m^{-2}), before the net heat flux becomes totally positive after the 20th March.

378 3.2.2 The MLD, the $Z_{0.415}$ and the $Z_{0.415}/\text{MLD}$ ratio

379 The seasonal evolution of the MLD in both bioregions is similar (**Fig. 4c**), with a minimum in
 380 summer, a progressive deepening in autumn and a maximum reached in late winter followed by a
 381 rapid shallowing in spring. The main differences between the MLDs associated to both
 382 bioregions are observed in winter. In the “High Bloom” bioregion, the deepening of the MLD
 383 (when $\text{MLD} > 200 \text{ m}$) starts in January and ends (when $\text{MLD} < 25 \text{ m}$) in April, with a very deep
 384 MLD observed in February (two mean MLD maxima $> 880 \text{ m}$). It should be recalled that MLD
 385 estimates are underestimated because profiles are only recorded down to 1000 m , while vertical
 386 mixing has been found to reach far greater depths ($> 2300 \text{ m}$) in February in the Gulf of Lion
 387 [Houpert *et al.*, 2016]. On the contrary, the MLD deepening is shorter and shallower in the
 388 “Bloom” bioregion (from February to March only, with a mean MLD maximum $\sim 475 \text{ m}$ reached
 389 within a couple of days only).

390 The temporal evolutions of $Z_{0.415}$ and $Z_{1\%}$ are similar in both bioregions, showing deeper values
 391 in summer and autumn, and shallower values during winter/spring (**Fig. 4d**). At the transition
 392 periods in autumn and spring, *in situ* evaluations of $Z_{1\%}$ and $Z_{0.415}$ (dark and red points in **Fig.**
 393 **4d**) are in accordance with the estimates obtained from satellite data (see Sect. 2.3.5). In winter,
 394 the shallower $Z_{1\%}$ and $Z_{0.415}$ derived from satellite compared to the *in situ* evaluations could be
 395 due to an overestimation of the $[\text{Chl-a}]_{\text{sat}}$, which induced an higher K_{PAR} . Nevertheless, $Z_{1\%}$ and
 396 $Z_{0.415}$ show differences in the autumnal shallowing, with a faster shallowing of $Z_{0.415}$ than $Z_{1\%}$,
 397 which support the use of $Z_{0.415}$, than $Z_{1\%}$, in order to not overestimate Z_{eu} .

398 The difference in the extent of winter MLD between bioregions can impact phytoplankton
 399 retention differently above the Z_{eu} , defined here as $Z_{0.415}$. This impact was addressed through the
 400 $Z_{0.415}/\text{MLD}$ ratio (**Fig. 4e**). This ratio can be considered as a proxy of the time when the
 401 phytoplankton is mixed below the euphotic zone ($Z_{0.415}/\text{MLD} < 1$) or above ($Z_{0.415}/\text{MLD} > 1$). A
 402 transition period from a $Z_{0.415}/\text{MLD} > 1$ state to a $Z_{0.415}/\text{MLD} < 1$ state (and vice versa) means
 403 important changes in light conditions experienced by phytoplankton. In summer, the $Z_{0.415}/\text{MLD}$
 404 ratio is largely greater than 1 ($Z_{0.415} \gg \text{MLD}$), whereas it is considerably lesser than 1 in winter

405 ($Z_{0.415} \ll \text{MLD}$). Between these two contrasted situations, two transition periods with a MLD
 406 close to $Z_{0.415}$ can be identified ($Z_{0.415}/\text{MLD} \approx 1$).

407 A first transition period occurs in late autumn (early December) in both bioregions. At this time
 408 of the year, the MLD deepens in response to an increase in average wind speed and surface heat
 409 loss, while the $Z_{0.415}$ shallows due to the seasonal decrease in PAR_0 (the day length is reduced),
 410 and both induced a $Z_{0.415}/\text{MLD} < 1$. A second transition period occurs in spring (in March).
 411 During the spring transition period, the $Z_{0.415}/\text{MLD}$ ratio is highly variable, mostly driven by
 412 variations of the mean MLD. After the maximum of MLD that is observed in February, a first
 413 event of $Z_{0.415}/\text{MLD} > 1$ occurs. Then a last annual event of very deep MLD is observed in mid-
 414 March and can be related to surface heat loss (**Fig. 4**), before the $Z_{0.415}$ and the MLD come closer
 415 again ($Z_{0.415}/\text{MLD} > 1$). The temporal dynamics of the $Z_{0.415}/\text{MLD}$ ratio associated with both
 416 bioregions, illustrated by color bars (below **Fig. 4f**, with black bars representing $Z_{0.415}/\text{MLD} = 1$),
 417 are further compared with the observed vertical distribution of [Chl-a] and with the [POC] and
 418 [NO₃] within the MLD.

419 3.3 The MLD, $Z_{0.415}$ and [Chl-a] interplay in the two bioregions

420 For the two bioregions, the reconstructed time-series of surface [Chl-a] (i.e., [Chl-a] averaged in
 421 Z_{pd} , $[\text{Chl-a}]_{Z_{\text{pd}}}$) retrieved from *in situ* observations (**Fig. 4f**) are similar to those obtained from the
 422 $[\text{Chl-a}]_{\text{sat}}$. The low summer and winter $[\text{Chl-a}]_{\text{sat}}$ values are confirmed, as well as the delayed and
 423 stronger $[\text{Chl-a}]_{\text{sat}}$ increase in the “High Bloom”. Then, all [Chl-a] data from the available
 424 profiles in both bioregions were averaged every 10 m and every two days, in order to describe
 425 the vertical distribution of [Chl-a] throughout the annual cycle (**Fig. 5**).

426 Typical patterns in the vertical distribution of [Chl-a] are associated with the key periods
 427 identified thanks to the $Z_{0.415}/\text{MLD}$ ratio. During summer, when the $Z_{0.415}/\text{MLD}$ is greater than 1
 428 ($Z_{0.415} \gg \text{MLD}$, **Fig. 5**), the vertical distribution of [Chl-a] is characterized by very low surface
 429 concentrations ($[\text{Chl-a}] < 0.25 \text{ mg m}^{-3}$) and the presence of a [Chl-a] maximum at depth (DCM),
 430 generally above $Z_{0.415}$. These summer features in the vertical distribution of [Chl-a] are observed
 431 in both bioregions. The [Chl-a] integrated over the $Z_{0.415}$ ($[\text{Chl-a}]_{Z_{0.415}}$) and over 0-1000 m ($[\text{Chl-}$
 432 $\text{a}]_{1000}$) are similar ($\sim 25\text{-}50 \text{ mg m}^{-2}$, **Fig. 6**).

433 When the autumnal transition period of the $Z_{0.415}/\text{MLD}$ ratio occurs (in December, **Fig. 5 and 6**),
 434 and when the MLD deepens for the first time after the summer, the surface [Chl-a] distribution
 435 appears to be homogenous (**Fig. 5**), indicating that the DCM has already vanished (vertical [Chl-
 436 $\text{a}]$ profiles in **Fig. 6**). The $[\text{Chl-a}]_{Z_{0.415}}$ and $[\text{Chl-a}]_{1000}$ begin to diverge, with the $[\text{Chl-a}]_{1000}$
 437 increasing more rapidly than the $[\text{Chl-a}]_{Z_{0.415}}$ (**Fig. 6**).

438 Thereafter, in winter, the $Z_{0.415}/\text{MLD}$ ratio is lower than 1 ($Z_{0.415} \ll \text{MLD}$, **Fig. 5**). In January
 439 when MLDs are lower than 400 m, $[\text{Chl-a}]_{1000}$ continues to increase until a maximum in late
 440 January ($\sim 25\text{-}50 \text{ mg m}^{-2}$, **Fig. 6**). Then, when MLDs reach their maximum with a homogeneous
 441 [Chl-a] over the mixed layer, a decrease of the $[\text{Chl-a}]_{1000}$ is observed in both bioregions (~ 50
 442 mg m^{-2}), as well as the annual minimum of $[\text{Chl-a}]_{Z_{\text{pd}}}$ ($\sim 0.05 \text{ mg m}^{-3}$ in the “Bloom” bioregion,
 443 and $\sim 0.1 \text{ mg m}^{-3}$ in the “High Bloom” bioregion, **Fig. 4f**) and $[\text{Chl-a}]_{Z_{0.415}}$ ($\sim 25 \text{ mg m}^{-2}$ in the
 444 “Bloom” bioregion, and $\sim 11 \text{ mg m}^{-2}$ in the “High Bloom” bioregion, **Fig. 6**). The lowest surface
 445 *in situ* [Chl-a] associated with the “High Bloom” bioregion confirms a higher surface dilution of
 446 [Chl-a] in this bioregion, induced by a very deep winter MLD.

447 At the spring transition period, the MLD becomes lower than $Z_{0.415}$ and the [Chl-a] increase at
 448 the surface (**Fig. 4, 5 and 6**). The high availability of [Chl-a] profiles in the “High Bloom”
 449 bioregion allows a better description of the temporal dynamics of such spring [Chl-a] increase,
 450 analyzed here with $r = \partial[\text{Chl} - a]_{Z_{0.415}}/\partial t$ (the growth of the [Chl-a] integrated in $Z_{0.415}$). The
 451 MLD becomes shallower than $Z_{0.415}$ during two successive events: March 9 and March 25. Each
 452 time, r starts to be positive one week before $Z_{0.415}/\text{MLD} > 1$, and a couple of days before the
 453 surface heat flux begins to be positive. Then, r is maximal at the time of $Z_{0.415}/\text{MLD} > 1$, or a
 454 couple of days before (and five or six days after the heat flux became positive).

