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1 **Unexpected winter phytoplankton blooms in the North Atlantic Subpolar Gyre**

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12 **Introductory paragraph: In mid- and high-latitude oceans, winter surface cooling and**
13 **strong winds drive turbulent mixing that carries phytoplankton to depth of several**
14 **hundred meters, well below the sunlit layer. This downward mixing, in combination with**
15 **low solar radiation, drastically limits phytoplankton growth during the winter, especially**
16 **that of the diatoms and other species that are involved in seeding the spring bloom. Here**
17 **we present observational evidence for widespread winter phytoplankton blooms in a large**
18 **part of the North Atlantic Subpolar Gyre from autonomous profiling floats equipped with**
19 **biogeochemical sensors. These blooms were triggered by intermittent restratification of**
20 **the mixed layer when mixed layer eddies led to a horizontal transport of lighter water**
21 **over denser layers. Combining a bio-optical index with complementary chemotaxonomic**
22 **and modelling approaches, we show that these restratification events increase**
23 **phytoplankton residence time in the sunlight zone, resulting in greater light interception**

24 **and the emergence of winter blooms. Restratification also caused a phytoplankton**
25 **community shift from pico- and nanophytoplankton to phototrophic diatoms. We**
26 **conclude that transient winter blooms can maintain active diatom populations throughout**
27 **the winter months, directly seeding the spring bloom and potentially making a significant**
28 **contribution to over-winter carbon export.**

29

30 The Sverdrup paradigm ¹ postulates that deep winter mixing prevents phytoplankton biomass
31 accumulation since losses exceed light-limited production. However, few wintertime in situ
32 observations revealed significant phytoplankton stock in deep mixed layers ^{2,3}. Based on
33 modelling simulations, orbital motions triggered by deep convection have been suggested to
34 allow recurrent incursions of phytoplankton to the surface lit layer, and thus supporting a winter
35 production ⁴. Furthermore, winter deepening of the mixed layer would dilute plankton
36 concentration, thus reducing grazing pressure, and consequently, phytoplankton loss
37 (disturbance-recovery hypothesis) ^{5,6}. Despite low phytoplankton growth, biomass may
38 accumulate throughout winter in deep mixed layers.

39 Modelling studies have shown that mixed layer eddies (MLEs) growing from horizontal
40 density gradients can generate vertical restratification of the mixed layer at spatial scales of 1-
41 10 km and time scales of days ^{7,8}, thus allowing patchy blooms to be initiated before the vernal
42 stratification ⁹. MLEs being potentially much more frequent in winter ¹⁰, such restratification
43 mechanism may provide an additional mechanism for winter phytoplankton growth.

44 In addition, other studies have proposed that a reduction in turbulent mixing, due to a
45 relaxation in atmospheric forcing, may allow phytoplankton to grow, before the vernal
46 restratification (critical turbulence hypothesis) ¹¹⁻¹³.

47 In this context, distinguishing the mixing layer depth from the mixed layer depth is
48 important when dealing with phytoplankton dynamics¹⁴⁻¹⁶. In the following, we improved the
49 determination of the mixed layer depth to be the closest to the mixing layer depth (see
50 Supplementary Methods 1.4) given that there are no large scale, autonomous measurements of
51 turbulence so far.

52 **Winter mixing intermittency**

53 The common view is that the North Atlantic subpolar ocean is continuously deeply
54 mixed during winter^{17,18}. However, around 25% of Argo density profiles in this area were
55 stratified (mixed layer depth (MLD) < 100 m, Supplementary Methods 1.4) during the winters
56 of 2014 and 2015 (Fig. 1a and Supplementary Fig. 4). The vertical stratification was particularly
57 strong in areas of significant horizontal density gradients (Fig. 1b), suggesting the potential role
58 of MLEs. MLEs drive net horizontal transfer of lighter water above heavier water that can
59 locally stratify the mixed layer. Similar temperature and salinity structure (i.e. Turner angle¹⁹)
60 between horizontal and vertical density gradients in the subpolar gyre (Fig. 1c, Supplementary
61 Methods 1.3) confirm the crucial role of lateral processes in restratifying the deep winter mixed
62 layer in the North Atlantic Subpolar Gyre.

