nature geoscience

ARTICLES

PUBLISHED ONLINE: 2 OCTOBER 2017 | DOI: 10.1038/NGEO3035

Unexpected winter phytoplankton blooms in the North Atlantic subpolar gyre

L. Lacour[1]*, M. Ardyna[1], K. F. Stec[2], H. Claustre[1], L. Prieur[1], A. Poteau[1], M. Ribera D'Alcala[2] and D. Iudicone[2]

In mid- and high-latitude oceans, winter surface cooling and strong winds drive turbulent mixing that carries phytoplankton to depths of several hundred metres, well below the sunlit layer. This downward mixing, in combination with low solar radiation, drastically limits phytoplankton growth during the winter, especially that of the diatoms and other species that are involved in seeding the spring bloom. Here we present observational evidence for widespread winter phytoplankton blooms in a large part of the North Atlantic subpolar gyre from autonomous profiling floats equipped with biogeochemical sensors. These blooms were triggered by intermittent restratification of the mixed layer when mixed-layer eddies led to a horizontal transport of lighter water over denser layers. Combining a bio-optical index with complementary chemotaxonomic and modelling approaches, we show that these restratification events increase phytoplankton residence time in the sunlight zone, resulting in greater light interception and the emergence of winter blooms. Restratification also caused a phytoplankton community shift from pico- and nanophytoplankton to phototrophic diatoms. We conclude that transient winter blooms can maintain active diatom populations throughout the winter months, directly seeding the spring bloom and potentially making a significant contribution to over-winter carbon export.

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

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

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

In this context, distinguishing the mixing layer depth from the mixed-layer depth is important when dealing with phytoplankton dynamics[14–16]. In the following, we improved the determination of the mixed-layer depth to be the closest to the mixing layer depth (see Supplementary Methods 1.4) given that there are no large-scale, autonomous measurements of turbulence so far.

Winter mixing intermittency

The common view is that the North Atlantic subpolar ocean is continuously deeply mixed during winter[17,18]. However, around 25% of Argo density profiles in this area were stratified (mixed-layer depth (MLD) <100 m, Supplementary Methods 1.4) during the winters of 2014 and 2015 (Fig. 1a and Supplementary Fig. 4). The vertical stratification was particularly strong in areas of significant horizontal density gradients (Fig. 1b), suggesting the potential role of MLEs. MLEs drive net horizontal transfer of lighter water above heavier water that can locally stratify the mixed layer. Similar temperature and salinity structure (that is, Turner angle[19]) between horizontal and vertical density gradients in the subpolar gyre (Fig. 1c and Supplementary Methods 1.3) confirm the crucial role of lateral processes in restratifying the deep winter mixed layer in the North Atlantic subpolar gyre.

Restratification mechanisms compete with vertical mixing induced mainly by surface wind and cooling[9]. Thus, restratification events require sufficiently long calm periods with a relaxation of this atmospheric forcing. While analysing wind speed and heat fluxes, we observed that some regions of the subpolar gyre presented up to 30% of calm periods (Fig. 1d and Supplementary Fig. 5 and Supplementary Methods 1.6). A proxy of the sea state (that is, wave height, Supplementary Methods 1.7), derived from BGC-Argo floats, also confirmed evidence of calm periods (that is, 20% of the winter profiles, Supplementary Fig. 7). Therefore, transient calm periods appear to be frequent across the North Atlantic subpolar gyre, allowing restratification to be a recurrent feature in winter.

Mixing intermittency triggers winter blooms

Restratification events triggered winter phytoplankton accumulations in the surface layer in the whole subpolar gyre (based on two different proxies of phytoplankton biomass: chlorophyll *a* (chl*a*) and particulate optical backscattering (b_{bp}); Fig. 2 and Supplementary Fig. 9). These restratification events maintain phytoplankton cells in the euphotic zone (surface to Ze; see Fig. 2b and Supplementary Fig. 15), enhancing the light availability for their growth. Indeed,

[1]Sorbonne Universités, UPMC Univ Paris 06, CNRS, Laboratoire d'Océanographie de Villefranche (LOV), Observatoire Océanologique, 06230 Villefranche-sur-Mer, France. [2]Laboratory of Ecology and Evolution of Plankton, Stazione Zoologica Anton Dohrn, 80121 Naples, Italy. *e-mail: leo.lacour@obs-vlfr.fr