455 Finally, and in both bioregions, when the $\text{MLD}/Z_{0.415}$ is definitively greater than 1 (i.e., on the 7-
 456 9th of April), the maximal annual values of [Chl-a] are observed (**Fig. 4, 5 and 6**). Note however,
 457 that the surface [Chl-a] increase is larger in the “High Bloom” bioregion ([Chl-a] _{$Z_{0.415}$} increased
 458 from 25 to 100 mg m⁻², **Fig. 6b**, with higher surface values > 6 mg m⁻³, **Fig. 5b**) than in the
 459 “Bloom” bioregion ([Chl-a] _{$Z_{0.415}$} increased from 40 to 70 mg m⁻², **Fig. 6a**, with [Chl-a] surface
 460 values < 3 mg m⁻³, **Fig. 5a**).

461 3.4 The [POC]_{MLD} and [NO₃]_{MLD} in both bioregions

462 As a reminder, the availability of [POC] and [NO₃] profiles is higher after February 2013, thanks
 463 to the BGC-Argo floats. Therefore, time series of [POC]_{MLD} and of [NO₃]_{MLD} were only
 464 computed between February 2013 to July 2013. The temporal dynamics of [POC]_{MLD} is
 465 comparable in both bioregions. In February 2013, [POC]_{MLD} is low (< 30 mg m⁻³). In March and
 466 April, during the spring transition period, the [POC]_{MLD} increases with surface [Chl-a] (**Fig. 7**).
 467 Finally, in summer the [POC]_{MLD} decreases, but is still higher than in winter.

468 From February to early April, [NO₃]_{MLD} is generally high with peak values around 8 μM and on
 469 average ~6 μM for the “High Bloom” and ~5 μM for the “Bloom” bioregion (**Fig. 7**). High
 470 variability around the mean values is also observed (**Fig 7**), most probably due to the low
 471 availability of [NO₃] profiles during this period (**Fig. 3**).

472 Later, from late February to the end of March, [NO₃]_{MLD} data become scarce, as only a single
 473 BGC-Argo float is available for this period. The float initially samples the “Bloom” bioregion
 474 measuring [NO₃]_{MLD} values of ~4 μM and then moves to the “High Bloom” bioregion, where it
 475 detects a rapid increase in [NO₃]_{MLD} from ~4.5 to 8 μM. The timing of this nitrate increase
 476 coincides with a late mixing event occurring around the 10th March, which deepens the mixed
 477 layer down to about 2000 m in the Gulf of Lion [Houpert *et al.*, 2016]. In April, [NO₃]_{MLD}
 478 uniformly decreases in both bioregions. These significant decreases in [NO₃]_{MLD} are followed by
 479 a brief increase in both bioregions (20th-23rd April), before rapidly and definitely decreasing
 480 down to summer values of ~0.5 μM (**Fig. 7**).

481 4 Discussion

482 By coupling satellite data with *in situ* physical and biogeochemical observations, the influence of
 483 environmental factors on phytoplankton seasonal cycles in the NWM were analyzed from July
 484 2012 to July 2013. Ocean color data ([Chl-a]_{sat}) indicated that surface phytoplankton distribution
 485 was structured in two large areas. The later are referred to as the “Bloom” and “High Bloom”
 486 bioregions (**Fig. 2**, following the results of Mayot *et al.*, [2016]) due to the contrasted timing and
 487 intensity of their phytoplankton spring blooms. Using this satellite spatial framework, coherent
 488 annual time series of physical and biogeochemical properties associated with these two
 489 bioregions were estimated and analyzed.

490 *Mayot et al.*, [2016] demonstrated a relationship between the inter-annual occurrences in the
 491 “High Bloom” bioregion and deep winter convection events. Therefore, a better understanding of
 492 the environmental factors controlling the observed spatial distinction between the “Bloom” and
 493 “High Bloom” bioregions will also improve our understanding of the inter-annual variability in
 494 phytoplankton dynamics. In the following sections, we will discuss (1) the processes regulating
 495 the temporal dynamics of phytoplankton biomass, with a focus on the autumnal and spring
 496 blooms, and (2) the environmental and biological factors inducing differences in phytoplankton
 497 biomass between bioregions during the spring bloom.

498 **4.1 The temporal dynamics of phytoplankton in the NWM**

499 For both bioregions, two phenological metrics (i.e., “Heat Flux” and “Max Roc”) identified a
 500 spring bloom (in March/April in Fig 2), while two different criteria (i.e., “Med +5%” and “15%
 501 Cum”) identified an autumnal bloom. The existence of these two blooms coincide with a typical
 502 temperate dynamic.

503 In temperate seas, the phytoplankton spring bloom is generally thought to begin when the MLD
 504 starts to shallow (e.g., [Cullen *et al.*, 2002; Chiswell *et al.*, 2015]). This concept was founded on
 505 the “critical depth” definition of Sverdrup, [1953], the depth at which the vertically integrated
 506 phytoplankton production and losses are equal. Stating that a “critical depth” exists, Sverdrup,
 507 [1953] proposed that the date at which the MLD shallows above this critical depth marks the
 508 establishment of the phytoplankton spring bloom. [Chiswell, 2011] demonstrated that the
 509 Sverdrup theory could be used to explain the occurrence of the autumnal bloom, following the
 510 definition of an “entrainment bloom” [Cullen *et al.*, 2002]. For the NWM, which lies at the limit
 511 between the sub-tropical and sub-polar regimes [Follows and Dutkiewicz, 2001; Henson *et al.*,
 512 2009; Bernardello *et al.*, 2012], the importance of MLD shallowing for spring bloom dynamics
 513 has already been mentioned [Lavigne *et al.*, 2013].

514 However, several recent hypotheses challenged the Sverdrup’s theory, by arguing that the
 515 vertical mixing in the mixed layer could be significantly reduced, which allow the onset of
 516 blooms in surface and prior to stratification (e.g. [Townsend *et al.*, 1994; Huisman *et al.*, 1999;
 517 Taylor and Ferrari, 2011a; Franks, 2014]). Similarly, mesoscale features could locally weaken
 518 surface turbulence, inducing favorable conditions for bloom onsets [Lévy *et al.*, 1999;
 519 Mahadevan *et al.*, 2012]. Another hypothesis is based on trophic interactions within the mixed
 520 layer. [Behrenfeld, 2010] suggested that the phytoplankton biomass accumulation could start in
 521 winter when the MLD increase due to the dilution of both phytoplankton and grazers that induce
 522 low losses (i.e. “dilution-recoupling model”, see also [Boss and Behrenfeld, 2010; Behrenfeld
 523 and Boss, 2014]).

524 In our study, the autumnal and spring bloom periods were unambiguously identified by changes
 525 in the $Z_{0.415}$ /MLD ratio. Therefore in the next section, we will focus on the environmental and
 526 biological factors controlling the link between the $Z_{0.415}$ /MLD ratio and the phytoplankton bloom
 527 periods, by accounting for the above-mentioned theories.

528 **4.1.1 The autumnal bloom to the winter period**

529 In autumn, the $Z_{0.415}$ and MLD interfaces overlapped, with a $Z_{0.415}$ /MLD < 1 in both bioregions
 530 (in November/December, Fig. 4). This transition period was associated with the surface
 531 autumnal increase in [Chl-a] (i.e. [Chl-a]_{sat} and [Chl-a]_{Zpd}) and an homogenous vertical
 532 distribution of [Chl-a] (Fig. 6). A couple of months before (in September/October), the vertical

533 distribution of [Chl-a] was on the contrary characterized by a DCM (**Fig. 5**). The surface
534 increase in [Chl-a] was likely related to a change in the vertical distribution of the phytoplankton.
535 Such modification could be due to a progressive reduction of the DCM and a redistribution of the
536 phytoplankton biomass over a more uniform shape [Morel and André, 1991; Lavigne et al.,
537 2015a].

538 Whatever the bioregion, our data indicated that the DCM progressively shallows in late
539 summer/autumn following the $Z_{0.415}$ interface (**Fig. 5**), thus suggesting a light-driven control of
540 the [Chl-a] vertical distribution [Mignot et al., 2014; Lavigne et al., 2015a]. To support such
541 DCM shallowing, a rise in the nitracline would also be required. During this season, the
542 intensification of the large scale cyclonic circulation over the whole NWM actually uplifted the
543 nitracline [Pasqueron de Fommervault et al., 2015a]. Then, the slight autumnal deepening of the
544 MLD lead to the mixing-up of the top layer of the summer shallowing DCM. This autumnal
545 MLD deepening was related to processes affecting the vertical mixing at this season: water-
546 column stratification, the integrated effects of air sea fluxes, and advection processes (as
547 discussed for the 2012-2013 particular year in [Estournel et al., 2016; Houpert et al., 2016;
548 Waldman et al., accepted]).