63 Restratification mechanisms compete with vertical mixing induced mainly by surface
64 wind and cooling⁹. Thus, restratification events require sufficiently long calm periods with a
65 relaxation of this atmospheric forcing. While analysing wind speed and heat fluxes, we
66 observed that some regions of the subpolar gyre presented up to 30% of calm periods (Fig. 1d,
67 Supplementary Fig. 5 and Methods 1.6). A proxy of the sea state (i.e. wave height,
68 Supplementary Methods 1.7), derived from BGC-Argo floats, also confirmed evidence of calm
69 periods (i.e. 20% of the winter profiles, Supplementary Fig. 7). Therefore, transient calm
70 periods appear to be frequent across the North Atlantic Subpolar Gyre, allowing restratification
71 to be a recurrent feature in winter.

72

73 **Mixing intermittency triggers winter phytoplankton blooms**

74 Restratification events triggered winter phytoplankton accumulations in the surface
75 layer in the whole subpolar gyre (based on two different proxies of phytoplankton biomass:
76 chlorophyll *a* (chl_a) and particulate optical backscattering (b_{bp}); Fig. 2 and Supplementary Fig.
77 9). These restratification events maintain phytoplankton cells in the euphotic zone (surface to
78 Z_e; see Fig. 2b and Supplementary Fig. 15), enhancing the light availability for their growth.
79 Indeed, the light level (i.e. the daily-integrated Photosynthetically Available Radiation (PAR)
80 averaged over the MLD) increased ten-fold in average in stratified conditions (MLD < 100 m;
81 1.3 mol photons m⁻²) compared to deeply mixed conditions (MLD > 100 m; 0.13 mol photons
82 m⁻²). For 70% of the stratified profiles (Fig. 2b, top panel), an increase in light exposure led to
83 the occurrence of winter blooms, defined here as a biomass increase of 5% above the winter
84 median value (75% of the stratified profiles using b_{bp} instead of chl_a). These observations
85 suggest that most of the calm periods lasted long enough to initiate locally transient winter
86 phytoplankton blooms.

87 Importantly, distinct light environments between stratified and deeply mixed conditions
88 impacted not only phytoplankton production but also the structure of the community^{20,21}. An
89 optical community index (chl_a to b_{bp} ratio²²) derived from BGC-Argo float measurements,
90 revealed a clear shift in the phytoplankton community structure during restratification events.
91 In typical winter conditions (i.e., deep mixed layers with low surface daily-integrated PAR),
92 pico- and nanophytoplankton clearly dominated the overall phytoplankton community in the
93 subpolar gyre (Fig. 3a). By contrast, the proportion of diatoms temporarily increases during
94 transient restratification events when their growth was evidently boosted by more favourable
95 light conditions (Fig. 3a, b). These blooms became particularly frequent in late February and
96 March (10-25% of the all profiles, n = 30, Fig. 3b), when frequency of restratification events

97 increased (20-40% of the all profiles, $n = 86$; $r = 0.94$, p -value < 0.01) and surface daily-
98 integrated PAR was higher due to longer daylength (Fig. 3c). Variation of the cloudiness (dot
99 size in Fig. 3c) also reinforced the critical role of light level, and its impact on changing the
100 community composition in winter. During calm periods with clear sky conditions, higher
101 surface daily-integrated PAR significantly boosted the growth of diatoms (Fig. 3c; $r = 0.56$, p -
102 value < 0.01 , see supplementary Table.3). These findings have been corroborated by rare
103 phytoplankton pigment samples collected during a winter cruise in the Newfoundland Basin
104 (CATCH, January-February 1997, Fig. 2a and Supplementary Methods 1.10 and 2.5). While
105 deep mixing layers were dominated by chryso- and pelagophytes, contributing to almost 50%
106 of the total chl a , diatoms became a relevant group contributing to almost 20% of the total chl a
107 when MLD shoaled above 100 m (Supplementary Fig. 16).