549 The surface [Chl-a] increase in autumn lasted until the end of January. The [Chl-a] integrated
550 between 0 and 1000 m also increased. Assuming that [Chl-a] is a proxy for phytoplankton
551 biomass, and following the “critical-depth theory” of Sverdrup, this suggests the MLD did not
552 reach the critical depth. Conversely, the shallowing of the nitracline and the concomitant
553 deepening of the MLD could induce an effective injection of nitrates into the surface layers and
554 the development of a typical “entrainment bloom” [Cullen et al., 2002; Chiswell, 2011].
555 Consequently, the autumnal increase in [Chl-a] that is recurrently observed in the NWM [Morel
556 and André, 1991; Volpe et al., 2012; D’Ortenzio et al., 2014] could be an effective biomass
557 increase.

558 However, during this period, PAR_0 level was low and could have led to reduced light availability
559 in the MLD, in conjunction with the later’s deepening. Both of these environmental factors may
560 have induced an intracellular increase of [Chl-a] in the phytoplankton cells due to the
561 photoacclimation (a low carbon to chlorophyll ratio, [Behrenfeld et al., 2005]), and could
562 explain a part of the observed autumnal [Chl-a] increase [Mignot et al., 2014]. This suggests that
563 the increase in surface [Chl-a] in November/December probably does not reveal an effective
564 increase in the phytoplankton biomass. Unfortunately, simultaneous *in situ* data of [Chl-a] and
565 b_{bp} were unavailable at this period of the year, thus preventing us from evaluating the
566 photoacclimation processes (like in [Mignot et al., 2014]).

567 Then, during the very deep winter MLD period, the $[Chl-a]_{1000}$ decreased in both bioregions.
568 This suggests that the winter integrated losses of phytoplankton biomass over the water column
569 exceeded the integrated phytoplankton production. In addition, in winter, there was no trend
570 towards an increase in the $[Chl-a]_{1000}$, which suggests that, contrary to the “decoupling-
571 recoupling model” of Behrenfeld, [2010], and results obtained by model simulations [Herrmann
572 et al., 2013], the deep winter MLDs do not induce a positive net increase of the phytoplankton
573 biomass.

574 4.1.2 The spring bloom temporal dynamics

575 The spring transition period, coincided with the strongest annual increase in [Chl-a]. The
576 availability of *in situ* data in the “High Bloom” bioregion allows to investigate the environmental
577 factors that may explain this relationship.

578 During the winter to spring transition, two successive events of surface [Chl-a] increase were
579 identified and separated by a one-week period of strong MLD deepening. The last mixing event
580 in mid-March was well identified with *in situ* data and described as a late deep mixing event that
581 occurred this year in the NWM [Houpert *et al.*, 2016]. Nevertheless, the temporal dynamics of
582 the [Chl-a] increase were similar during these two successive events and were typical of a
583 temperate spring bloom.

584 At the beginning of each of the two spring bloom transition periods, the MLD remained deep but
585 the mixed layer might not be actively mixing [Townsend *et al.*, 1994; Chiswell, 2011; Taylor and
586 Ferrari, 2011b; Franks, 2014]. [Taylor and Ferrari, 2011b] supposed that after the winter
587 mixing period, lowered vertical mixing occurs mainly at the surface and is caused by the
588 reduction of net surface heat loss by the ocean. According to the authors, the spring bloom
589 should initiate when the heat flux becomes positive. In our case, the [Chl-a] started to increase in
590 surface only two days before the surface heat flux became positive. Therefore, the hypothesis of
591 a reduction of the mixing in surface due to net heat gains could be relevant, although buoyancy
592 gain by horizontal processes may be important for the deep convection process of the NWM
593 [Estournel *et al.*, 2016].

594 One week later, the MLD overlapped with $Z_{0.415}$ ($Z_{0.415}/\text{MLD} > 1$) and the increase in the [Chl-a]
595 integrated over the $Z_{0.415}$ was maximal. Assuming that $Z_{0.415}$ is a good proxy for the Z_{eu} , this
596 depth also represents the equivalent depth, where the instantaneous production and losses are
597 equal [Sverdrup, 1953]. Therefore, when $Z_{0.415}/\text{MLD} > 1$, the integrated phytoplankton
598 production in the $Z_{0.415}$ should largely overcome the integrated losses. Using a dedicated model,
599 [Llort *et al.*, 2015] demonstrated that the maximal annual increase in phytoplankton production
600 occurs during the spring restratification, and they attributed this maximal annual increase to a
601 change in the light condition. Here, we showed that during the spring transition period, the
602 surface [Chl-a] (i.e. $[\text{Chl-a}]_{Z_{0.415}}$) corresponds to an increase in the phytoplankton production
603 (since it is simultaneous with the spring increase of [POC]) and that its maximal increase is
604 related to a change in the light condition since the $Z_{0.415}/\text{MLD}$ ratio became > 1 (a large part of
605 the phytoplankton remain in the Z_{eu}).

606 However, the autumnal mixing as well as the spring restratification are not monotonous
607 processes. In both bioregions, the $Z_{0.415}/\text{MLD}$ were indeed characterized by an important
608 variability, oscillating between values < 1 and > 1 with three-week intervals, from December to
609 March (Fig. 4e). These observations highlight that, during these critical transition periods, sub-
610 seasonal processes influence both the mixing and the restratification of the water column and
611 therefore the response of phytoplankton [Franks, 2014; Thomalla *et al.*, 2015]. Similar
612 conclusions were obtained by model simulations [Bernardello *et al.*, 2012]. However, it is
613 noteworthy that our analysis was conducted over large areas (i.e., bioregions) in order to identify
614 key environmental factors influencing the phytoplankton blooms, and did not focus on the
615 smaller scale processes that could obviously influence phytoplankton growth [Franks, 2014].

616 4.2 The spring bloom magnitude

617 After the 9th of April, the water column was definitely stratified in both bioregions ($Z_{0.415}/MLD >$
618 1, **Fig. 4e**). At that time, most of the phytoplankton biomass was concentrated in the $Z_{0.415}$ layer
619 (**Fig. 5**). However, bioregions displayed different spring bloom intensities. In the “High bloom”
620 bioregion, higher surface values ($> 6 \text{ mg m}^{-3}$, **Fig. 5**) than in the “Bloom” bioregion (surface
621 values $< 3 \text{ mg m}^{-3}$, **Fig. 5**) were found, and were in the range of values previously reported for
622 the NWM [*Conan et al.*, 1999; *Estrada and Vaqué*, 2014]. This suggests higher surface net
623 accumulation rates (more gains than losses) of phytoplankton in the “High Bloom” bioregion
624 than in the “Bloom” bioregion.

625 Differences in phytoplankton community composition, which influence the net accumulation rate
626 of phytoplankton biomass, could explain the observed difference in the [Chl-a] magnitude within
627 bioregions. Diatoms are characterized by a higher maximal growth rate than the smaller
628 phytoplankton species, and higher light levels requirements [*Edwards et al.*, 2015]. They
629 generally dominate the phytoplankton spring bloom community in March-April [*Marty et al.*,
630 2002; *Siokou-Frangou et al.*, 2010; *Estrada and Vaqué*, 2014; *Thyssen et al.*, 2014; *Romagnan et*
631 *al.*, 2015; *Mayot et al.*, accepted]. However, the relative abundance of diatoms within the
632 phytoplankton spring bloom community exhibited strong inter-annual variability in the NWM
633 [*Organelli et al.*, 2013]. High concentrations of diatoms were observed after strong winter
634 mixing events [*Estrada et al.*, 1999; *Marty et al.*, 2002; *Rigual-Hernández et al.*, 2013; *Mayot et*
635 *al.*, accepted]. Therefore, a stronger accumulation of diatoms in the “High Bloom” bioregion
636 rather than in the “Bloom” bioregion could explain the differences in the net accumulation rate
637 of phytoplankton biomass. As a matter of fact, *Mayot et al.*, [accepted] (in this special issue)
638 found a higher proportion of diatoms in the phytoplankton community in the “High Bloom”
639 bioregion (~48 %) than in the “Bloom” bioregion (~36 %), from the DEWEX ship survey
640 stations performed in April 2013.

641 The higher diatom concentration could be explained by a change in silicates surface availability
642 that was induced by strong winter mixing [*Severin et al.*, 2014]. Therefore, we suggest that the
643 difference in net phytoplankton accumulation rates cannot be ascribed to higher nitrates surface
644 availability in the “High Bloom” bioregion. Indeed, $[NO_3]_{MLD}$ were quite constant since the end
645 of winter (**Fig. 7**) and more importantly, they were particularly high ($> 6 \mu\text{M}$) compared to the
646 rest of the Mediterranean basin [*Pujo-Pay et al.*, 2011]. In the NWM, the nitracline is generally
647 close to the surface [*Pasqueron de Fommervault et al.*, 2015a, 2015b], in association with the
648 thermocline [*Diaz et al.*, 2000; *Pujo-Pay et al.*, 2011], and can be reached by a relatively shallow
649 MLD [*D’Ortenzio et al.*, 2014]. In addition, nitrates concentration sharply increases in
650 subsurface waters [*Pasqueron de Fommervault et al.*, 2015b] (**Fig. 8a**). In other terms, although
651 maximum winter MLDs were very different between both bioregions (**Fig 4c**), the $[NO_3]$ that is
652 available for the next spring should remain similar in both areas.

653 On the contrary, silicates concentration in the NWM progressively increases downwards from
654 the surface [*Pasqueron de Fommervault et al.*, 2015b] (**Fig. 8b**). Deep winter convection events
655 which reach the deep water masses are necessary to strongly increase the surface availability of
656 silicates for the coming spring bloom. Thus, the stronger and longer winter mixing in the “High
657 Bloom” bioregion could have enhanced silicates availability, generating more favorable
658 conditions for diatoms, and leading to the development of an enhanced diatom spring bloom.
659 *Severin et al.* [submitted] showed that the DEWEX ship surveys stations performed in February

660 2013 inside the deep convection area presented higher surface $[\text{Si}(\text{OH})_4]$ and higher silicates to
661 nitrates (Si:N) ratio ($[\text{Si}(\text{OH})_4] \sim 7.1 \mu\text{M}$ and Si:N ~ 0.86) than the ship surveys stations
662 performed in the surrounding mixed area ($[\text{Si}(\text{OH})_4] \sim 3.63 \mu\text{M}$ and Si:N ~ 0.70).

663

664 **5 Conclusion**

665 The main objective of this study was to understand the influence of the physical and
666 biogeochemical properties driving the phytoplankton annual cycle in the temperate regime of the
667 NWM. An unprecedented sampling effort was carried out over a year from July 2012 to July
668 2013 and coupled data from several platforms. Combined with a satellite-based
669 bioregionalization, an exceptional dataset was collected in terms of number of profiles and
670 parameters (both physical and biogeochemical). Therefore, an analysis with *in situ* data of the
671 primary drivers of the phytoplankton blooms was made possible over a complete annual cycle
672 and not, as usual, restricted to a short period or area.

673 During the year 2012-2013, ocean color observations, supported by *in situ* measurements,
674 revealed the existence of two large-scale areas (or bioregions) bearing similar phytoplankton
675 autumnal blooms but contrasted spring blooms. The timing of the bloom events identified by
676 existing methods (mostly based on remotely sensed ocean color data) confirmed the temperate
677 nature of the NWM area with both autumnal and spring blooms. However, the use of these
678 phenological metrics only provided a partial vision of the phytoplankton annual cycle. The
679 $Z_{0.415}/\text{MLD}$ ratio, by inferring the time when the phytoplankton is mixed below or above the
680 euphotic zone, provided an accurate alternative to detect the dates of the main bloom events in
681 the NWM.

682 The phytoplankton autumnal bloom, that occurs when $Z_{0.415}/\text{MLD}$ ratio changes from > 1 to < 1 ,
683 is likely explained by overlapping processes, related to the erosion of the summer water column
684 stratification and light availability. In fact, the deepening of the MLD and the light driven
685 displacement to the surface of the DCM may have induced a redistribution of the [Chl-a] within
686 the surface layer. The MLD deepening could also have injected nutrients into the surface layer
687 thus sustaining phytoplankton growth, while the reduced light availability at this season should
688 also generate [Chl-a] increases through photoacclimation. In spring, the $Z_{0.415}/\text{MLD}$ ratio
689 becomes > 1 again and is related to the timing of the highest accumulation rate of phytoplankton
690 biomass, while the spring bloom onset appears more related to a less intense mixing in surface
691 winter mixed layer.

692 Finally, our analysis evidenced an unusually high net accumulation rate of phytoplankton
693 biomass in spring where winter deep water convection events had occurred. However, the winter
694 availability of nitrate in the surface layer was homogeneously high over the whole NWM (not
695 restricted to the deep convection area), suggesting that a higher availability of nitrate can
696 probably not explain the unusually high spring phytoplankton biomass. Instead, we suggest that
697 very deep winter MLD lead to an increased silicates availability in the surface, which could also
698 explain the dominance of diatoms in the underpinning spring phytoplankton community, as well
699 as the unusually high accumulation rates of phytoplankton.

700 The results obtained in the NWM provide a new framework to characterize the phytoplankton
701 seasonality in temperate seas (i.e., oceanic regions submitted to strong seasonality). The
702 combined use of satellites, ship-based sampling and mainly *in situ* autonomous platforms (i.e.

703 Argo and BGC-Argo floats, and bio-optical gliders) allowed us to retrieve physical and
704 biogeochemical properties along the water column, and to enhance our interpretation of the
705 physical-biological coupling in the NWM.

706 **Acknowledgments and Data**

707 The authors would like to thank the NASA Ocean Biology Processing Group (OBPG) for the
708 access to MODIS data (<http://oceancolor.gsfc.nasa.gov>). The Argo-floats data were collected and
709 made freely available by the Coriolis project and programs that contribute to it
710 (<http://www.coriolis.eu.org>). Bio-Argo float data used in this work are made available online
711 (http://www.oao.obs-vlfr.fr/BD_FLOAT/NETCDF/). This work is a contribution to the MerMEX
712 project (Marine Ecosystem Response in the Mediterranean Experiment, WP1) from the
713 MISTRALS international program. This work was supported by the remOcean (remotely sensed
714 biogeochemical cycles in the Ocean) project, funded by the European Research Council (GA
715 246777), by the French “Equipement d’avenir” NAOS project (ANR J11R107-F), and by the
716 PACA region. The authors are also grateful to the French Bio-Argo project funded by CNES-
717 TOSCA, and to LEFE Cyber and GMMC programs that supported this work. We also thank F.
718 Benedetti for reviewing the manuscript. Finally, we are grateful to two anonymous reviewers for
719 their valuable comments and suggestions.

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- 1044
1045

1046 Table 1. Result of the linear regressions for the calibration of the fluorimeters. All the scaling
 1047 factor values were significantly different from 0 (t-test, p -value < 0.001). See Sect. 2.3.2 for
 1048 more details.

Name	n	r ²	scaling factor (slope)
Ship cruises			
MOOSE-GE 2012	283	0.95	3.50
DOWEX 2012	127	0.71	1.51
DEWEX 2013 – Leg 1	225	0.98	2.17
DEWEX 2013 – Leg 2	264	0.98	2.03
MOOSE-GE 2013	80	0.93	3.18
BioArgo Floats			
SBEE	16	0.81	0.44
NAOS 001	11	0.97	0.65
NAOS 017	13	0.86	0.88
NAOS 035	18	0.96	0.59

1049

1050 **Figure 1.** (a) Positions of the profiles performed by the different sampling platforms from July
 1051 2012 to July 2013. (b) Temporal distribution (five days bin intervals) of the number of available
 1052 profiles for each sampling platform. Note the irregular scale of the color bar.
 1053

1054 **Figure 2.** (a) Spatial distribution of the two bioregions determined by satellite in the NWM from
 1055 July 2012 to July 2013. The “Bloom” bioregion is in blue, and the “High Bloom” bioregion is in
 1056 red. (b) The respective mean time-series of $[\text{Chl-a}]_{\text{sat}}$ of the two bioregions, (c) with the dates of
 1057 the phytoplankton blooms derived from different phenological metrics.
 1058

1059 **Figure 3.** Temporal distribution (five days bin intervals) of the number of available density,
 1060 fluorescence, $[\text{NO}_3]$, $[\text{POC}]$ and PAR profiles, from July 2012 to July 2013, (a) for the “Bloom”
 1061 and (b) “High Bloom” bioregions.
 1062

1063 **Figure 4.** Annual time series of physical and biogeochemical properties associated with the two
 1064 bioregions the “Bloom” (in blue) and “High Bloom” bioregions (in red). Time series of (a) wind
 1065 speed, (b) heat flux, (c) MLD, (d) $Z_{0.415}$ and $Z_{1\%}$, (e) $Z_{0.415}/\text{MLD}$ and (f) $[\text{Chl-a}]_{Z_{\text{pd}}}$. The lines
 1066 represent the mean values median filtered (i.e., five days), the dots the single *in situ* values and
 1067 the shaded areas the standard deviations. The time-series of the $Z_{0.415}/\text{MLD}$ ratio is calculated
 1068 with the mean $Z_{0.415}$ and MLD values (i.e., lines in c and d), and the black line represents when
 1069 $Z_{0.415}/\text{MLD} = 1$. The color bars below each plot describe the state of the $Z_{0.415}/\text{MLD}$ ratio, with
 1070 the phenological metrics from the figure 2c reported and two spring transition events highlighted
 1071 (i.e., numbers 1 and 2). Note the logarithmic scale of the y-axis for the $Z_{0.415}/\text{MLD}$ ratio (e), and
 1072 the $[\text{Chl-a}]_{Z_{\text{pd}}}$ (f).
 1073

1074 **Figure 5.** Time series of $[\text{Chl-a}]$, (a) for the “Bloom” and (b) “High Bloom” bioregions. The
 1075 color bar for the $[\text{Chl-a}]$ applies to both panels (i.e., a and b). The $[\text{Chl-a}]$ data have been
 1076 averaged every 10 m and two days. The thickest white line represents the contour line 0.25 mg
 1077 m^{-3} . The solid red line represents the MLD, and the dashed red line the $Z_{0.415}$. The color bars
 1078 above each plot describe the state of the ratio $Z_{0.415}/\text{MLD}$, with the phenological metrics from the
 1079 figure 2c reported and two spring transition events highlighted (i.e., numbers 1 and 2).
 1080

1081 **Figure 6.** Time series of depth integrated $[\text{Chl-a}]$, (a) for the “Bloom” and (b) “High Bloom”
 1082 bioregions. Depth integrations were performed from the surface to $Z_{0.415}$ (red line) and 1000 m
 1083 (black line). The values of the $[\text{Chl-a}]$ integrated were averaged daily and a five-day median
 1084 filter was applied. The color bars below each plot describe the state of the ratio $Z_{0.415}/\text{MLD}$, with
 1085 the phenological metrics from the figure 2c reported and two spring transition events highlighted
 1086 (i.e., numbers 1 and 2). $[\text{Chl-a}]$ profiles realized the 1st December 2012 in the “Bloom” and
 1087 “High Bloom” bioregions are also reported.
 1088

1089 **Figure 7.** Times series of the (a) $[\text{POC}]_{\text{MLD}}$ and (b) the $[\text{NO}_3]_{\text{MLD}}$ for the “Bloom” (blue) and
 1090 “High Bloom” (red) bioregions. The lines represent the mean values, median filtered (i.e., five
 1091 days), and the dots the single values. The colour bars above the plot describe the state of the
 1092 $Z_{0.415}/\text{MLD}$ ratio, with the phenological metrics from the figure 2c reported and two spring
 1093 transition events highlighted (i.e., numbers 1 and 2).
 1094

1095 **Figure 8.** Mean profiles of (a) $[\text{NO}_3]$ and (b) $[\text{Si}(\text{OH})_4]$ in February 2013 in the “Bloom” (blue)
 1096 and “High Bloom” (red) bioregions. The lines represent the mean values and the dots the single
 1097 values.