108

109 **Reassessing the winter as an active phytoplankton period**

110 Moderate to high light-adapted diatoms thriving in spring are not likely able to survive
111 in deep winter mixed layers. A set of suitable overwintering strategies, e.g. formation of resting
112 cells or spores^{23,24}, have been highlighted as means to survive harsh winter conditions. Here,
113 we show that diatoms can remain physiologically active throughout winter by benefiting from
114 transient restratification events and thus more favourable light environments (Supplementary
115 Fig. 17 and 19). By contrast, the persistence of pico- and nanophytoplankton, especially small
116 flagellates, and their dominance in deep mixing layers may be explained by mixotrophy, the
117 combined use of phototrophy and heterotrophy within a single organism²⁵. The shift to
118 heterotrophy during long period of darkness at depth could confer to these organisms a serious
119 ecological advantage and bring an alternative hypothesis to the disturbance-recovery hypothesis
120 ⁵.

121 An extraordinary number of studies emerged during the last decade to understand the
122 dynamics of the high-latitude spring bloom (i.e. timing and magnitude). However, the vigorous
123 debate on spring bloom dynamics has remained mainly focused on physical controls of
124 phytoplankton biomass accumulation. Our observations reveal that the physical environment
125 plays a key role also in shaping the community structure during the preconditioning period of
126 the spring bloom. Although transient winter blooms, supported by mixing intermittency, are
127 not intense in term of biomass, they maintain an active diatom population throughout winter.
128 Unlike resting cells or spores that require a germination period ²⁶, active winter diatoms can
129 directly seed the spring bloom, hence impacting the bloom timing and potentially its magnitude.

130

131 **Implications for spring bloom and carbon export dynamics**

132 Results of a parallel subpolar phytoplankton community model (Supplementary
133 Methods 2.7) support the claim that intermittent winter stratification can affect spring bloom
134 characteristics. Restratification events in winter boost diatom net growth rate (Supplementary
135 Fig. 17), increasing the standing stock of diatoms towards spring. Mixing intermittency may
136 increase by up to 2 fold the bloom magnitude and bring the bloom peak timing forward by up
137 to 19 days (Supplementary Fig. 19 and Table 7). These results not only corroborate in situ
138 observations (i.e. BGC-Argo and CATCH data) but further suggest a possible impact of winter
139 mixing intermittency on the observed yet unexplained ²⁷ interannual variability of spring
140 blooms.

141 Unexpected wintertime occurrence of diatom blooms in the subpolar gyre could also
142 challenge our perception of the spring bloom-dependent carbon export. Alternation of
143 stratification and deep mixing allows transient diatom blooms along with non-sinking particles
144 and dissolved organic and inorganic carbon to be transferred rapidly to depth (the so-called

145 mixed layer pump^{28–30}). Even though a single event transfers only a low carbon stock compared
146 to the spring bloom, cumulative events over the winter months may contribute significantly to
147 the annual carbon export.

148

149 **Methods**

150 Methods and supplementary figures are available in the supplementary information.

151 Data availability

152 Argo data were collected and made freely available by the International Argo Program and the
153 CORIOLIS project that contribute to it (<http://www.coriolis.eu.org>). BGC-Argo data are
154 publicly available at <ftp://ftp.ifremer.fr/ifremer/argo/dac/coriolis/>. Net heat flux and wind data
155 were extracted from the ECMWF ERA Interim dataset (reanalysis) freely available at
156 <http://apps.ecmwf.int/datasets/data/interim-full-daily/levtype=sfc>. The MLD climatology was
157 provided by Ifremer (<http://www.ifremer.fr/cerweb/deboyer/mld/home.php>).