Figure 1.

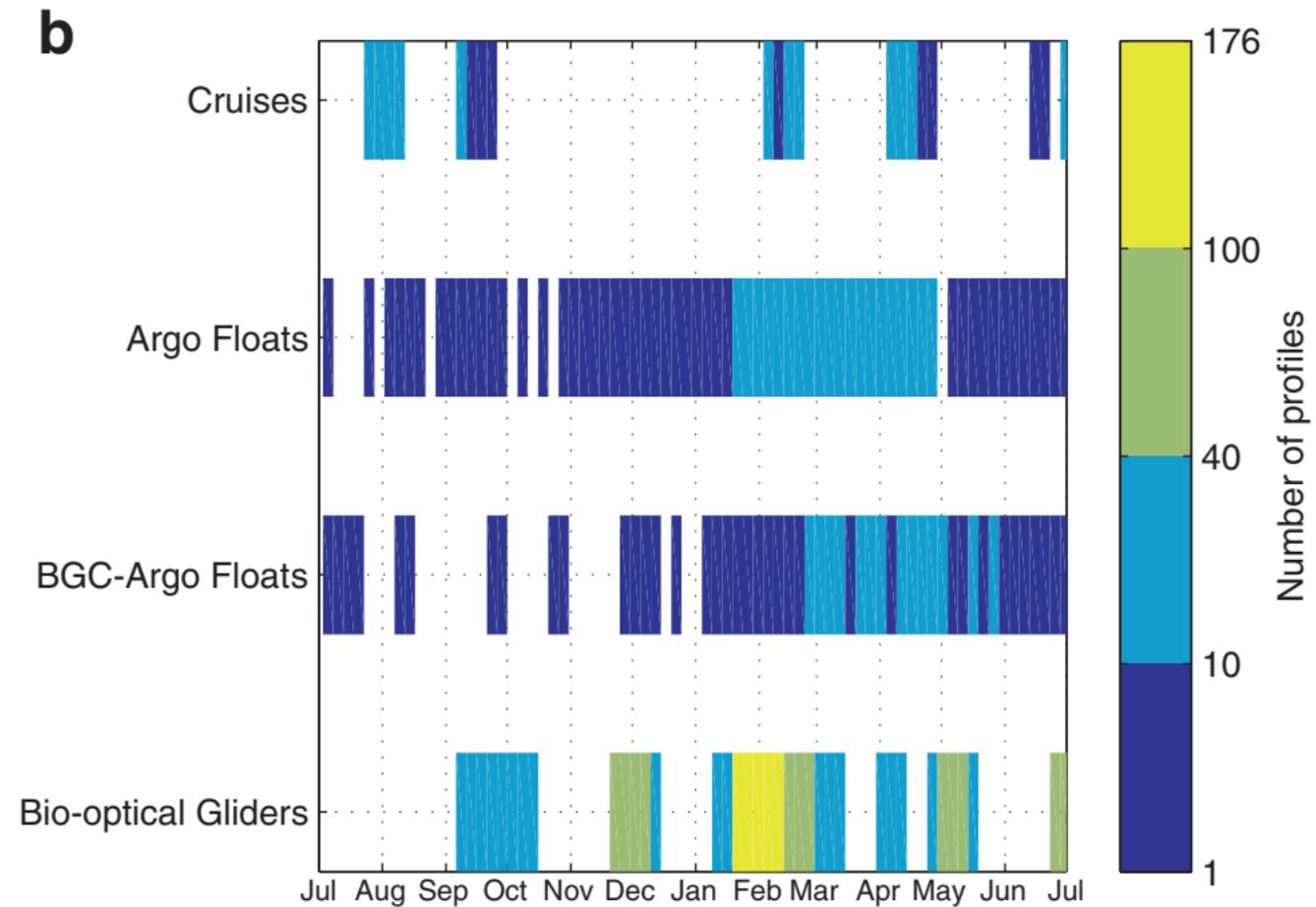
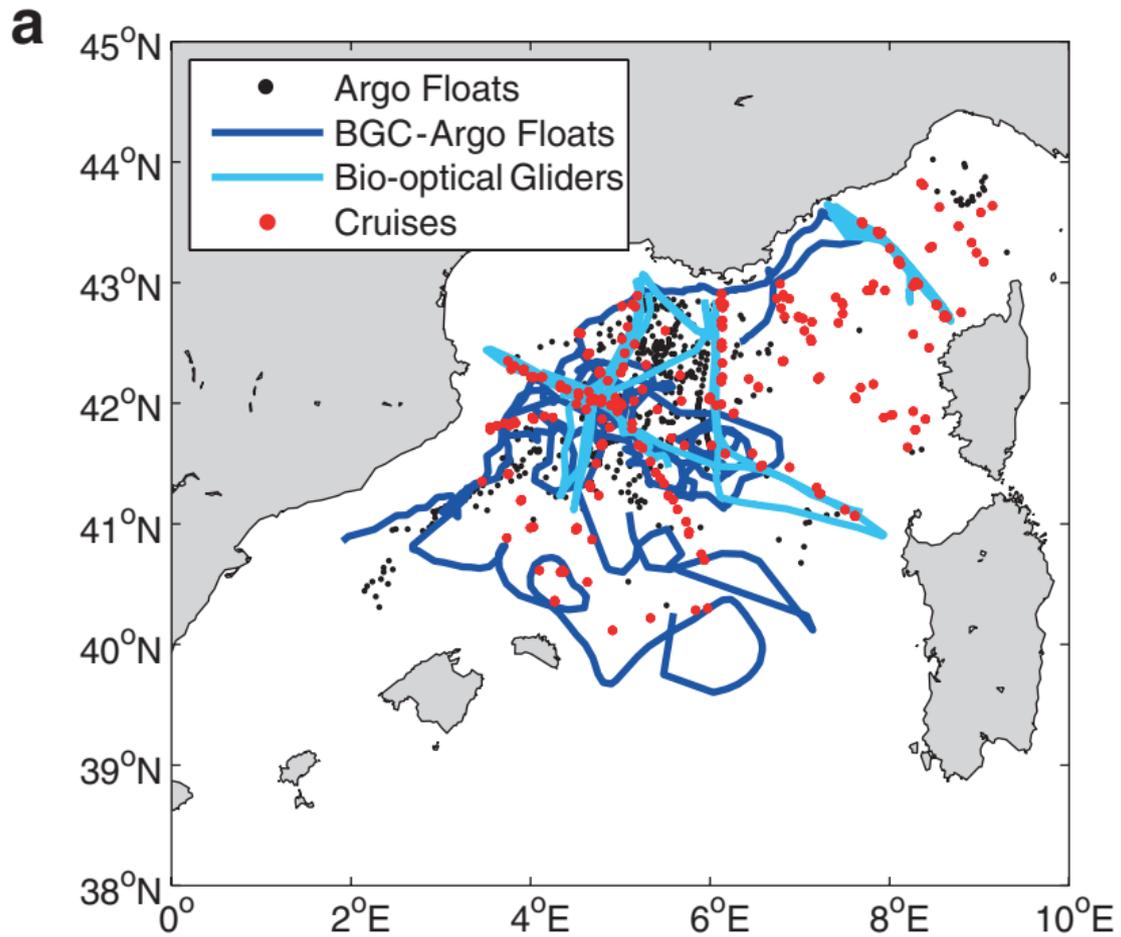


Figure 2.

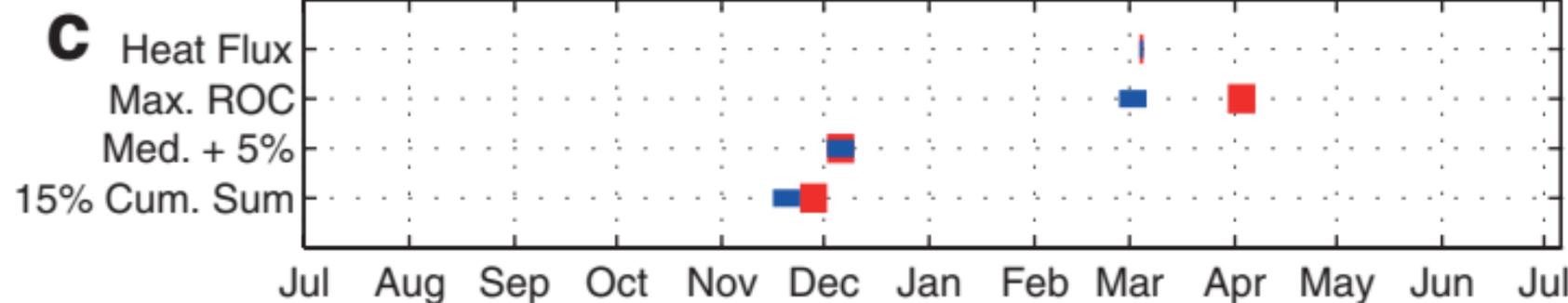
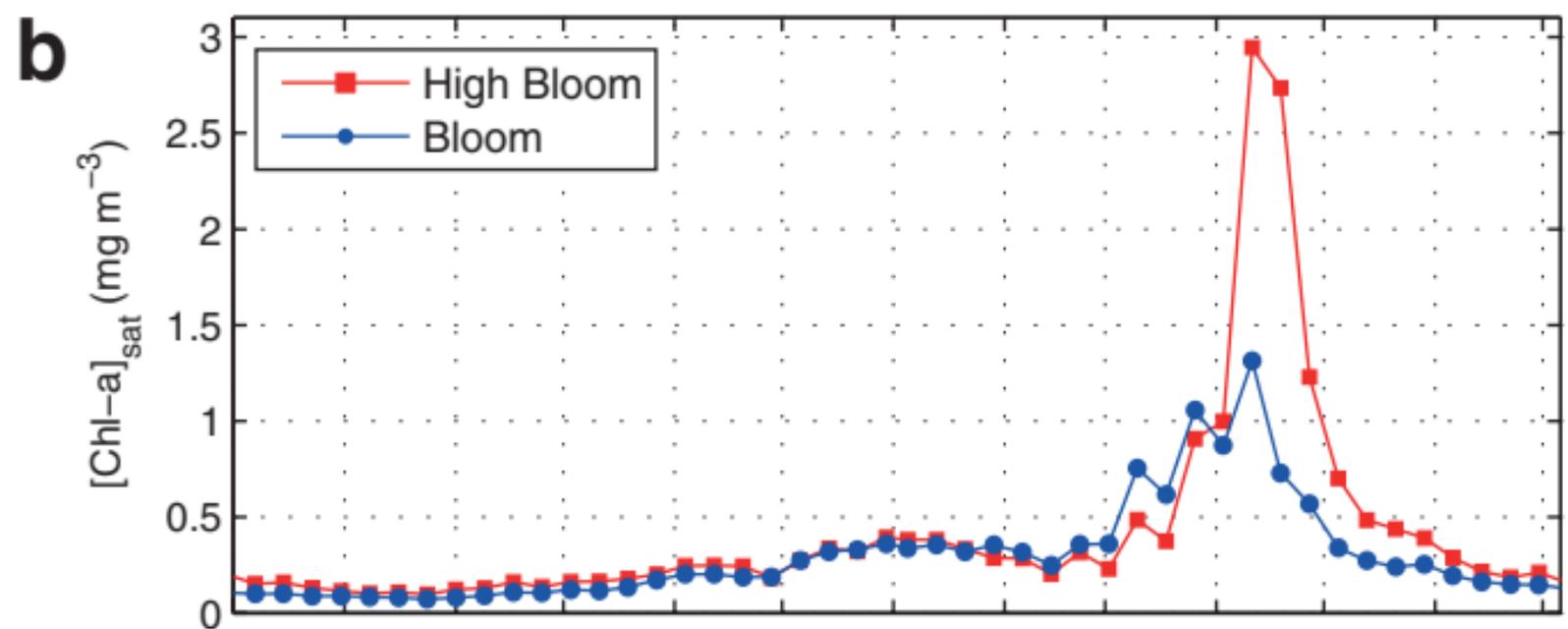
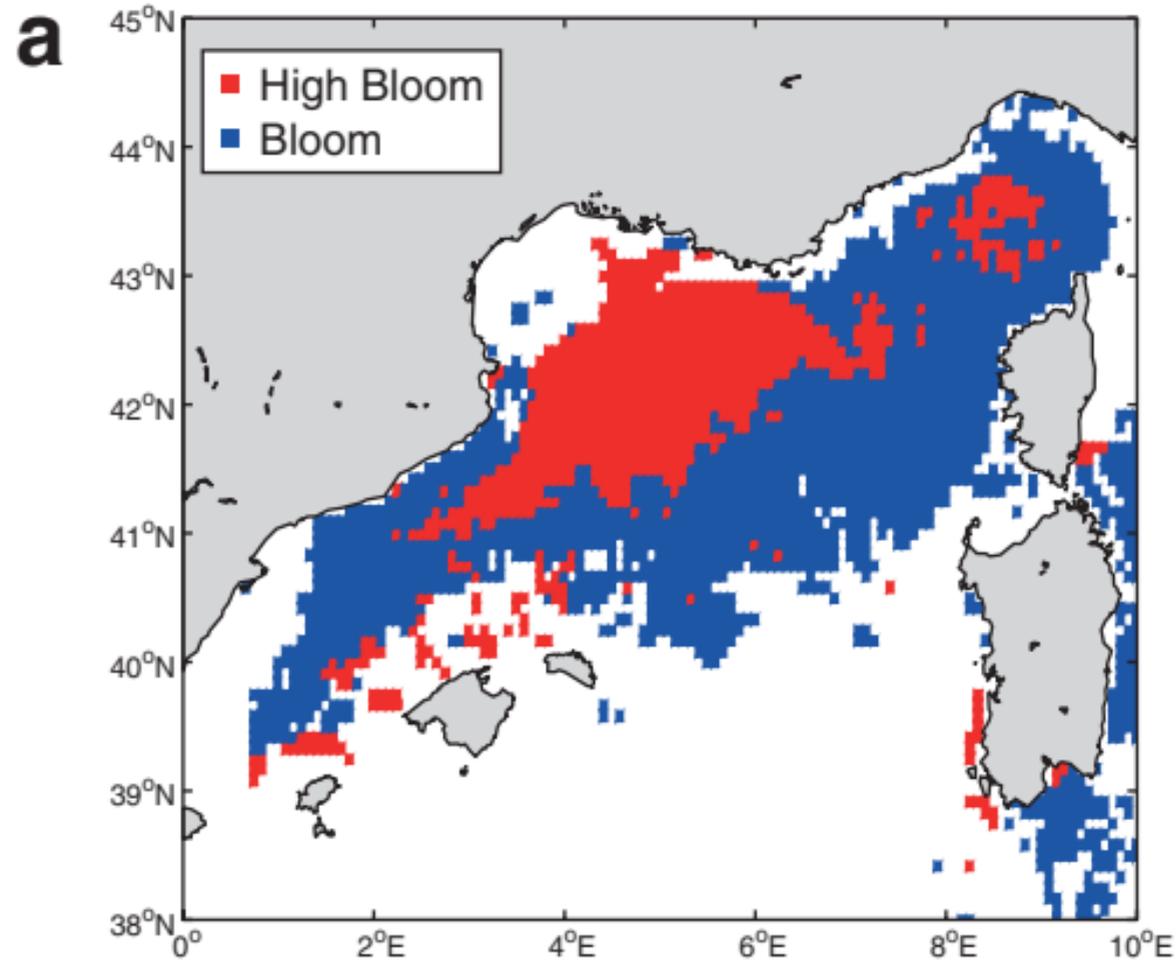


Figure 3.