158

159 **References**

- 160 1. Sverdrup, H. U. On conditions for the vernal blooming of phytoplankton. *J. du Cons.*
161 *Int. pour l'exploitation la mer* **18**, 287–295 (1953).
- 162 2. Backhaus, J. O. *et al.* Convection and primary production in winter. *Mar. Ecol. Progr.*
163 *Ser.* **251**, 1–14 (2003).
- 164 3. Dale, T., Rey, F. & Heimdal, B. R. Seasonal development of phytoplankton at a high
165 latitude oceanic site. *Sarsia* **84**, 419–435 (1999).
- 166 4. Große, F., Lindemann, C., Pätsch, J. & Backhaus, J. O. The influence of winter

- 167 convection on primary production: A parameterisation using a hydrostatic three-
168 dimensional biogeochemical model. *J. Mar. Syst.* **147**, 138–152 (2015).
- 169 5. Behrenfeld, M. J. Abandoning Sverdrup’s Critical Depth Hypothesis on phytoplankton
170 blooms. *Ecology* **91**, 977–989 (2010).
- 171 6. Behrenfeld, M. J., Doney, S. C., Lima, I., Boss, E. S. & Siegel, D. A. Annual cycles of
172 ecological disturbance and recovery underlying the subarctic Atlantic spring plankton
173 bloom. *Global Biogeochem. Cycles* **27**, 526–540 (2013).
- 174 7. Boccaletti, G., Ferrari, R. & Fox-Kemper, B. Mixed Layer Instabilities and
175 Restratification. *J. Phys. Oceanogr.* **37**, 2228–2250 (2007).
- 176 8. Fox-Kemper, B., Ferrari, R. & Hallberg, R. Parameterization of Mixed Layer Eddies.
177 Part I: Theory and Diagnosis. *J. Phys. Oceanogr.* **38**, 1145–1165 (2008).
- 178 9. Mahadevan, a., D’Asaro, E., Lee, C. & Perry, M. J. Eddy-Driven Stratification
179 Initiates North Atlantic Spring Phytoplankton Blooms. *Science (80-.)*. **337**, 54–58
180 (2012).
- 181 10. Callies, J., Ferrari, R., Klymak, J. M. & Gula, J. Seasonality in submesoscale
182 turbulence. *Nat. Commun.* **6**, 6862 (2015).
- 183 11. Huisman, J. & Weissing, F. J. Biodiversity of plankton by species oscillations and
184 chaos. *Nature* **402**, 407–410 (1999).
- 185 12. Taylor, J. R. & Ferrari, R. Shutdown of turbulent convection as a new criterion for the
186 onset of spring phytoplankton blooms. *Limnol. Ocean.* **56(6)**, 2293–2307 (2011).
- 187 13. Ferrari, R., Merrifield, S. T. & Taylor, J. R. Shutdown of convection triggers increase
188 of surface chlorophyll. *J. Mar. Syst.* **147**, 116–122 (2015).

- 189 14. Brainerd, K. E. & Gregg, M. C. Surface mixed and mixing layer depths. *Deep. Res.*
190 *Part I* **42**, 1521–1543 (1995).
- 191 15. Franks, P. J. S. Has Sverdrup’s critical depth hypothesis been tested? Mixed layers vs.
192 turbulent layers. *ICES J. Mar. Sci.* **72**, 1897–1907 (2015).
- 193 16. Brody, S. R. & Lozier, M. S. Changes in dominant mixing length scales as a driver of
194 subpolar phytoplankton bloom initiation in the North Atlantic. *Geophys. Res. Lett.* **41**,
195 3197–3203 (2014).
- 196 17. Behrenfeld, M. J. & Boss, E. S. Resurrecting the ecological underpinnings of ocean
197 plankton blooms. *Ann. Rev. Mar. Sci.* **6**, 167–194 (2014).
- 198 18. Lindemann, C. & St. John, M. A. A seasonal diary of phytoplankton in the North
199 Atlantic. *Front. Mar. Sci.* **1**, 37 (2014).
- 200 19. Johnson, L., Lee, C. M. & D’Asaro, E. A. Global Estimates of Lateral Springtime
201 Restratification. *J. Phys. Oceanogr.* **46**, 1555–1573 (2016).
- 202 20. Litchman, E. Growth rates of phytoplankton under fluctuating light. *Freshw. Biol.* **44**,
203 223–235 (2000).
- 204 21. Walter, B., Peters, J., Van Beusekom, J. E. E. & St. John, M. A. Interactive effects of
205 temperature and light during deep convection: A case study on growth and condition of
206 the diatom *Thalassiosira weissflogii*. *ICES J. Mar. Sci.* **72**, 2061–2071 (2015).
- 207 22. Cetinić, I. *et al.* A simple optical index shows spatial and temporal heterogeneity in
208 phytoplankton community composition during the 2008 North Atlantic Bloom
209 Experiment. *Biogeosciences* **12**, 2179–2194 (2015).
- 210 23. Smetacek, V. S. Role of sinking in diatom life-history cycles: ecological, evolutionary
211 and geological significance. *Mar. Biol.* **84**, 239–251 (1985).

- 212 24. McQuoid, M. R. & Hobson, L. A. Diatom resting stages. *J. Phycol.* **32**, 889–902
213 (1996).
- 214 25. Caron, D. A. Mixotrophy stirs up our understanding of marine food webs. *Proc. Natl.*
215 *Acad. Sci. U. S. A.* **113**, 2806–2808 (2016).
- 216 26. Smayda, T. J. & Mitchell-Innes, B. Dark survival of autotrophic, planktonic marine
217 diatoms. *Mar. Biol.* **25**, 195–202 (1974).
- 218 27. Barton, A. D., Lozier, M. S. & Williams, R. G. Physical controls of variability in North
219 Atlantic phytoplankton communities. *Limnol. Oceanogr.* **60**, 181–197 (2014).
- 220 28. Gardner, W. D., Chung, S. P., Richardson, M. J. & Walsh, I. D. The oceanic mixed-
221 layer pump. *Deep Sea Res. Part II Top. Stud. Oceanogr.* **42**, 757–775 (1995).
- 222 29. Dall’Olmo, G. & Mork, K. A. Carbon export by small particles in the Norwegian Sea.
223 *Geophys. Res. Lett.* **41**, 2921–2927 (2014).
- 224 30. Koeve, W., Pollehne, F., Oschlies, A. & Zeitzschel, B. Storm-induced convective
225 export of organic matter during spring in the northeast Atlantic Ocean. *Deep. Res. Part*
226 *I Oceanogr. Res. Pap.* **49**, 1431–1444 (2002).