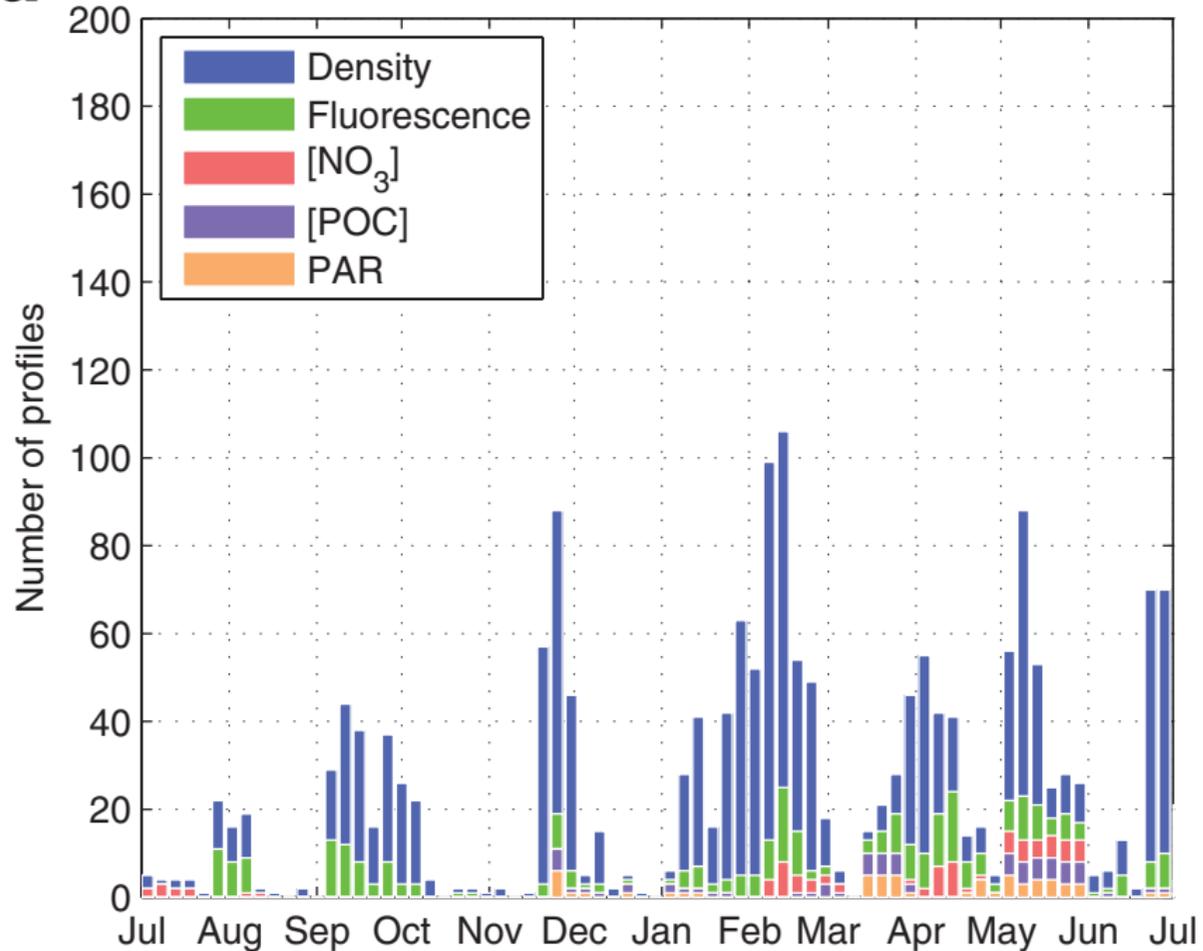
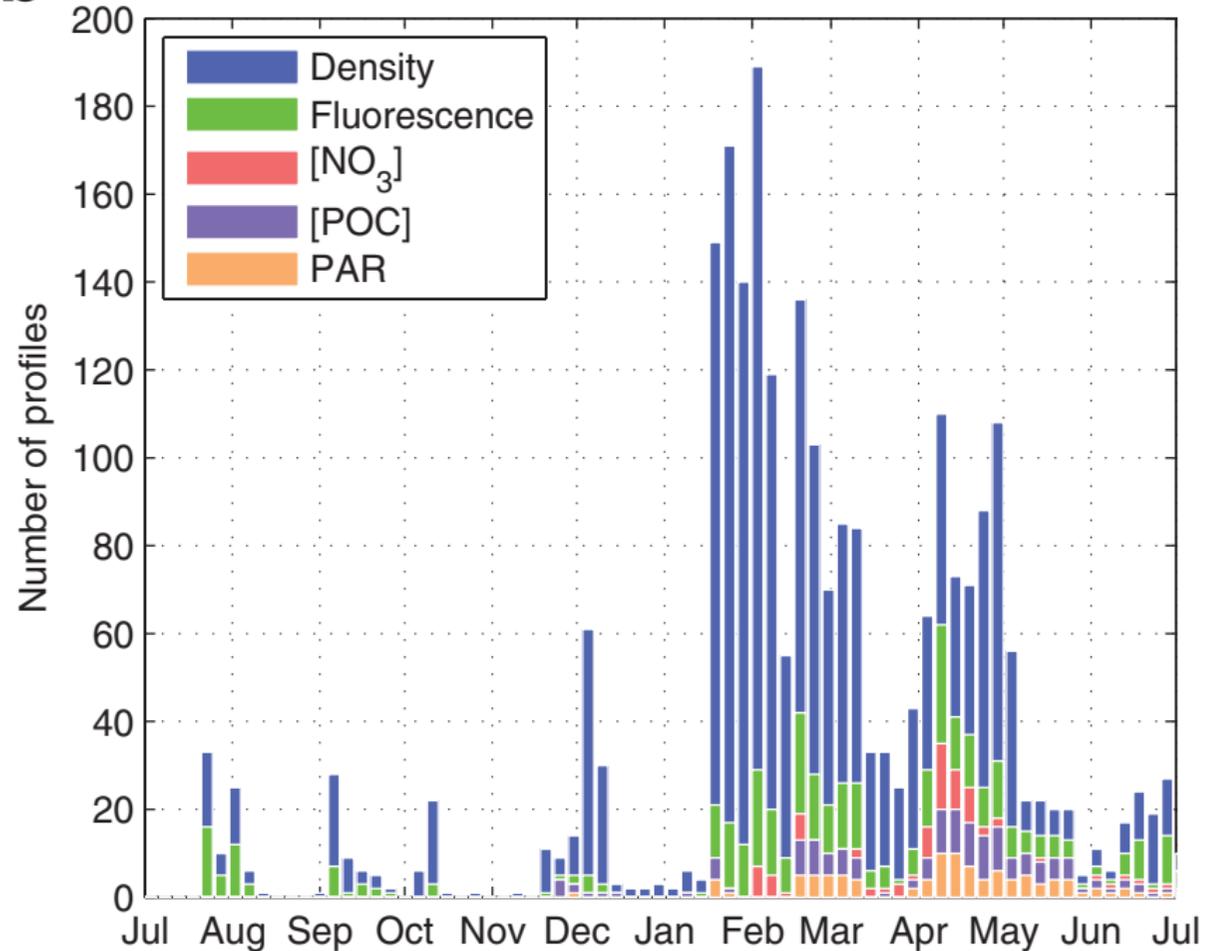
a High Bloom Bioregion**b** Bloom Bioregion

Figure 4.

Figure 5.

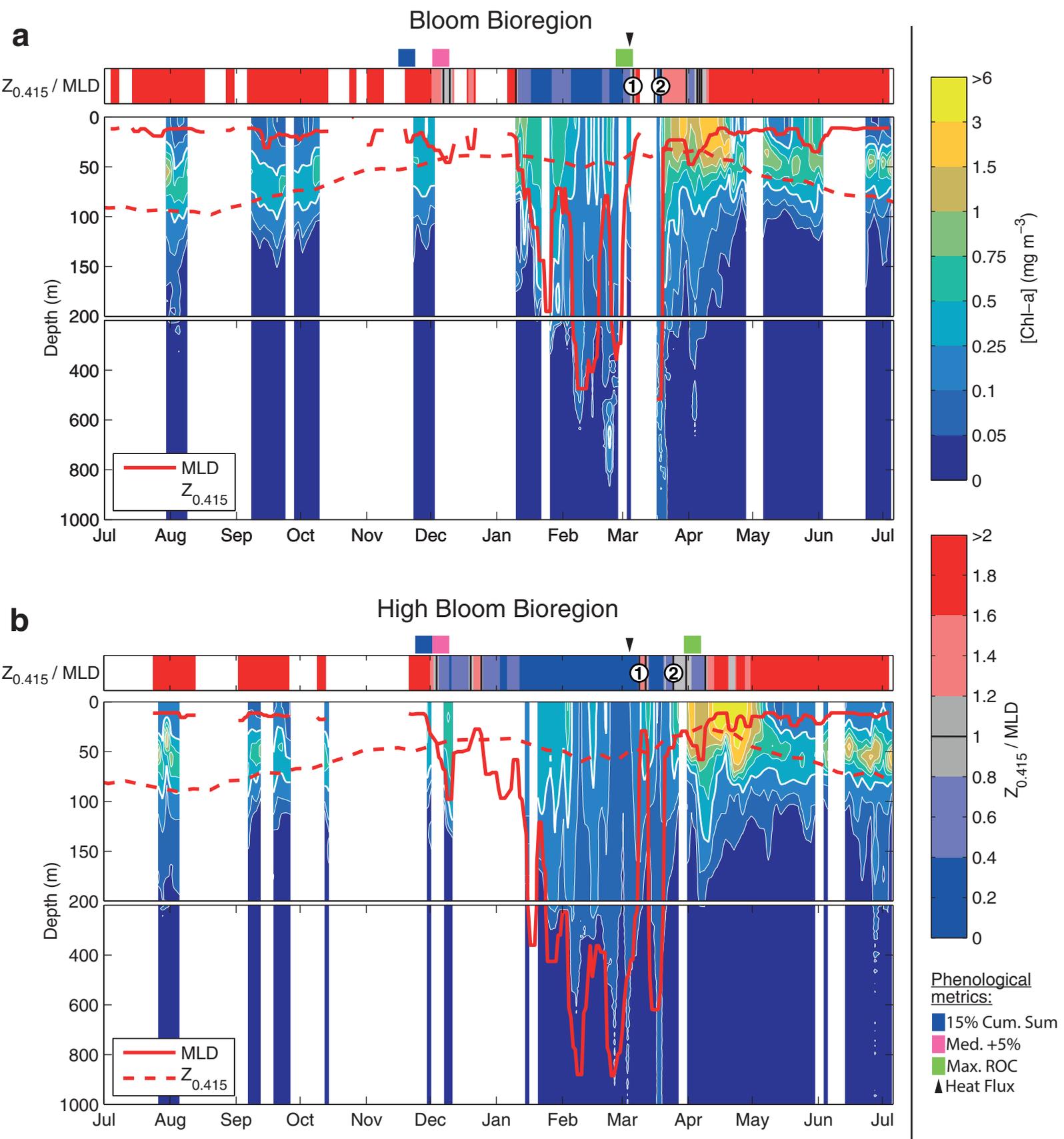
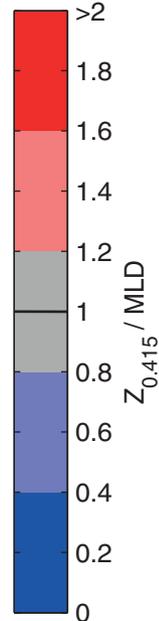
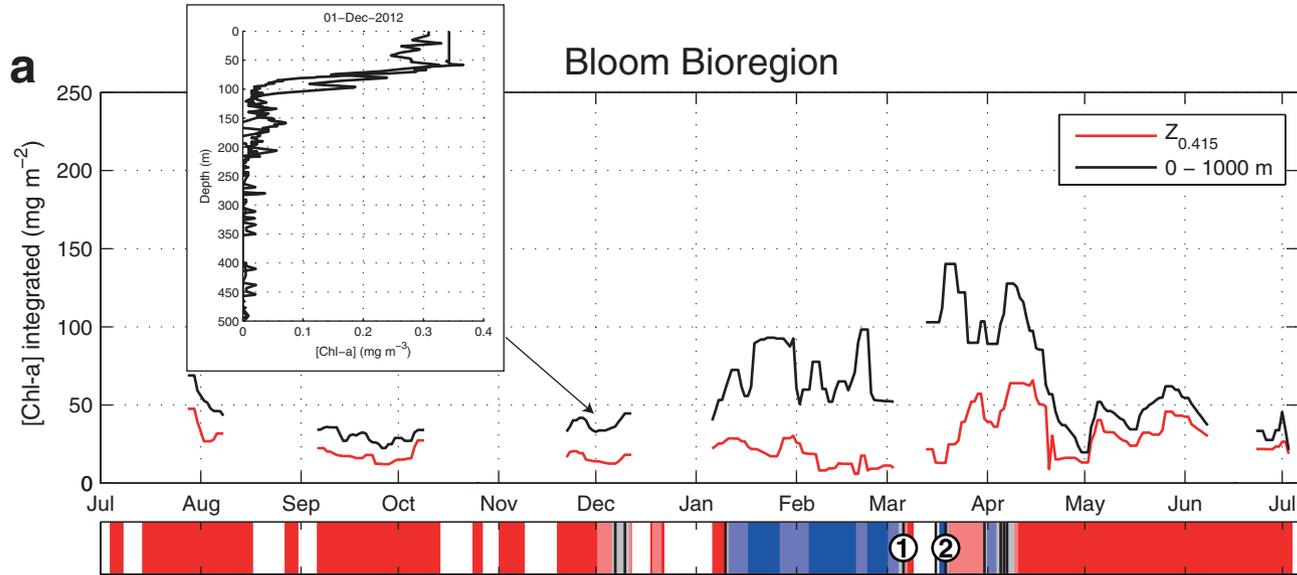