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230

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240

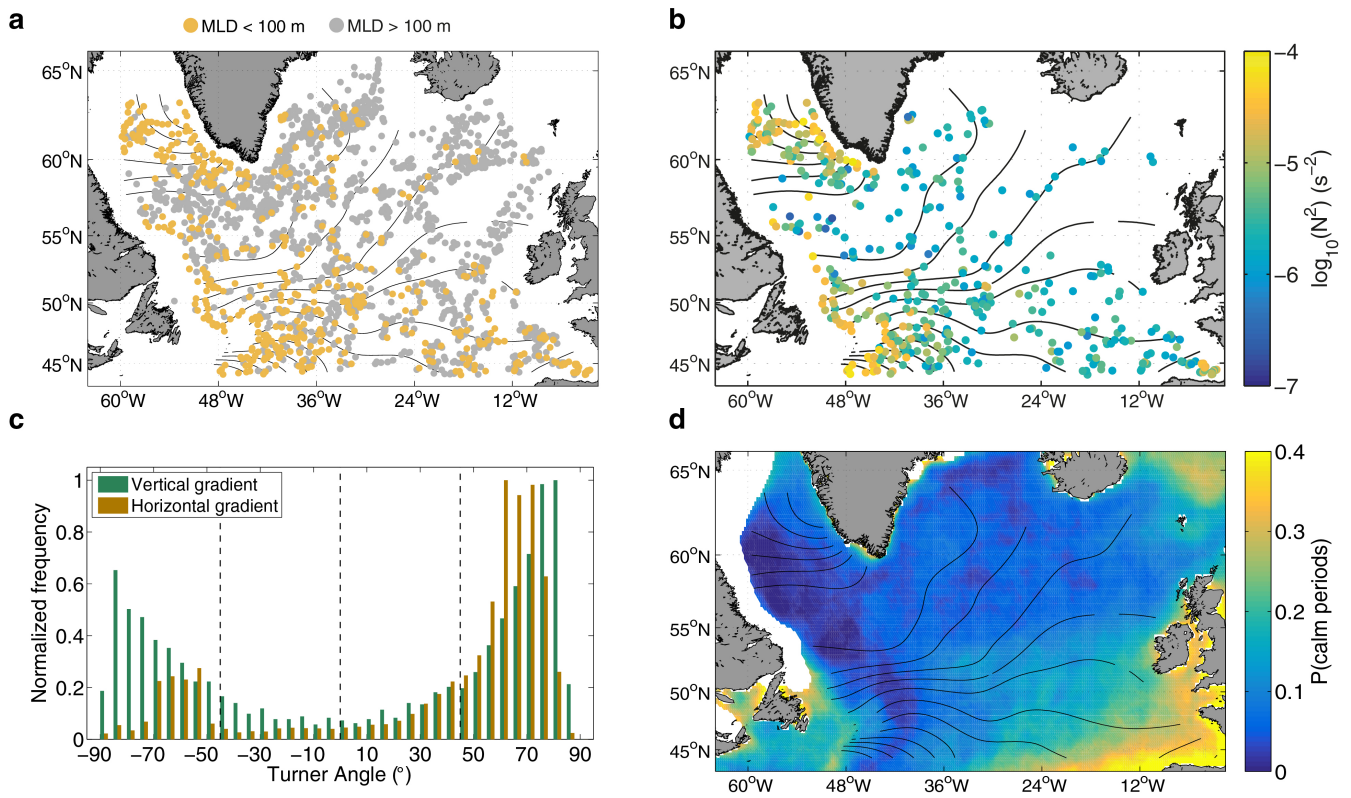
241 **Author contributions**

242 D.I. and L.L. designed the study. L.L., M.A., K.F.S., H.C., A.P., M.R.D. and D.I. conducted
243 the data analysis. L.L. and M.A. wrote the manuscript. All authors commented on the
244 manuscript.

245

246 **Competing financial interests**

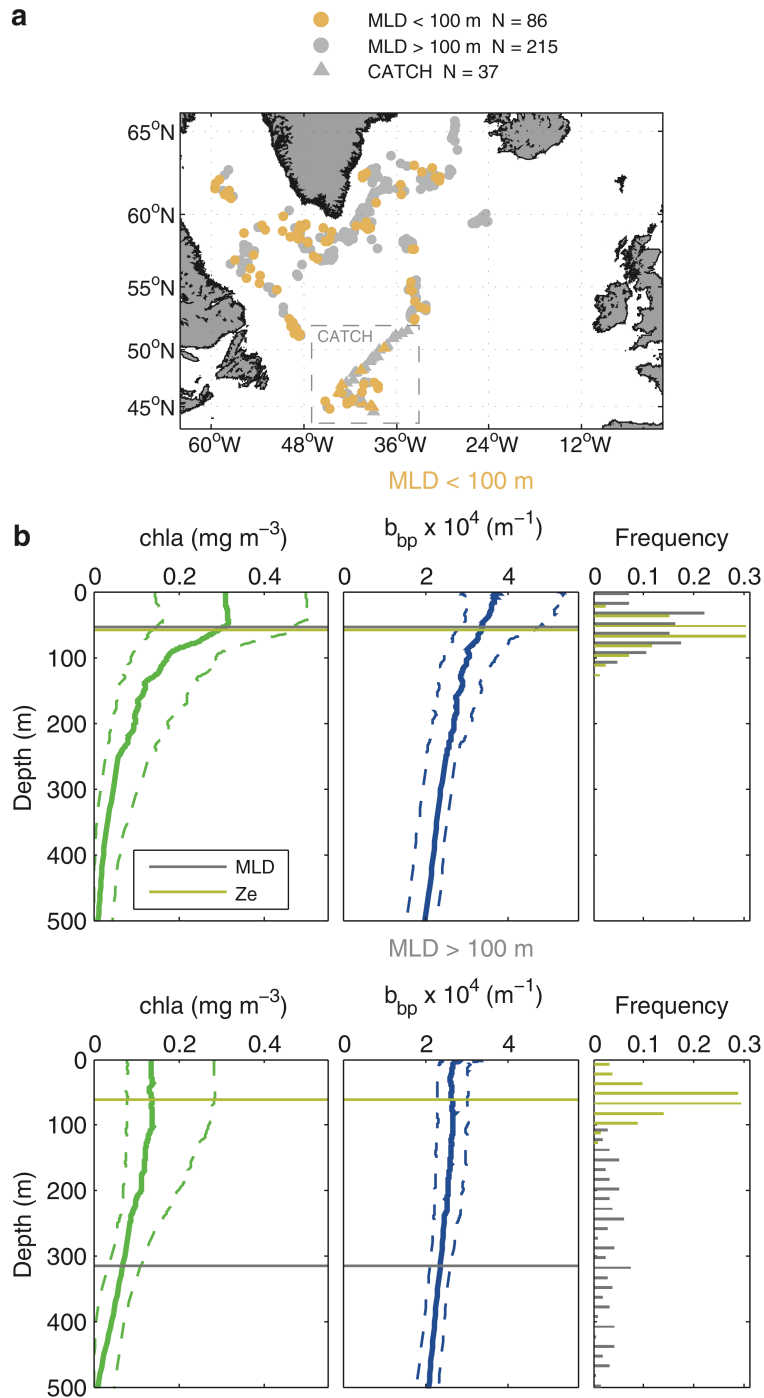
247 The authors declare no competing financial interests.