Figure 6.

a

Phenological metrics:

- 15% Cum. Sum
- Med. +5%
- Max. ROC
- ▲ Heat Flux

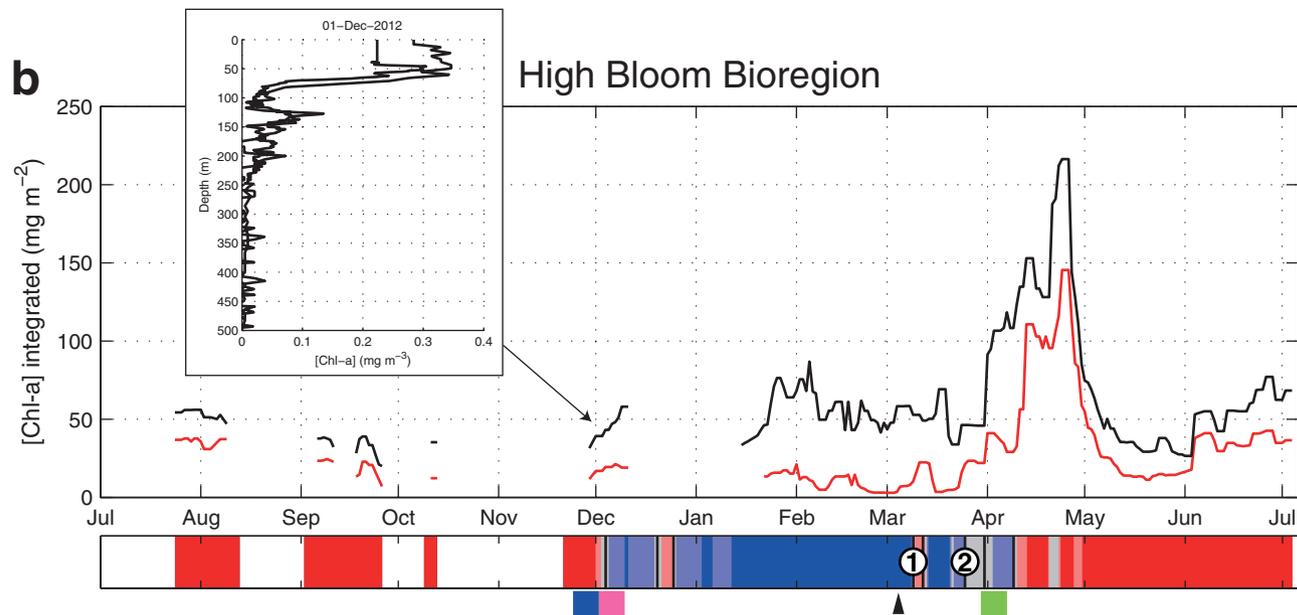
b

Figure 7.

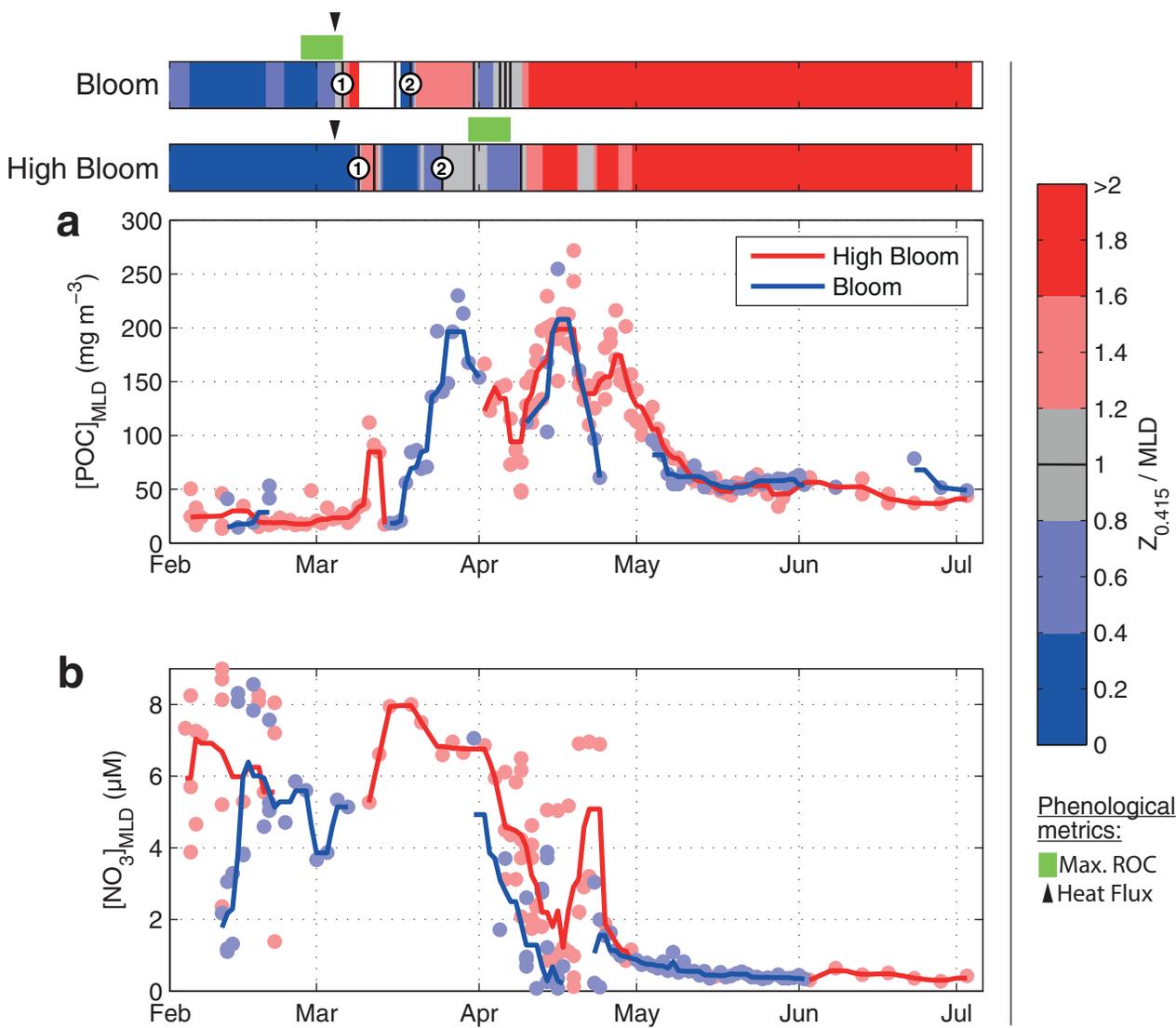


Figure 8.