248

249 **Fig. 1.** Winter mixing intermittency in the North Atlantic Subpolar Gyre. (a) 2022 Argo float
 250 profiles (January-March 2014-2015). Orange dots mark the location of stratified profiles (MLD
 251 < 100 m) and grey dots mark the deep mixed profiles (MLD > 100 m). (b) Stratification
 252 intensity (average value of N^2 between 5 and 100 m) of profiles with MLD < 100 m. (c)
 253 Frequency distribution of Turner angle for horizontal (orange) and vertical (green) density
 254 gradients. Each distribution is normalized by its maximum frequency. Vertical dashed lines
 255 mark angle 0° , where both temperature and salinity contribute equally to the density gradient,
 256 and angle -45° and 45° where salinity and temperature respectively are the only contributor.
 257 Angles $> 45^\circ$ or $< -45^\circ$ indicate that salinity is working against temperature and vice versa. (d)
 258 Probability to have calm periods lasting at least 24 hours during January-March 2014-2015. A
 259 calm period is defined as a > 24 hour period with wind speed $< 10 \text{ m s}^{-1}$ and net heat flux $> -$
 260 100 W m^{-2} . White pixels indicate the presence of sea ice (Supplementary Methods 1.2). Black

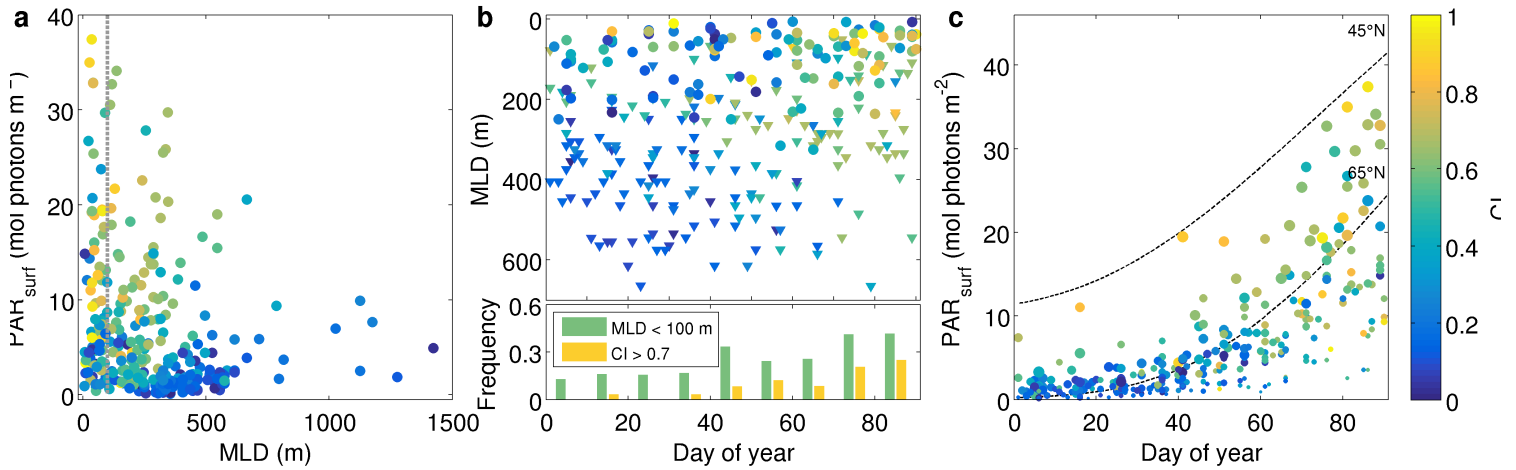
261 lines in (a), (b) and (d) denote contours of surface density (contour interval of 0.1 kg m^{-3} ,
262 maximum and minimum density of 27.74 and 25.90 kg m^{-3} respectively).



263

264 **Fig. 2.** Winter phytoplankton blooms in the North Atlantic Subpolar Gyre. (a) Location of the
 265 301 BGC-Argo float profiles (dots, January-March 2014-2015) and the 37 pigment profiles
 266 from the CATCH cruise (triangles, January-February 1997). Orange symbols indicate stratified
 267 profiles (MLD < 100 m, 35% of the profiles, including CATCH profiles) and grey symbols
 268 indicate deep mixed profiles (MLD > 100 m). The dashed rectangle delineates the study area

269 for the CATCH expedition. **(b)** Median profile and quartiles of chlorophyll *a* (chl_a) and
270 backscattering (b_{bp}) from BGC-Argo floats shown in (a), for MLD < 100 m (top) and MLD >
271 100 m (bottom). The two sets of data (MLD < 100 m and MLD > 100 m) are statistically
272 different in term of both surface chl_a and b_{bp} (Wilcoxon test, p-value < 0.01). Every single chl_a
273 and b_{bp} profile is shown in Supplementary Fig. 9. Horizontal grey and yellow lines indicate the
274 median MLD and euphotic depth (Z_e) respectively. Z_e is defined as the depth of the 0.1 mol
275 photons m⁻² daily isolume (Supplementary Methods 1.8). Panels on the right show the
276 frequency distribution of MLD (grey) and euphotic depth (yellow).



277

278 **Fig. 3.** The light environment impacts the phytoplankton community structure. Colour scale
 279 denotes the optical community index CI (normalized chlorophyll *a* to backscattering ratio). CI
 280 close to 1 indicates a large contribution of diatoms to the community whereas CI close to 0
 281 indicates a pico- and nanophytoplankton-dominated community (Supplementary Methods 1.9).
 282 (a) Surface daily-integrated photosynthetically available radiation (PAR) and MLD derived
 283 from all BGC-Argo float profiles shown in Fig. 2a. Vertical dashed grey line marks 100 m
 284 depth. (b) MLD as function of day of year (from 1st January to 31 March, top). Circles and
 285 triangles represent positive and negative MLD anomalies respectively (i.e. deviation from the
 286 climatological seasonal cycle, supplementary Methods 2.2). Frequency of stratified profiles
 287 (MLD < 100 m) and frequency of profiles with CI > 0.7 over a ten days period (bottom). (c)
 288 Surface daily-integrated PAR as function of day of year. Dot size denotes the cloudiness (large
 289 for clear sky and small for dark sky). Dashed black lines indicate temporal evolution of
 290 modelled clear sky surface PAR for the minimum and maximum latitudes of the domain (45°N
 291 and 65°N).